Persistence, size, trends and productivity in populations of two Critically Endangered Indonesian cockatoos

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General abstract

The aim of this thesis was to understand patterns of persistence, size, trends and productivity in populations of two Critically Endangered and heavily traded Indonesian cockatoos: the Yellow-crested Cockatoo *Cacatua sulphurea* and Citron-crested Cockatoo *Cacatua citrinocristata*. The Yellow-crested Cockatoo was formerly common and widespread on many islands of Wallacea. Its former subspecies on Sumba, the Citron-crested Cockatoo, was recently elevated to species level. After dramatic declines information on the remnant populations of both species is essential to guide future conservation management. A challenge with species that have disappeared from most of their range is to identify correlates of local persistence. The Yellow-crested Cockatoo and Citron-crested Cockatoo have undergone catastrophic declines due to habitat loss and especially trapping. The former is now extinct in much of its range across Indonesia while the latter has lost substantial numbers and some of its old sites on Sumba. Of 144 sites supporting cockatoos in 1950 only 76 did so in 2015. I compared socio-ecological conditions between the occupied and unoccupied sites, using ‘random forests’. Tree cover, sparse human densities and low road densities promoted cockatoo survival but site-specific conditions (e.g. sacred groves, NGO activities) were also important. These local influences offer exciting possibilities for low-cost conservation prescriptions tailored to individual sites.

One of the few Yellow-crested Cockatoo populations still numbering >100 individuals survives on Komodo Island. Distance sampling was combined with density surface modelling (DSM) to predict local densities and estimate total population size for this island. The population estimate of 1,113 (95% CI: 587–2,109) individuals on Komodo was considerably larger than previous conservative estimates. Coincidence between the DSM and a set of independent cockatoo observations was high (93%). Standardised annual counts by national park staff showed increases in cockatoo records from <400 in 2011 to ~650 in 2017. Taken together, the results indicate that Komodo National Park, alongside and indeed because of preserving its iconic Komodo Dragons *Varanus komodoensis*, is succeeding in protecting a significant population of Indonesia’s rarest cockatoo species. This study’s findings highlight the potential of

DSM for locating abundance hotspots and estimating global population size in a range of threatened taxa.

Although the importance of long-term monitoring is widely recognised, very few tropical bird species have been monitored over the span of 25 years. A multi-species distance sampling survey from 1992 was replicated in 2017, and present data on five parrot species and a hornbill, with three threatened island endemics, Citron-crested Cockatoo *Cacatua citrinocristata* (CR), Sumba Eclectus *Eclectus cornelia* (EN) and Sumba Hornbill *Rhyticeros everetti* (EN), two restricted-range species, Great-billed Parrot *Tanygnathus megalorynchos* and Marigold Lorikeet *Trichoglossus capistratus*, and one Wallacean-Papuan species, Red-cheeked Parrot *Geoffroyus geoffroyi*. Densities of the three large parrots and the hornbill in 2017 were similar to 1992 but densities of the smaller Red-cheeked Parrot and Marigold Lorikeet declined significantly in the same time span. Quantity of forest on Sumba is assessed for both years, presence data and local density estimates to gauge island-wide population sizes. The Marigold Lorikeet may need a re-assessment of its global Red List status. The uncertainty in trends for the threatened cockatoo, eclectus and hornbill is of concern as they show no definite sign of sustainable recovery from the extensive trapping of past decades.

Knowledge of breeding success and its limiting factors is crucial in assessing species' conservation needs. As hole-nesters, parrots are particularly influenced by the availability of suitable cavities and low breeding output. On Sumba, the Citron-crested Cockatoo has to compete with an unusually rich hole-nesting bird community affected by forest loss. Ninety-five nesting cavities of cockatoos were monitored including competitors and potential nest-predators, over one to four breeding seasons, using a combination of camera-traps, direct checks on nest contents, and observations from the ground. Competition for suitable cavities was intense among three large parrot species, two owls and a hornbill. The Endangered Sumba Hornbill dominated observed direct confrontations and was the most frequent visitor to active parrot nests, suggesting a further role as a potential nest-predator. Cockatoos prospected many cavities but rarely then attempted to nest. At the few cavities where cockatoos did breed, predation pressure was likely low, and observed success rate high (10 successful of 15 nests). Intense competition for cavities suggests a shortage of suitable nest-sites, the need to preserve old hole-bearing trees and a role for nestboxes. Both studied cockatoo species would benefit from targeted local awareness-raising and law enforcement, with the whole endeavour backed up by longer-term forest restoration.

The recent split of the Citron-crested Cockatoo leaves the resultant two species at higher risk of extinction than when they were assessed combined. The population on Sumba remains under pressure from illegal trapping, habitat loss, nest site competition and appears to have low productivity. Only two of the six Yellow-crested Cockatoo subspecies retain wild populations > 300 individuals but for each subspecies recovery is still possible, if conservation management tailored to each location is implemented, including public awareness programmes, provision of nestboxes, logistical and capacity building support, habitat protection and law enforcement.

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Contents

1 Introduction

1.1 Parrots

Habitat loss and deterioration have rendered almost one in ten tropical bird species at risk of extinction (Sodhi et al., 2010; BirdLife International, 2018, 2021a). Species that are large, long-lived, forest dependent, hole-nesting or evolved on small islands are at particular risk (Olah et al., 2016; van der Hoek et al., 2017; Vergara-Tabares et al., 2020). Attractive, relatively easy-to-keep species such as parrots face the additional impact of unsustainable direct exploitation for the pet trade (Bush et al., 2014; Tella and Hiraldo, 2014). As a result of this double pressure, parrots are among the most endangered bird orders in the world (Olah et al., 2016; BirdLife International, 2018), with 175 (43%) of the 404 species either Threatened or Near Threatened (BirdLife International, 2021a). Capture for the international pet trade and continuous habitat loss and degradation are regarded the main cause of worldwide parrot population declines (Snyder et al., 2000). Since the establishment of CITES in 1975, the international trade in parrots, of which only four species are not included in its appendices (CITES, 2020), has become increasingly regulated, but evidence of a direct benefit to threatened species is inconclusive (Martin, 2000), not least because of a severe lack of reliable abundance data (Marsden and Royle, 2015).

1.1.1 Systematics

The order of parrots (Psittaciformes) contains three groups: New Zealand parrots Strigopidea, cockatoos Cacatuidea and True Parrots Psittacidea (Rowley and Collar, 1997; del Hoyo and Collar, 2014; HBW and BirdLife International, 2021). The number of known parrot species differs between different taxonomies and has varied over the decades as some have become extinct, new species were discovered and others were taxonomically split or lumped: e.g. the parrot order contained 332 extant species in 1963 (Brereton, 1963), 345 species in 1989 (Forshaw, 1978) and 404 species today (BirdLife International, 2021a).

Parrots are predominantly found in the tropics and subtropics in lower latitudes and most species (94%) inhabit forests, whereas much fewer species use savannas 29% and shrubland (31%) (BirdLife International, 2021a; IUCN, 2021). Owing to the extensive conversion of natural habitats most species (60%) have also adapted to using some type of artificial habitat such as severely degraded forests, plantations, gardens and other agricultural land uses, some of them have even been found in urban areas (13%)(Collar, 1997; BirdLife International, 2021a; IUCN, 2021).

1.1.2 Threats to the world's parrots

The parrot order included 21 Critically Endangered and 35 Endangered species (BirdLife International, 2021a; IUCN, 2021). The situation is reflected in the cockatoo family (22 species) with 41% of cockatoos Threatened or Near Threatened, including 14% Critically Endangered and 14% Endangered species.

Parrots as a group are so threatened because their ecology and morphology make them particularly vulnerable to two of the main threats for avian species: trade and habitat loss (Collar and Juniper, 1992; Collar, 1997). Additional disadvantages are the group's (near-)restriction to the tropics where biodiversity loss has been more severe than in other climate zones (Loh et al., 2005; Collen et al., 2011) and their almost universal dependence on old-growth forests (Rowley and Collar, 1997; Bucher and Aramburú, 2014) which have been subject to more destruction, fragmentation and degradation than other habitats (Keenan et al., 2015; Olah et al., 2016).

Many parrot species — particularly those restricted to small islands — are also threatened by introduced predators (Snyder et al., 1987; Jones et al., 2013), competitors (Pell and Tidemann, 1997; Port and Brewer, 2004), alien diseases (Fogell et al., 2016), introduced parasites (Berkunsky et al., 2005) and inbreeding (White et al., 2015). Although much more research effort has been dedicated to parrots than to some other animals and plants, baseline data for many species is missing on population estimates, trends, local or species-specific threats (Marsden and Royle, 2015; BirdLife International, 2021a). This lack of knowledge limits the ability to allocate conservation effort optimally to the species that need it most.

Trapping and trade

Due to their size, colourful appearance and ability to imitate human speech parrots are popular as pets and display birds (Marešová and Frynta, 2008; Gunnthorsdottir, 2015) creating a demand for wildlife trade (Romero-Vidal et al., 2020). Aside from trapping for the pet trade parrots are also hunted or trapped for various other purposes (Collar, 1997; Juniper and Parr, 2003:35), e.g. for human food (Burger and Gochfeld, 2003), for their feathers as decoration or for spiritual use (McCormack and Künzlé, 1996; Mack and Wright, 1998; Assou et al., 2021), or as part of pest control to protect crops (Masello and Quillfeldt, 2002; Reuleaux et al., 2014).

Legal and illegal trade in wild birds is a multi-million-dollar business globally (Pires, 2012) and parrots represent a large proportion of the most frequently traded species and fetch high prices (Homberger and Beissinger, 2006). While humans have taken parrots from the wild for hundreds of years, it only became problematic when it grew into a large-scale commercial business (Pires, 2012). During most of the last century trade in parrot species was still legal and negatively impacted 55% of threatened and near-threatened parrot species (Pain et al., 2006). This was mainly due to international trade with the majority being imported to the US and Europe (Thomsen and Mulliken, 1992). After the introduction of international and national legislation to regulate trade (see section 1.1.3), and consequent reduction of legally exported and imported birds (Wright et al., 2001; Pain et al., 2006), the illegal component of parrot trade has started to dominate over the legal part (Pires, 2012; Pires et al., 2016). Today targeted hunting and trapping is considered a threat for 78% of Threatened and Near-Threatened parrot species (BirdLife International, 2021a; IUCN, 2021). Regulations of international trade aim to interrupt the supply chain late, when captured parrots move from one country to another. Other stages to consider are the trappers and their motivations, as well as in-country trade (Cook et al., 2002; Pires et al., 2021). Parrots are often trapped by local farmers, not by outsiders or by professional poachers (Pires et al., 2016) and the areas where remnant populations of parrots occur, are often remote and offer few other opportunities for villagers to generate income. This dependency of livelihoods on parrot trade must be considered when planning conservation action against trade (see 1.1.3). On the other end of the chain, demand for wild-caught birds (usually by pet-owners, collectors and formerly by zoos) determines if the price the birds fetch, outweighs the effort and risk for each previous person in the supply chain (Pires et al., 2021).

Habitat loss and deterioration

Habitat loss due to conversion of forest for agricultural and other human uses is one of the major causes for the loss of biodiversity. Forest loss has been more severe in the tropics although recently the annual rate of tropical forest loss has almost halved compared to the 1990s (Keenan et al., 2015). As most parrots are compulsory secondary hole-nesters they depend on these old-growth forest habitats (Forshaw, 1978; van der Hoek et al., 2017). If the forest is logged or disturbed the parrots may not disappear immediately due to the long lifespan of adults and naturally relatively low annual productivity but reproduction will be impacted by cavity shortages and the population will likely decline slowly and may disappear with a delay (Kuussaari et al., 2009; Manning et al., 2012). This delay may prevent detection of the problem by conservationists until it is too late and makes it harder to see the connection between cause and effect.

The effects of habitat fragmentation on parrots – although less of a direct problem for strong fliers – resemble the consequences of habitat destruction: fragmentation interacts with other threats via increased accessibility for trappers, introduced predators, competitors and plants; it may decrease food availability and increase potential for parrot-human conflicts in the edge zones (Simberloff, 1998; Snyder et al., 2000; Renton and Salinas-Melgoza, 2004; Nunes and Galetti, 2007). Intelligent birds with a history of trapping also tend to learn to avoid areas where they could encounter trappers (Marsden and Jones, 1997; Bunbury et al., 2018).

Additional future problems are expected from climate change, which tends to affect existing forests negatively (Allen et al., 2010; Mátyás, 2010) and is another concern for parrot habitat worldwide. While parrots do not tend to be habitat specialists they are at disadvantage in adapting to changed climates due to their long generation times and compulsory hole-nesting (Şekercioğlu et al., 2012). Natural disasters such as earthquakes, tsunamis, storms, fires and floods also have the potential to harm parrots either directly (e.g. through chicks drowning in nest sites) or indirectly through habitat changes or causing socio-economic changes that in turn affect the birds.

1.1.3 Parrot conservation

Parrots' attractiveness to humans is both blessing and curse in regard to conservation. Their perceived beauty and suitability as pet has made them a preferred target for tapping and trade (Collar, 1997; Frynta et al., 2010; Tella and Hiraldo, 2014; Pires et al., 2021) but also gives them an advantage over less striking species when it comes to attracting conservation funding (Frynta et al., 2010; Gunnthorsdottir, 2015) and legal protection. Governments and NGOs are likely to devote more attention to them (Metrick and Weitzman, 1996), in particular if they attract tourism. Pet owners and zoos tend to donate for wild populations of species they keep (Marešová and Frynta, 2008). Therefore, many parrot species function as flagship species for their communities and habitats (Snyder et al., 2000; McGowan et al., 2020) both locally and internationally. Conservation actions for parrots generally follow from the list of major threats to parrots, with differences in priorities resulting from feasibility, amount of effort and occasionally prestige. Unfortunately the two major threats habitat loss and trade — although known for decades — are not easily remedied (Collar and Juniper, 1992).

Trapping and trade

Parrot trade has been addressed initially with regulation of international trade and national export quota. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) came into force in 1975. Since 1981 all but four parrot species have been listed in Appendix I or II, meaning that trading these species commercially is either completely prohibited (I) or strictly regulated (II) (Collar, 1997). CITES relies however on Countries joining the convention and putting legislation in place to implement it (Collar, 1997). Further progress was made when major parrot import counties passed additional legislation e.g. the US Wild Bird Conservation Act in 1993 (Wright et al., 2001; Pain et al., 2006) and the EC Wildlife Trade regulations in 1997 (Ó Crídáin, 2007). As imports to some countries were curbed, other countries may have taken their roles, therefore exporting countries' legislation also play a major role in the effectiveness of the regulations. Legal parrot trade was regulated with capture quotas, that were deemed sustainable harvesting. This approach has the potential to be a solution to consolidate needs of the local parrot and human populations (Beissinger, 2001). Legal harvesting can provide an incentive for stakeholders to preserve parrot habitat and otherwise crate favourable conditions for parrots to multiply (Collar, 1997), but which amount of removal is sustainable for each species and population is however debatable and would depend on much better data on each species' population numbers, trends and ecology than is generally available (Martin, 2000; Marsden and Royle, 2015; Valle et al., 2018). Allowing some legal trade with wild captures also makes identification of illegal trade much harder.

While legal parrot trade could still be directed and controlled, an unknown part of it undoubtedly continues illegally without supervision or monitoring (Pires, 2012; Nandika et al., 2021). Law enforcement is needed to make the legislation effective but there are also less adversary approaches, that work with the people of the supply chain, not against them. Crime prevention methods can also be effective in creating obstacles to parrot trapping, such as restricting access to trapping areas, employing guards, restricting access to specialized trapping gear (e.g. glue, nets, ladders etc.), removing climbing gear from trees (Pires, 2012) or changing attitudes towards trapping in the communities around the trappers. Public awareness programmes for the communities of trappers often go hand in hand with creation of alternative livelihoods for the trappers (e.g. other products to trade, sustainable forest uses). Following an approach that has been successful in large mammal conservation (Gibson and Marks, 1995), trappers can be employed as guardians of the parrot population that they used to trap (Widmann and Lacerna-Widmann, 2008).

Raising awareness in local communities with access to parrot habitat can also target related topics such as the fragility of ecosystems and their functions (e.g. water retention), possibility of species extinctions in general, concept of endemism and instilling local pride (Christian et al., 1996; Snyder et al., 2000). An approach targeting the other end of the parrot-trade chain aims to reduce demand by raising awareness in importing countries or regions for the harm caused by wild-captures or by creating a sufficient supply of captive bred birds (Marshall et al., 2019; Ribeiro et al., 2019; Pires et al., 2021).

Habitat loss and deterioration

Ideally habitat loss and deterioration are prevented rather than mitigated. Legal protection of areas has been shown to benefit biodiversity in many cases (Gaveau et al., 2009; Brun et al., 2015; Higginbottom et al., 2019; Cazalis et al., 2020) as they can be effective at reducing deforestation in the tropics (Nelson and Chomitz, 2009). Parks have shown the ability to stop land clearing and to reduce logging, fire, hunting and grazing (Bruner et al., 2001). However, these effects are far from guaranteed. In addition to preventing habitat loss, deterioration and fragmentation of remaining forest has to be prevented as well (Sitompul et al., 2004). When habitat has already been lost, restoration is only a long-term option, although some characteristics of primary forest can never be recovered (Gibson et al., 2011). However, to prevent immediate extinctions conservation management can temporarily replace some of the habitat’s nesting feeding and roosting functions artificially (Snyder et al., 2000; Renton et al., 2015): nest site shortage can be mitigated with artificial nest boxes (e.g. White et al., 2005), improvement of existing cavities (e.g. Snyder et al., 1987; Clout and

Merton, 1998), initiation of natural cavity formation or control of cavity competitors (Jones and Duffy, 1993; Pell and Tidemann, 1997; Arendt, 2000; Jones et al., 2013); food shortages can be reduced by supplementary feeding (e.g. Clout and Craig, 1994) or planting of fast-growing trees or shrubs (e.g. Rocamora and Laboudallon, 2013). Although these measures have contributed to prevent parrot extinctions in the short term, it is important to note that they require continued effort until the natural habitat has recovered sufficiently which can take many decades.

1.1.4 Estimating parrot abundance

Estimates of population sizes and ranges are cornerstones of conservation science at both the global and local scale and are instrumental in assessing extinction risks, conservation priorities and Red List status (Mace et al., 2008; Collen et al., 2011). These essential data are however lacking for many rare and threatened species (MacKenzie et al., 2005), which are often difficult to survey on account of their biology and/or the areas they inhabit (McDonald, 2004). Even for relatively well-known groups such as parrots, around 75% of species are lacking abundance estimates (Marsden and Royle, 2015), a worrying statistic given that almost one-third of parrots are currently threatened (BirdLife International, 2021a). A variety of methods have been used to calculate population size in parrots. For very rare species it may be possible to count every individual. For others, marked or identifiable individuals allow mark-recapture or mark re-sighting methods, but these conditions are not the norm (Dénes et al., 2018). For most species, roost counts, flyway counts and distance sampling have been used more or less effectively (Casagrande and Beissinger, 1997; Marsden and Royle, 2015). Distance sampling, despite difficulties in meeting method assumptions, has become a well-established method for estimating sizes of animal populations generally (Buckland et al., 2001; Thomas et al., 2010) and parrots in particular (Marsden, 1999; Marsden and Royle, 2015; Dénes et al., 2018).

Local densities are a key driver of population sizes and are usually assessed as the first step before extrapolating to the whole population. Estimates derived from distance sampling have become the most commonly used method, involving 84% of published parrot abundance estimates (Marsden and Royle, 2015), despite question marks over reliability related to lack of records in rare species, and idiosyncrasies of parrot behaviour (Marsden, 1999; Buckland et al., 2008; Dénes et al., 2018). Alternative methods fail to measure absolute bird abundance (Bibby et al., 2000), face the same (and additional) challenges (Casagrande and Beissinger, 1997) or remain largely untested (Dénes et al., 2018).

Extrapolating from density estimates to absolute population numbers requires an estimate of range or distribution. A spectrum from simple to sophisticated methods are available for the task: basic options like simple multiplication of average densities with the known occupied area require the distribution to be uniform over the study area or representative sampling which is often hard to achieve in parrot habitat. Using stratified densities (e.g. regions or habitat tapes) allows compensation for less uniform sampling and renders strata specific results (Buckland et al., 2001). Modelling the locally observed densities based on environmental predictors and assigning them to unsurveyed areas involves more complicated analysis but can generate spatially explicit results including maps of predicted population densities (Miller et al., 2013). Density surface models are not widely used for population estimates at present but have been successfully applied to other species (Petersen et al., 2011; Winiarski et al., 2013, 2014; Bradbury et al., 2014). With temporal replication of presence data it becomes possible to estimate site-specific detection probability and use occupancy models to estimate the percentage of sites occupied (Mackenzie et al., 2002; Tyre et al., 2003). Aside from predicting an animal's distribution, species distribution models allow examination of the relationship between the species and environmental variables which can also be used to predict response to changes (Elith and Leathwick, 2009; Miller, 2010).

Passive acoustic monitoring using recorders is a survey method that has become more feasible with technological development and has not been widely applied in parrots (Marques et al., 2013; Dénes et al., 2018). Although it has been applied to parrot presence (Figueira et al., 2015) it also has potential for density and abundance estimates in parrots, solving the problem of poor visibility in dense forest habitats (Dénes et al., 2018).

1.2 Study species

The Yellow-crested Cockatoo *Cacatua sulphurea* is endemic to the islands of western Wallacea, (BirdLife International, 2021b), with the Citron-crested Cockatoo *C. citrinocristata*, restricted to Sumba in the south-west of the same region (BirdLife International, 2022a). Like many other parrots the species are negatively affected by habitat loss and trade, as a consequence of which they have disappeared from almost all of their range and been listed as Critically Endangered all this century (Collar et al., 2001; BirdLife International, 2021b). Once the species were so numerous in parts of their ranges that their flocks made trees appear white, and crops had to be guarded against them (Kendall, 1979; Setiawan, 1996; Collar et al., 2001). As obligate hole-nesters the cockatoos are highly vulnerable to trapping when breeding or communally roosting (Marsden and Jones, 1997; Walker et al., 2005; Imansyah et al., 2016). Consequently they were trapped and exported in the thousands for the international pet market (Inskipp et al., 1988; Cahill et al., 2006). Estimated annual exports from Sumba, for example, were as high as 1600 birds in 1992 (Cahill et al., 2006) when a population of only 3200 individuals was estimated to remain (Jones et al., 1995). A number of regional studies were produced (Mallo and Setiawan, 1996; Catterall, 1997; Agista et al., 2001) along with a species recovery plan (PHPA et al., 1998) and a comprehensive status review (Collar et al., 2001). Although export effectively became illegal in 1994 (Cahill et al., 2006), difficulties in enforcement allowed trapping and trade to continue (Collar et al., 2001; CITES, 2002; Persulessy et al., 2003). Although local studies have been carried out in the past 20 years, data on persistence, abundance, trends and limiting factors was urgently needed for a comprehensive assessment of the conservation status of each species.

To avoid informing trappers and traders on current cockatoo locations (Meijaard and Nijman, 2014; Collar et al., 2017), in this thesis I only refer to the former ranges. I avoid giving specific locations (which includes small island names) of remnant populations and do not present any updated maps. The locations and maps are however available for bona-fide researchers or conservation purposes on request.

Figure 1.1: Study species; left: Yellow-crested Cockatoo *Cacatua sulphurea*, here a captured male of the subspecies *djampeana* in the Selayar Islands; middle; Citron-crested Cockatoo *Cacatua citrinocristata* at its nest on Sumba; right: female Citron-crested Cockatoo with red iris colour, which is distinguishable only in good light.

1.2.1 Yellow-crested Cockatoo

Taxonomy

In the past the Yellow-crested Cockatoos *Cacatua sulphurea* included between four (Collar et al., 2001) and seven subspecies (Collar and Marsden, 2014). The former subspecies *citrinocristata* on Sumba has now been recognized as separate species (BirdLife International, 2022a), which leaves six subspecies of *C. sulphurea*. The nominate form *C. s. sulphurea* occurred on Sulawesi and its satellites including Buton and Muna (Figure 1.2, Figure 1.3). The subspecies *djampeana* is restricted to the Selayar islands (sometimes referred to as Tanah Jampea but this name only covers one of the islands in the cockatoo's range) located between Sulawesi and Flores. Historically this taxon was often grouped with the nominate form. The population on the Tukangbesi islands southeast of Buton was separated by Marsden and Collar (2014) as subspecies *paulandrewi* based on its smaller bill and ear covert patch and brighter colouration. Timor and its satellites support the subspecies *parvula*. Collar and Marsden (2014) reinstated the subspecies *occidentalis* for the cockatoos on the chain of islands from Bali to Alor, which some taxonomies continue to group as *parvula*. The subspecies *abbotti* on the Masalembu islands is the most distinctive due to its larger size. Owing to its isolated location in the Java Sea, on the 'wrong' side of the Wallace line, hundreds of kilometres away from the next cockatoo presence, *abbotti* has been referred to as a mystery population with a possibility of relatively recent introduction (Collar and Marsden, 2014).

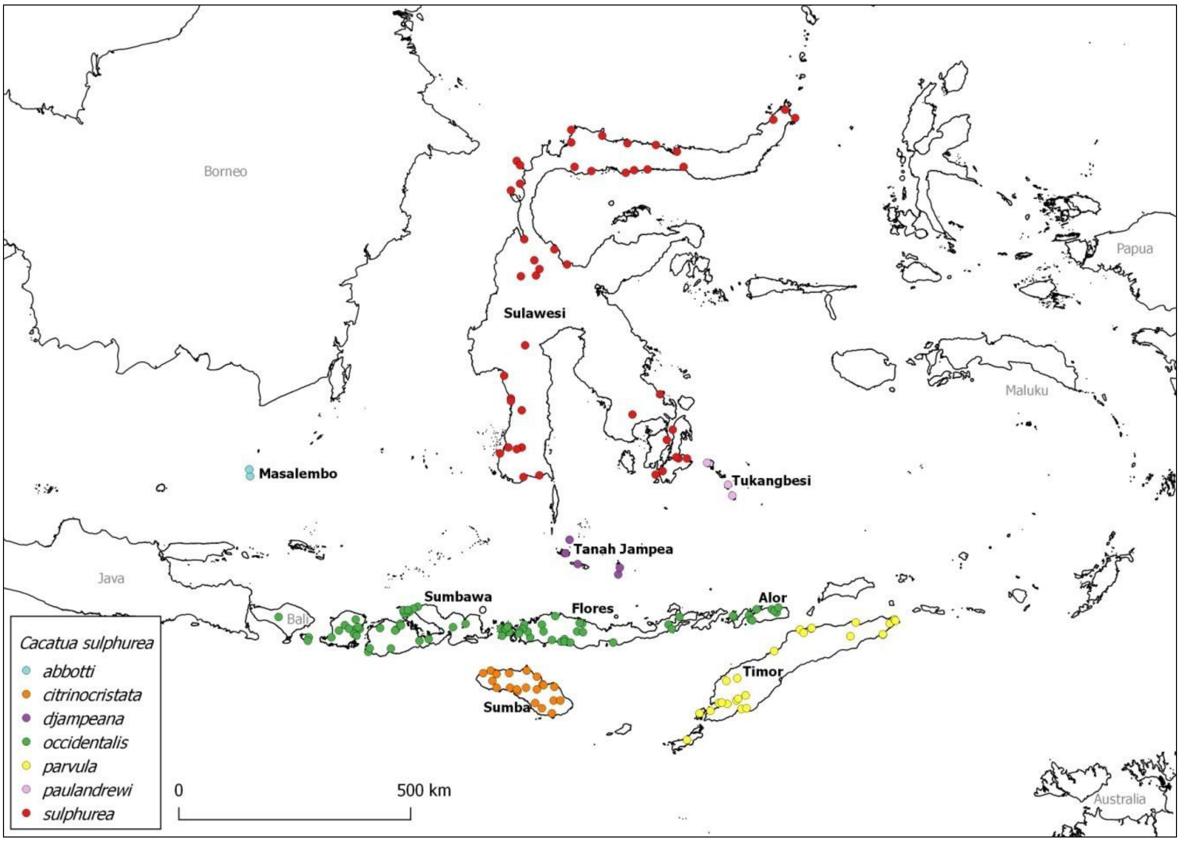

Figure 1.2: Past distribution of Yellow-crested cockatoo *Cacatua sulphurea* subspecies and Citron-crested Cockatoo *Cacatua citrinocristata* based on records from 1850 – 2016 in BirdLife International (2001) supplemented with data from online platforms and unpublished reports.

Distribution

The Yellow-crested Cockatoo has a vast distribution area mostly within Wallacea (apart from Masalembu and Nusa Penida) and is endemic to Indonesia and Timor-Leste. Naturalized populations are known from Hong Kong and Singapore (Lim, 1997; Leven and Corlett, 2004; Neo, 2012; Andersson et al., 2021). The Yellow-crested cockatoo's range does not naturally overlap with any other cockatoo, but in the long history of parrot trade, feral populations of other cockatoos have been reported from various areas in the range (e.g. Kelly and Marples, 2010).

While there have been no records of the species above 1200 m (Rensch, 1931; PHPA et al., 1998; Collar, 2001), these elevations are rare within its range. In the past the cockatoo was generally reported as wide-ranging in the lowlands and can be presumed to have been present in most areas below ca. 1000 m of all islands in its range (Collar et al., 2001). Most dense populations were reported below 500 m in the past (Forshaw, 1978; PHPA et al., 1998).

On Sulawesi the cockatoo has been reported as historically widespread but unevenly distributed (Forshaw, 1989). The range on Sulawesi included all four peninsulas (Figure 1.2), but occurrences on the northern peninsula were probably always rare (PHPA et al., 1998). Strongholds were considered to be mainly National Parks of Central Sulawesi, South Sulawesi and South-East Sulawesi (Collar, 2001). At the start of this study in 2017 survival at all but two of these sites was in doubt (Mallo and Setiawan, 1996; Agista et al., 2001; Collar and Marsden, 2014). Remnants were only known from a tiny island off Central Sulawesi and one national park in South-East Sulawesi (BirdLife International, 2016). Survival on Buton and Muna was also in doubt (Catterall, 1997; Martin et al., 2012). The Tukangbesi islands and some of the Selayar islands have supported small populations in the past which were thought to be close to extinction by 2017 (Dutson, 1995; PHPA et al., 1998; Kelly and Marples, 2010; Bashari and Arndt, 2016). Only one of the Masalembu islands continued to support cockatoos and numbers dropped as low as five individuals before recovering to 23 by 2017 (Nandika and Agustina, 2018; Nandika et al., 2020).

Although occasional observations are reported from Bali it is uncertain if the island ever had a permanent population, or if the birds present there were brought by humans or were seasonal dispersers (Collar, 2001). The neighbouring Nusa Penida supported a substantial (native or non-native) population at least for some time (Meise, 1941) which had already started to decline in 1986 (van Helvoort cited in Collar, 2001).

Originally cockatoos were present on all large islands of the Lesser Sundas: Lombok, Sumbawa, Moyo, Komodo, Rinca, Flores, Adonara, Solor, Lembatar (=Lomblen), Pantar, Alor, Timor, Semau and Sumba with the status of smaller islands unknown (PHPA et al., 1998). Survival was doubtful on Lombok, Flores and Pantar before this survey (Mochtar, 1989; Butchart et al., 1996; Collar, 2001; BirdLife International, 2016). In 2017 only one population of > 300 individuals was known for the species, which was located on Komodo and reported to be declining in 2006 (Imansyah et al., 2016).

Habitat

The Yellow-crested cockatoo uses a large variety of habitats and reported forest types vary between regions. On Sulawesi it is described as a forest species using primary and tall secondary forest in lowlands and hills (Cahyadin, Jepson and Syarief, 1994; Coates and Bishop, 1997; PHPA et al., 1998) but its formerly large range included woodland, scrub, cultivated fields, agricultural areas and forest edges (Forshaw, 1989). It is reported to be absent from the interior of wet forests on Sulawesi which would explain its historically patchy distribution on the large island. In the Lesser Sunda Islands semi-evergreen forest, moist deciduous monsoon forest and gallery forest are reported as core habitats but it can also be found in other forest types and adjacent areas including modified habitat such as cultivations and scrub (Butchart et al., 1996; PHPA et al., 1998; Prijono, 2008; Trainor et al., 2008, 2012). The large population on Komodo uses palm savannah, mangroves and gallery forests (Agista and Rubyanto, 2001; Imansyah et al., 2016). In the remnant populations on small islands, where the original forest has been cleared (e.g. one of the Masalembu islands or some of the Tukangbesi islands) it shows its adaptability to modified habitats, persisting for decades in highly modified forest fragments, mangroves and cultivation (Cahyadin, Jepson and Arif, 1994; Kelly and Marples, 2010; Nandika et al., 2020). The need for old forests is grounded in the cockatoo’s dependence on trees old enough to form large cavities for nesting and trees big enough to be used as safe roosts. If these functions can be fulfilled by old palm groves (Coconut *Cocos nucifera*, Lontar Palm *Borassus flabellifer* or Cabbage Palm *Corypha utan*), mangrove forests, or remnant forest strips along river valleys, the cockatoos can survive in open habitats, provided there is enough food (PHPA et al., 1998).

Feeding ecology

Like many other cockatoos the species is known to feed on a wide variety of seeds, nuts, berries, fruits and flowers (Forshaw, 1989). Although the list of known Yellow-crested Cockatoo food plants is long, it is based mainly on opportunistic observations and includes food plants reported by farmers (Cahyadin, Jepson and Arif, 1994; Mallo and Setiawan, 1996; Setiawan, 1996; Agista and Rubyanto, 2001; Aziz, 2012; Nandika and Agustina, 2018). The methods lead to a dominance of cultivated species (e.g. maize *Zea mays*, mango *Mangifera indica*, tamarin *Tamarindus indica,* moringa *Moringa oleifera*, coconut palm *Cocos nucifera* flowers and young fruits) and open habitats where behaviour is more easily observed than in closed canopy forest. In times before cockatoos were captured in the thousands and still occurred in large flocks, they were feared crop pests (Kendall, 1979; PHPA et al., 1998; Prijono, 2008). Since their decline this role is negligible and restricted to exceptional locations. Much less is known about feeding observations on uncultivated wild plants; the list includes various *Ficus, Canarium* and *Protium* species (PHPA et al., 1998). It is highly likely that many of the wild plants consumed by the better studied Citron-crested Cockatoo on Sumba (see 1.2.2) also play a role in the nutrition of Yellow-crested Cockatoos. The cockatoos — like other parrots — tend to consume fruits and seeds before they are ripe and destroy most seeds with their beaks, acting mainly as seed predator (Collar, 1997) but their ability of carrying seeds in their bill, crop or stuck to their plumage allows them to act as accidental seed dispersers (Collar, 1997; Tella et al., 2015).

Breeding ecology

Studies of the Yellow-crested Cockatoo's breeding biology in the wild have been very limited and most were just side notes in studies of population size, usually involving <10 nests whose contents were not investigated (Agista and Rubyanto, 2001; Hidayat, 2012; Nandika and Agustina, 2012; Imansyah et al., 2016; Ihsannudin et al., 2020; Nandika et al., 2020).

Yellow-crested cockatoos, like the majority of parrot species nest in tree cavities (Collar, 1997, 2001; van der Hoek et al., 2017). Only once Yellow-crested Cockatoo nesting in borrows in a 10 m tall vertical soil riverbank was reported from Central Sulawesi (Mallo and Setiawan, 1996; Collar, 2001). Similar behaviour is observed in other parrot species (Lawson and Lanning, 1981; Bucher et al., 1987; Arcos-Torres and Solano-Ugalde, 2008). In Yellow-crested Cockatoos tree and palm cavities are however the normal choice for nests. Preferred species vary widely across the range and include e.g. *Tetrameles nudiflora*, *Metrosideros petiolate*, *Ceiba pentandra*, *Alstonia scholaris*, *Ficus benyamina, Sterculia foetida, Gossampinus sp.*, and *Borassus flabellifer* (Forshaw, 1989; Setiawan, 1996; PHPA et al., 1998; Agista and Rubyanto, 2001; Collar, 2001).

As so few nests have been accessed by researchers, most conclusions about the timing of the breeding season are deducted from pairs entering nest holes, observations of nestlings being fed by their parents in the cavity entrance or after fledging, chicks removed by trappers, and enlarged gonads in dissection of specimens killed in the early days of ornithological exploration (Forshaw, 1989; Collar, 2001). This has rendered a variety of seasons reported as breeding period for the species (Forshaw, 1989; Cahyadin, Jepson and Arif, 1994; Catterall, 1997; Coates and Bishop, 1997; Agista and Rubyanto, 2001; Collar, 2001; BirdLife International, 2022b). As typical for large parrots (Rowley and Collar, 1997), a successful Yellow-crested Cockatoo nest attempt takes multiple months from prospecting to fledging (>3 weeks incubation and >9 weeks nesting stage alone take almost 3 months) or even fledgling independence (Kendall, 1979; Forshaw, 1989; Setiawan, 1996; Djawarai et al., 2014). Allowing for some individual, regional, and annual variation, breeding reported for both September–October and Mach–April is not contradictory if the former refers to prospecting and egg laying and the latter to fledging and feeding of dependent fledglings.

Another typical trait of most parrot species is the formation of long-lasting socially monogamous pairs (Forshaw, 1978; Collar, 1997; Spoon, 2006) and the Yellow-crested Cockatoo does not appear to be an exception, although this is only supported by anecdotal evidence (Schmutz 1977 in Collar, 2001) and no studies with individually identifiable wild pairs have been carried out. Unlike the majority of parrots where the female incubates alone while the male provisions her with food (Forshaw, 1978; Collar, 1997), most cockatoos — including those of the genus *Cacatua* — exhibit biparental incubation without one parent providing for the other (Rowley, 1990; Spoon, 2006).

In captivity up to three eggs have been reported per nesting attempt, in the wild usually only two. Incubation lasted 23–28 days and nestling period is given as ca 65–70 days in and chicks depend on their parents for several months (Forshaw, 1989; Setiawan, 1996; Coates and Bishop, 1997; Putra et al., 1999; Prijono, 2008; IUCN, 2021).

Yellow-crested Cockatoo trapping and trade

The Yellow-crested Cockatoo has a long history of heavy trade: It was a common species in the past and was considered the most easily available cockatoo for many years (Inskipp et al. 1988). It was traded in large numbers for low prices until the mid-1970s when prices started rising (Inskipp et al., 1988). Major importers were the US and European countries (PHPA et al., 1998). The species was added to CITES Appendix 2 in 1981. An annual capture quota was introduced in the 1980s and the number of captures permitted gradually decreased until it was set to zero from 1994 onwards. Export from Indonesia was already outlawed by a moratorium in 1992 and the Yellow-crested Cockatoo had become the highest priced of the parrots in Wallacea (Marsden, 1995). However, this did not stop the illegal trade (PHPA et al., 1998) and according to anecdotal reports by trappers their activities were not significantly disrupted until the early 2000s (pers. obs.). Although there is very little known about the population numbers in the 1970s, the reported export and import numbers in the 1980s suggest that populations must still have been substantial enough to support the import of 5,200–12,000 wild-caught Yellow-crested Cockatoos to CITES countries via Singapore every year for more than a decade (Inskipp et al., 1988; PHPA et al., 1998; BirdLife International, 2021b). The species was granted formal national protection by the Ministry of Forestry in 1997 (Cahill et al., 2006) and in 2004 it was moved to CITES Appendix 1. When legislation became stricter in the traditional importing countries, the demand was thought to have been replaced by other countries with less strict regulations (Pires, 2012), e.g. countries in the Middle East and India. Domestic demand for cockatoos as pets within Indonesia and even locally in the areas of origin remains high. Since trade has become illegal, it has been much harder to survey the trade (Pires, 2012), with information only available sporadically when it is either leaked or the trade is intercepted by law enforcement, as happened in 2015 when more than 20 Yellow-crested Cockatoos were discovered stuffed into water bottles on a boat arriving in Surabaya (McKirdy et al., 2015). Currently, the trade routes for Yellow-crested Cockatoos are thought to run by boat via Jakarta or Surabaya, from which cockatoos are shipped onwards via trade hubs such as Singapore, Hongkong or the Philippines (PHPA et al., 1998; Budiani and Raharningrum, 2018). Online trading via social media platforms has taken on a more important role recently, especially for connecting middlemen and buyers (Budiani and Raharningrum, 2018).

1.2.2 Citron-crested Cockatoo

The Citron-crested Cockatoo *Cacatua citrinocristata* is endemic to the island of Sumba, East Nusa Tenggara, Indonesia (Figure 1.2, Figure 1.3). The taxon was recently elevated to species rank from a subspecies of the Yellow-crested Cockatoo due to its morphological distinctiveness (Figure 1.1), most obvious an orange crest instead of a yellow one (Collar and Marsden, 2014; Eaton et al., 2016; BirdLife International, 2022a).

As closely related species the Citron-crested Cockatoo and the Yellow-crested Cockatoo are generally assumed to be very similar ecologically, aside from adaptations to their native habitats. Some aspects of ecology, such as wild food plants and nesting ecology have been studied more intensively in the Sumba species than on its widespread relative (Marsden, 1995; Marsden and Jones, 1997; Hidayat, 2014). Nesting data on Sumba even include some nest access (Walker et al., 2005; Djawarai et al., 2014), but all studies were limited by low numbers of active nests found, preventing detailed analyses of nesting parameters in the wild (Marsden and Jones, 1997; Walker et al., 2001, 2005; Burung Indonesia, 2013; Djawarai et al., 2014; Hidayat, 2015). Citron-crested cockatoos feed on a wide variety of native and introduced, wild and cultivated species (Djawarai et al., 2014; Hidayat, 2014). Knowledge of the cockatoo's feeding ecology on Sumba is based mostly on incidental observations and reports by farmers (Persulessy et al., 2003; Djawarai et al., 2014; Hidayat and Kayat, 2020) but includes one study including forest habitat and food species availability and found preference *Melia azedarach, Quercus piriformis* and *Phaseolus lunatus* (Hidayat, 2014). In the past, before cockatoos were captured in the thousands, they were known as crop pests (Kendall, 1979; PHPA et al., 1998; Prijono, 2008). Older Sumba residents remember being tasked in their childhood with driving large flocks of cockatoos off the corn fields to protect the harvest (pers. comm. B. Paulus, D. Wali, B. Yohan 2018).

Over the history of ornithology on Sumba many authors have taken note of the Citron-crested Cockatoo, initially commenting on how common they were (Doherty 1891 in Inskipp et al., 1988) Formal population estimates were not attempted until the start of conservation concerns in the 1980s when an unpublished internal survey found an 80% decline in cockatoo densities from 8 individuals km^{-2} (12,000 individuals in 1986) to 1.9 individuals km^{-2} within three years (Riffel and Bekti 1991 in PHPA et al., 1998). In 1992 2.2 individuals km^{-2} were estimated (Jones et al., 1995). In the early 2000s different densities were reported ranging from 0.2 individuals km^{-2} in 2003 (Persulessy et al., 2003) and 0.1 in 2007 (Bashari and Wungo, 2011; Wungo, 2011) to 4.3 at the four core sites in 2002 (Cahill et al., 2006). Only the latter survey matched some of the sites from 1992 and was published, therefore, a recovery following the trade ban was generally assumed (Cahill et al., 2006). Although the surveys covered different areas and used different methods the discrepancy in results is not fully explained by this and some uncertainty remains about the island-wide population size during this period. The most recent population survey in 2012 was based on small sample sizes and resulted in 2.9 individuals km^{-2} at three forest sites (Nandika et al., 2012).

Citron-crested Cockatoo trapping and trade

As a subspecies of the Yellow-crested Cockatoo, the history of the Citron-crested Cockatoo is closely linked to the more widely spread cockatoo. Cockatoos from Sumba were at times even more sought after because of their orange crests. The numbers captured and exported from Sumba were estimated to still be in the low thousands in 1989, 1991 and 1992 by Marsden (1995), although the remaining populations did not appear to be much larger than the annual trapping rates (Jones et al., 1995; Cahill et al., 2006). Local regents banned the trapping and trade of cockatoos in East and West Sumba in 1992 and 1993, respectively (PHPA et al., 1998; Cahill et al., 2006). Some progress towards enforcing this ban was made through extensive public awareness campaigns conducted by NGOs (Djawarai et al., 2014) and the eventual dedication of two areas of prime cockatoo habitat on Sumba as national parks by the Indonesian government. According to former trappers, it became more risky to trap cockatoos in the early 2000s, especially in the national parks and in areas where NGOs operated; indeed, several arrests were made and one trapper received a jail sentence (Djawarai et al., 2014). From 2016 to 2019, we found evidence for at least 12 incidences of cockatoo trapping from roosts and nests on Sumba. The evidence found included climbing set-ups erected on cockatoo trees; the presence of large amounts of flight feathers, indicating recent trapping success; twigs with nylon nooses; and eye-witness reports. According to our informants, trade from Sumba has been ongoing for the past decades and has been increasing since 2017, with rising prices per individual (IDR 1,000,000 for the trapper in 2019) and improving logistics for transport and communication between trappers and traders.

1.3 Study area

1.3.1 Study area in Wallacea

The study area comprises the combined historic ranges of the Yellow-crested Cockatoo and Citron-crested Cockatoo with focus on the areas where either species has survived until today. The Citron-crested Cockatoo is endemic to Sumba Island in East Nusa Tenggara (Figure 1.3). The Yellow-crested Cockatoo’s range is mostly located in Wallacea and encompasses the Nusa Tenggara Islands (or Lesser Sundas/Lesser Sunda Islands), Sulawesi and its satellites and the Masalembu Archipelago in the Southern Java Sea (Figure 1.2). Most of the range belongs to Indonesia with the exception of the Eastern part of Timor Island which forms the Republic of Timor Leste. In this thesis Lesser Sunda Islands and Nusa Tenggara islands is used synonymously although historically the Lesser Sundas included Bali and usually excluded the territory of the present-day Timor-Leste (Monk et al., 1997:20). Nusa Tenggara only includes the island chain from Lombok through to Alor, plus Sumba, Timor, Wetar and their Satellites and is therefore the more useful term regarding ecological boundaries but is less widely used. Whenever this distinction becomes important in this thesis, the included islands are specified by name.

Wallacea is the biogeographical region between the Wallace-Line (between Bali and Lombok) in the West and the Lydekker-Line (between Maluku and Papua) in the East (Figure 1.3). It forms a transition zone between Indomalyan and Australian fauna (Orientalis to Australis) and is a hotspot for both biodiversity and endemism (Stattersfield et al., 1998; Myers et al., 2000). Maluku is part of Wallacea but — despite having cockatoos of other species — has never supported known populations of the study species (Coates and Bishop, 1997; Collar, 2001).

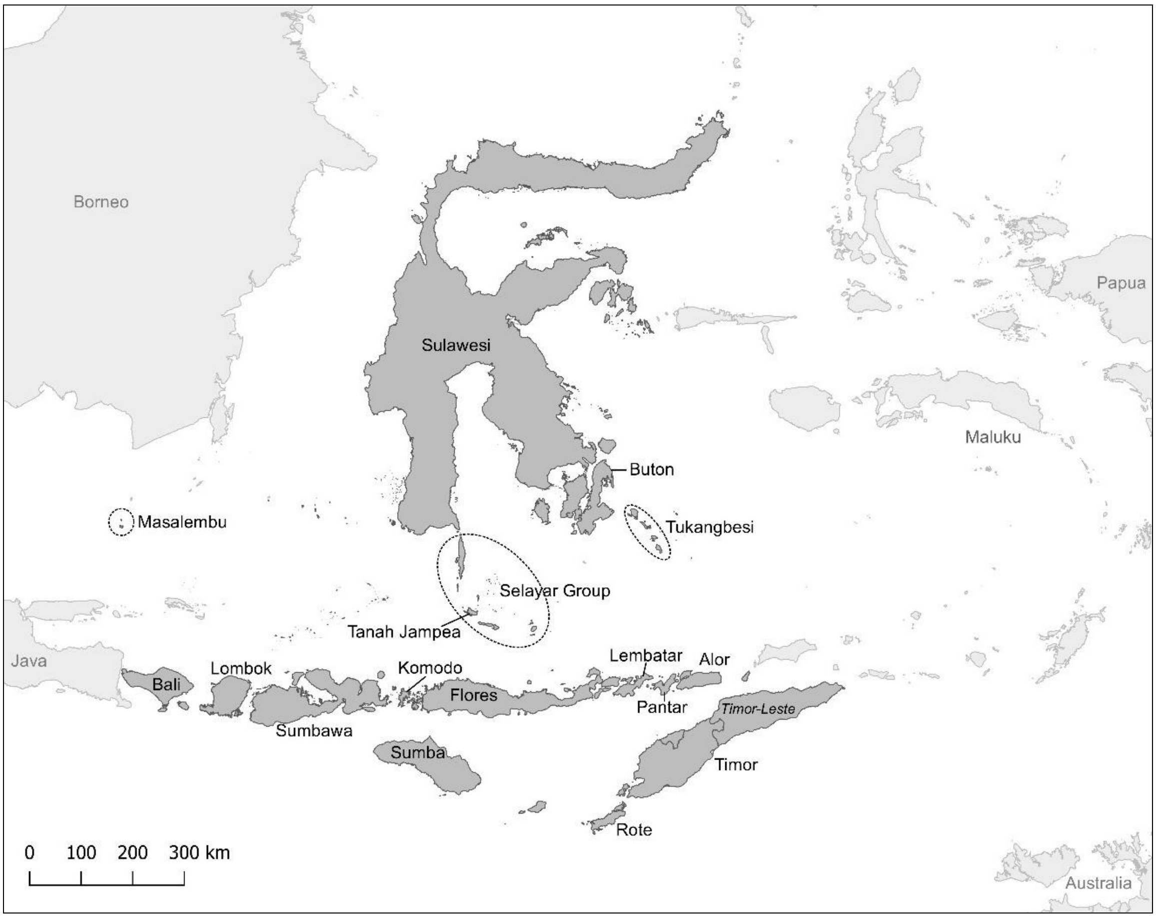

Figure 1.3: Study area (dark shading) within Indonesia and Timor-Leste with major islands

1.3.2 Indonesia

Indonesia is the world's largest island state, spanning almost 2 million km² on >17,000 islands and the 4th most populous country globally with 270 million people (Monk et al., 1997; World Bank Group, 2020a; Badan Pusat Statistik, 2021). Economic development was very steep in the 1970s and it is now regarded as 'newly industrialized country' (Bolt and van Zanden, 2021). Due to the county's size and island structure, it is culturally and economically very diverse. Beside very densely populated areas e.g. on Java, Indonesia also supports large contiguous areas of wilderness including primary tropical forest. Indonesian biodiversity is one of the largest worldwide (Harrison et al., 2020), supporting > 1700 bird species. With > 500 birds endemic to the country and 38 Endemic Bird Areas (BirdLife International, 2021a) levels of endemism are also high as typical for tropical archipelagos (Stattersfield et al., 1998) but Indonesia is also one of the countries most threatened by biodiversity loss (Monk et al., 1997; BirdLife International, 2021a) including 168 threatened bird species

(BirdLife International, 2021a). Indonesia as a country has been deemed the worldwide highest priority for parrot conservation considering the parrot species diversity, number of threatened species and number of country endemics (Olah et al., 2016; Pires et al., 2021).

1.3.3 Timor-Leste

Timor Island is politically split into two countries; most of the western half belongs to the Republic of Indonesia (Figure 1.3) whereas the eastern half is the Democratic Republic of Timor-Leste (formerly East Timor, Figure 1.3). A small enclave on Timor's north coast belongs to Timor-Leste and is surrounded on land by Indonesian territory. The republic of Timor-Leste covers 15,000 km² and has a population of 1.3 million people (World Bank Group, 2020b). The country's recent history was dominated by war and Indonesian occupation and the country only became independent in 2002. Although political borders do not stop bird dispersal, there are differences in conservation laws, administration, law enforcement and culture between the two countries. Despite rapid economic development after independence the new country has continued to emphasize protection of natural resources creating protected areas including two national Parks and identifying 16 Important Bird Areas (BirdLife International, 2008; Trainor et al., 2008; BirdLife International, 2021a).

1.3.4 Sumba

The island of Sumba (118.9–120.8°◦E, 9.3–10.3°◦S) in East Nusa Tenggara took a central role in the study because it supports only population of the Citron-crested Cockatoo. It comprises just over 11,000 km² and has 650,000 inhabitants (Badan Pusat Statistik, 2021). It is dominated by relatively low limestone hills reaching up to 1200 m asl (Monk et al., 1997). Sumba has a dry season from May to November and a rainy season from December to April (Monk et al., 1997). It is one of the economically least developed islands of Indonesia where many people rely on self-subsistence farming. Pastures for livestock and irrigated rice fields are the most important agricultural land uses (Russell-Smith et al., 2007; Badan Pusat Statistik, 2021). Many villages still do not have electricity, mobile phone network or a reliable source of water (Russell-Smith et al., 2007).

Owing to its relative isolation within the Lesser Sundas, Sumba is also distinctive in the composition of its avifauna (Monk et al., 1997): the island is a biodiversity hotspot with

15 restricted-range species, including nine island endemics (del Hoyo and Collar, 2014, 2016; Eaton et al., 2016; BirdLife International, 2021a).

1.4 Thesis aim and objectives

This thesis aims to understand patterns of persistence, size, trends and productivity in populations of two Critically Endangered and heavily traded Indonesian cockatoos: the Yellow-crested Cockatoo *Cacatua sulphurea* and Citron-crested Cockatoo *Cacatua citrinocristata*.

To achieve this aim, chapters of the thesis have the following objectives:

Chapter 2: Assess the status and viability of all populations of the Yellow-crested Cockatoo and investigate the environmental and socio-economic factors determining survival or extinction of populations in the past.

Chapter 3: Estimate the Yellow-crested Cockatoo densities and numbers in its stronghold population on Komodo island using density surface modelling.

Chapter 4: Determine the decadal population trajectory of the Citron-crested Cockatoo, other parrots and a hornbill on Sumba in association with forest change over 25 years.

Chapter 5: Investigate Productivity constraints on Citron-crested Cockatoos in a rich community of large hole-nesting birds on Sumba

Chapter 6: Use the outcomes of Chapter 2–5 to identify suitable conservation interventions for each subspecies to conserve or boost current populations and re-create extinct ones

1.5 Thesis structure

Chapter 2: Correlates of persistence in remnant populations of two Critically Endangered cockatoos

A challenge with endangered species that have disappeared in most of their range is to identify conditions allowing survival at just a few sites. Random forests classifiers based on socio-ecological variables are used in this chapter to explain why the Critically Endangered Yellow-crested Cockatoo has avoided local extinction. Conditions such as forest cover, human population density and infrastructure, and protected area status were compared between the occupied and unoccupied sites. Examination of local conditions at ‘false negative’ sites (where cockatoos survived contrary to model predictions) showed that, particularly in recent years, cockatoo survival has been promoted by site-specific protection due to traditional beliefs, NGO activities, dedicated individual residents and local topographic barriers. Implications of the local influences for the possibilities for conservation prescriptions tailored to individual sites are discussed. Studies combining field and remotely sensed data, and examining false negative sites for beneficial location-specific conditions, have broad application for the conservation of taxa with once-large ranges.

Chapter 3: Protected by dragons: Density surface modelling confirms large population of the critically endangered Yellow-crested Cockatoo on Komodo Island

Yellow-crested Cockatoo populations of more than 100 individuals remain at only a handful of sites. This chapter combines distance sampling with density surface modelling (DSM) to predict local densities and estimate total population size for one of these areas, Komodo Island, part of Komodo National Park in Indonesia. Local density is modelled based on topography (topographic wetness index) and habitat types (percentage of palm savanna and deciduous monsoon forest). Coincidence between the DSM and a set of independent cockatoo observations was high and the population estimate was considerably larger than previous conservative estimates. Standardized annual counts by Komodo National Park staff showed increases in cockatoo records in the six years before this survey. Taken together, the results indicate that Komodo National Park, alongside and indeed because of preserving its iconic Komodo Dragons *Varanus komodoensis*, is succeeding in protecting a significant population of Indonesia’s rarest cockatoo species. The findings highlight the potential of DSM for locating abundance hotspots, identifying habitat associations, and estimating global population size in a range of threatened taxa, especially if independent datasets can be used to validate model predictions.

Chapter 4: Population changes over 25 years in parrots and hornbills on Sumba

Although the importance of long-term monitoring of population density and distribution is widely recognised, very few tropical bird species have been monitored over the span of 25 years. This chapter is based on a replication of a multi-species distance sampling survey from 1992 in 2017, matching sampling seasons, locations of transects and methods as closely as possible. Data is presented on five parrot species and a hornbill, with three threatened island endemics, Citron-crested Cockatoo Cacatua citrinocristata (Critically Endangered), Sumba Eclectus Eclectus cornelia (Endangered) and Sumba Hornbill Rhyticeros everetti (Endangered), two restricted-range species, Great-billed parrot Tanygnathus megalorynchos and Marigold Lorikeet Trichoglossus capistratus, and one Wallacean-Papuan species, Red-cheeked Parrot Geoffroyus geoffroyi. Quantity of forest on Sumba for both years is assessed using satellite imagery and the size of the resulting forest patches paired with presence data and local density estimates from survey sites to gauge island-wide population sizes. Conservation implications for the surveyed species and methodological lessons are discussed.

Chapter 5: Productivity constraints on Citron-crested Cockatoos in a rich community of large hole-nesting birds

Knowledge of breeding success and its limiting factors is crucial in assessing species' conservation needs. As cavity-nesters, parrots are particularly influenced by the availability of suitable cavities and low breeding output. On Sumba the Citron-crested Cockatoo has the added problem of co-existing with an unusually rich hole-nesting bird community in a forested environment much constrained by habitat loss. Nesting cavities of cockatoos were monitored and their competitors and potential nest-predators, over one to four breeding seasons, using a combination of camera-traps, direct checks on nest contents, and observations from the ground. I investigated the occupancy and fate of potential cockatoo nest sites, seasonal cavity use across the community of large hole-nesters, and visitation rates to nests by potential competitors and predators, and I present new knowledge on the Citron-crested Cockatoo's breeding behaviour in the wild. The consequences of intense competition for cavities are discussed and suitable conservation management actions suggested.

Chapter 6: General conclusions and recommendations

This chapter brings together the conclusions from the previous chapters and uses them to assess the status of both study species and subspecies and Red List assessment is discussed. The conclusions lead to recommendations for the conservation of each taxon, for re introductions and for future research.

References

Agista, D. and Rubyanto, D. (2001) *Telaah awal status, penyebaran, dan populasi kakatua kecil jambul kuning,* Cacatua sulphurea parvula*: di Taman Nasional Komodo, Nusa Tenggara Timur*. Bogor, Indonesia: Birdlife International Indonesia Programme.

Agista, D., Sumardin, Hamid, A., Mallo, F. N., Alam, S., Harjun and Mamengko, C. (2001) *Status Kakatua-kecil Jambul-kuning di Sulawesi Tenggara dan Sulawesi Tengah*. Bogor, Indonesia: Birdlife International - Indonesia Programme.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (Ted., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J. H., Allard, G., Running, S. W., Semerci, A. and Cobb, N. (2010) 'A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests.' *Forest Ecology and Management*, 259(4) pp. 660–684.

Andersson, A. A., Gibson, L., Baker, D. M., Cybulski, J. D., Wang, S., Leung, B., Chu, L. M. and Dingle, C. (2021) 'Stable isotope analysis as a tool to detect illegal trade in critically endangered cockatoos.' *Animal Conservation*, 24(6) pp. 1021–1031.

Arcos-Torres, A. and Solano-Ugalde, A. (2008) 'First record of a nesting colony of the Military Macaw (Psittacidae: Ara militaris) in Ecuador.' *Ornitología Colombiana*, 6 pp. 69–73.

Arendt, W. J. (2000) 'Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery.' *Ornitologia Neotropical*, 11 pp. 13–63.

Assou, D., Elwin, A., Norrey, J., Coulthard, E., Megson, D., Ronfot, D., Auliya, M., Segniagbeto, G. H., Martin, R. O. and D'Cruze, N. (2021) 'Trade in African Grey Parrots for Belief-Based Use: Insights From West Africa's Largest Traditional Medicine Market.' *Frontiers in Ecology and Evolution*, 9, February, p. 29.

Aziz, F. A. (2012) *Telaah awal habitat dan populasi Kakatua-kecil Jambul-kuning di bentang alam Mbeliling Bagian Barat, Manggarai Barat*. Bogor, Indonesia: Burung Indonesia.

Badan Pusat Statistik (2021) *Statistical yearbook of Indonesia 2020*. [Online] [Accessed on 20th December 2021] www.bps.go.id.

Bashari, H. and Arndt, T. (2016) 'Status of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea djampeana* in the Tanahjampea islands, Flores Sea, Indonesia.' *FORKTAIL*, (32) pp. 62–65.

Bashari, H. and Wungo, E. (2011) *Survey burung di Taman Nasional Manupeu Tanah Daru, Sumba, Indonesia*. Borgor, Indonesia.

Beissinger, S. R. (2001) 'Trade of live wild birds: potencials, principles and practices of sustainable use.' *In* Reynolds, J. D., Mace, G. M., Redford, K. H., and Robinson, J. G. (eds) *Conservation of exploited species*. Cambridge, UK: Cambridge University Press, pp. 182–202.

Berkunsky, I., Formoso, A. and Aramburu, R. (2005) 'Ectoparasitic load of blue-fronted parrot (Amazona aestiva, Psittacidae) nestlings.' *Ornitología Neotropical*, 16 pp. 573–578.

Bibby, C. J., Burgess, N. D., Hill, D. A. and Mustoe, S. (2000) *Bird census techniques*. 2nd ed., Amsterdam, Netherlands: Academic Press.

BirdLife International (2008) *BirdLife worked with the Timor-Leste government to create the country's first National Park*. Datazone. [Online] [Accessed on 2nd March 2022] http://datazone.birdlife.org.

BirdLife International (2016) *Species factsheet:* Cacatua sulphurea. [Online] [Accessed on 2nd January 2017] http://www.birdlife.org.

BirdLife International (2018) *State of the world's birds: taking the pulse of the planet*. Cambridge, UK: BirdLife International.

BirdLife International (2021a) *Datazone*. [Online] [Accessed on 11th March 2021] http://datazone.birdlife.org/.

BirdLife International (2021b) *Species factsheet* Cacatua sulphurea. [Online] [Accessed on 16th July 2021] http://www.birdlife.org.

BirdLife International (2022a) *Species Factsheet* Cacatua citrinocristata. [Online] [Accessed on 6th January 2022] http://www.birdlife.org.

BirdLife International (2022b) *Species Factsheet* Cacatua sulphurea. [Online] [Accessed on 6th January 2022] http://www.birdlife.org.

Bolt, J. and van Zanden, J. L. (2021) 'The long view on economic growth: New estimates of GDP.' *In How Was Life? Volume II: New Perspectives on Well-being and Global Inequality since 1820*. Paris, France: OECD Publishing.

Bradbury, G., Trinder, M., Furness, B., Banks, A. N., Caldow, R. W. G. and Hume, D. (2014) 'Mapping seabird sensitivity to offshore wind farms.' Magar, V. (ed.) *PLoS ONE*, 9(9) p. e106366.

Brereton, J. L. G. (1963) 'Evolution within the Psittaciformes.' *Proc.Int.Ornithol.Congr.*, 13 pp. 499–517.

Brun, C., Cook, A. R., Lee, J. S. H., Wich, S. A., Koh, L. P. and Carrasco, L. R. (2015) 'Analysis of deforestation and protected area effectiveness in Indonesia: A comparison of Bayesian spatial models.' *Global Environmental Change*, 31, March, pp. 285–295.

Bruner, A. G., Gullison, R. E., Rice, R. E. and da Fonseca, G. A. B. (2001) 'Effectiveness of parks in protecting tropical biodiversity.' *Science*, 291(5501) pp. 125–128.

Bucher, E. H. and Aramburú, R. M. (2014) 'Land-use changes and monk parakeet expansion in the Pampas grasslands of Argentina.' *Journal of Biogeography*, 41 pp. 1160–1170.

Bucher, E. H., Bertin, M. A. and Santamaria, A. B. (1987) 'Reproduction and molt in the burrowing parrot.' *Wilson Bulletin*, 99 pp. 107–109.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. (2001) *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.

Buckland, S. T., Marsden, S. J. and Green, R. E. (2008) 'Estimating bird abundance: making methods work.' *Bird Conservation International*, 18 pp. 91–108.

Budiani, I. and Raharningrum, F. (2018) *Illegal online trade in Indonesian parrots. Global Initiative Against Transnational Organized Crime.* Geneva, Switzerland.

Bunbury, N., Haverson, P., Page, N., Agricole, J., Angell, G., Banville, P., Constance, A., Friedlander, J., Leite, L., Mahoune, T., Melton-Durup, E., Moumou, J., Raines, K., van de Crommenacker, J. and Fleischer-Dogley, F. (2018) 'Five eradications, three species, three islands: overview, insights and recommendations from invasive bird eradications in the Seychelles.' *Island Invasives 2017 Conference*, March, pp. 282–288.

Burger, J. and Gochfeld, M. (2003) 'Parrot behavior at a Rio Manu (Peru) clay lick: temporal patterns, associations and antipredator responses.' *Acta ethologica*, 6 pp. 23–34.

Burung Indonesia (2013) *The behavioural ecology of breeding the Yellow-crested Cockatoo* Cacatua sulphurea citrinocristata *in Manupeu Tanadaru National Park, Sumba Island. 1st Progress report 2011*. Bogor, Indonesia: Burung Indonesia.

Bush, E. R., Baker, S. E. and Macdonald, D. W. (2014) ‘Global trade in exotic pets 2006–2012.’ *Conservation Biology*, 28(3) pp. 663–676.

Butchart, S. H. M., Brooks, T. M., Davies, C. W. N., Dharmaputra, G., Dutson, G. C. L., Lowen, J. C. and Sahu, A. (1996) ‘The conservation status of forest birds on Flores and Sumbawa, Indonesia.’ *Bird Conservation International*, 6(4) pp. 335–370.

Cahill, A. J., Walker, J. S. and Marsden, S. J. (2006) ‘Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea citrinocristata* in Indonesia after 10 years of international trade control.’ *Oryx*, 40(2) pp. 161–167.

Cahyadin, Y., Jepson, P. and Arif, S. (1994) *The status of* Cacatua sulphurea abbotti *on the Masalembo Islands*. Bogor: PHPA/BirdLife International - Indonesia Programme.

Cahyadin, Y., Jepson, P. and Syarief, M. (1994) *A rapid status assessment of* Cacatua sulphurea sulphurea *in South Sulawesi Province*. Bogor, Indonesia: PHPA/BirdLife International - Indonesia Programme.

Casagrande, D. G. and Beissinger, S. R. (1997) ‘Evaluation of four methods for estimating parrot population size.’ *The Condor*, 99(2) pp. 445–457.

Catterall, M. (1997) *Results of the 1996 bird survey of Buton Island, Sulawesi, Indonesia*. Spilsby, UK: Operation Wallacea.

Cazalis, V., Princé, K., Mihoub, J. B., Kelly, J., Butchart, S. H. M. and Rodrigues, A. S. L. (2020) ‘Effectiveness of protected areas in conserving tropical forest birds.’ *Nature Communications*, 11(1) pp. 1–8.

Christian, C. S., Lacher, T. E., Zamore, M. P., Potts, T. D. and Burnett, G. W. (1996) ‘Parrot conservation in the Lesser Antilles with some comparison to the Puerto Rican efforts.’ *Biol.Conserv.*, 77 pp. 159–167.

CITES (2002) *Cacatua sulphurea - Consideration of proposals for amendment of appendices I and II - CoP13 Prop. 11*. [Online] https://cites.org/sites/default/files/eng/cop/13/prop/E13-P11.pdf.

CITES (2020) *Convention on International Trade in Endangered Species of Wild Fauna and Flora - Appendices*. [Online] [Accessed on 10th February 2021] https://cites.org/eng/app/appendices.php.

Clout, M. N. and Craig, J. L. (1994) ‘The conservation of critically endangered flightless birds in New Zealand.’ *Ibis*, 137 pp. 181–190.

Clout, M. N. and Merton, D. V (1998) ‘Saving the Kakapo: The conservation of the world’s most peculiare parrot.’ *Bird Conserv.Internatn.*, 8 pp. 281–296.

Coates, B. J. and Bishop, D. (1997) *A guide to the birds of Wallacea*. Queensland, Australia: Dove Publications.

Collar, N. J. (1997) ‘Order Psittaciformes, Family Psittacidae (Parrots).’ *In* del Hoyo, J., Elliott, A., and Sargatal, J. (eds) *Handbook of the Birds of the World, Vol. 4, Sandgrouse to Cuckoos*. Barcelona, Spain: Lynx Ediciones, pp. 280–477.

Collar, N. J. (2001) ‘Yellow-crested Cockatoo *Cacatua sulphurea*.’ *In* Collar, N. J., Andreev, A. V, Chan, S., Crosby, M. J., Subramanya, S., and Tobias, J. A. (eds) *Threatened birds of Asia: the BirdLife International Red Data Book*. Cambridge: BirdLife International, pp. 1643–1661.

Collar, N. J., Andreev, A. V, Chan, S., Crosby, M. J., Subramanya, S. and Tobias, J. A. (2001) *Threatened birds of Asia: The BirdLife International Red Data Book*. Cambridge, UK: BirdLife International.

Collar, N. J., Eaton, J. A. and Sykes, B. (2017) 'Conservation and the redaction of locality data.' *BirdingASIA*, 28 pp. 3–4.

Collar, N. J. and Juniper, A. T. (1992) 'Dimension and causes of the parrot conservation crisis.' *In* Beissinger, S. R. and Snyder, N. F. R. (eds) *New world parrots in crisis: solutions from conservation biology.* New York and London: Smithsonian Institution Press, pp. 1–24.

Collar, N. J. and Marsden, S. J. (2014) 'The subspecies of Yellow-crested Cockatoo *Cacatua sulphurea*.' *Forktail*, (30) pp. 23–27.

Collen, B., McRae, L., Deinet, S., De Palma, A., Carranza, T., Cooper, N., Loh, J. and Baillie, J. E. M. (2011) 'Predicting how populations decline to extinction.' *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1577) pp. 2577–2586.

Cook, D., Roberts, M. and Lowther, J. (2002) 'The international wildlife trade and organised crime: a review of the evidence and role of the United Kingdom.' *Cambridge: WWF/TRAFFIC*.

Dénes, F. V, Tella, J. L. and Beissinger, S. R. (2018) 'Revisiting methods for estimating parrot abundance and population size.' *Emu-Austral Ornithology*, 118(1) pp. 67–79.

Djawarai, Y., Bashari, H., Siregar, B. and Widyanto, A. (2014) *The breeding ecology of Sumba Cockatoo* Cacatua sulphurea citrinocristata *in Manupeu Tanadaru National Park and surrounding, Sumba*. *Burung Indonesia*. Bogor, Indonesia: Burung Indonesia.

Dutson, G. (1995) 'The birds of Salayar and the Flores Sea islands.' *Kukila*, 7(2) pp. 129–141.

Eaton, J. A., Van Balen, S. B., Brickle, N. W. and Rheindt, F. E. (2016) *Birds of the Indonesian Archipelago Greater Sundas and Wallacea*. Barcelona, Spain: Lynx Ediciones.

Elith, J. and Leathwick, J. R. (2009) 'Species Distribution Models: Ecological Explanation and Prediction Across Space and Time.' *https://doi.org/10.1146/annurev.ecolsys.110308.120159*, 40, February, pp. 677–697.

Figueira, L., Tella, J. L., Camargo, U. M. and Ferraz, G. (2015) 'Autonomous sound monitoring shows higher use of Amazon old growth than secondary forest by parrots.' *Biological Conservation*, 184 pp. 27–35.

Fogell, D. J., Martin, R. O. and Groombridge, J. J. (2016) 'Beak and feather disease virus in wild and captive parrots: an analysis of geographic and taxonomic distribution and methodological trends.' *Archives of Virology*, 161 pp. 2059–2074.

Forshaw, J. M. (1978) *Parrots of the world*. 2nd ed., London: David & Charles.

Forshaw, J. M. (1989) 'Lesser Sulphur-crested Cockatoo Cacatua sulphurea (Gmelin).' *In Parrots of the world*. London, UK: David&Charles, pp. 136–137.

Frynta, D., Lišková, S., Bü Ltmann, S., Burda, H., Bültmann, S. and Burda, H. (2010) 'Being attractive brings advantages: The case of parrot species in captivity.' *PLoS ONE*, 5(9) p. e12568.

Gaveau, D. L. A., Epting, J., Lyne, O., Linkie, M., Kumara, I., Kanninen, M. and Leader-Williams, N. (2009) 'Evaluating whether protected areas reduce tropical deforestation in Sumatra.' *Journal of Biogeography*, 36(11) pp. 2165–2175.

Gibson, C. C. and Marks, S. A. (1995) 'Transforming rural hunters into conservationists: An assessment of community-based wildlife management programs in Africa.' *World Development*, 23(6) pp. 941–957.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E. and Sodhi, N. S. (2011) 'Primary forests are irreplaceable for sustaining tropical biodiversity.' *Nature*, 478(7369) pp. 378–381.

Gunnthorsdottir, A. (2015) 'Physical Attractiveness of an Animal Species as a Decision Factor for its Preservation.' https://doi.org/10.2752/089279301786999355, 14(4) pp. 204–214.

Harrison, M. E., Ottay, J. B., D'Arcy, L. J., Cheyne, S. M., Anggodo, Belcher, C., Cole, L., Dohong, A., Ermiasi, Y., Feldpausch, T., Gallego-Sala, A., Gunawan, A., Höing, A., Husson, S. J., Kulu, I. P., Soebagio, S. M., Mang, S., Mercado, L., Morrogh-Bernard, H. C., Page, S. E., Priyanto, R., Ripoll Capilla, B., Rowland, L., Santos, E. M., Schreer, V., Sudyana, I. N., Taman, S. B. B., Thornton, S. A., Upton, C., Wich, S. A. and van Veen, F. J. F. (2020) 'Tropical forest and peatland conservation in Indonesia: Challenges and directions.' *People and Nature*, 2(1) pp. 4–28.

HBW and BirdLife International (2021) *Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 6*. [Online] http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v6_Dec21.zip%0D.

Hidayat, O. (2012) 'Lubang masa depan.' *Biodiversitas Indonesia*, 2 pp. 110–118.

Hidayat, O. (2014) 'Komposisi, preferensi dan sebaran jenis tumbuhan pakan Kakatua Sumba (*Cacatua sulphurea citrinocristata*) di Taman Nasional Laiwanggi Wanggameti.' *Jurnal Penelitian Kehutanan Wallacea*, 3(1) pp. 25–36.

Hidayat, O. (2015) 'Status terkini perdagangan Kakatua Sumba (*Cacatua sulphurea citrinocristata*).' *Warta Cendana*, 8(1) pp. 1–4.

Hidayat, O. and Kayat (2020) 'Pendekatan preferensi habitat dalam penyusunan strategi konservasi in situ Kakatua Sumba (*Cacatua sulphurea citrinocristata*, Fraser 1844).' *Jurnal Penelitian Hutan dan Konservasi Alam*, 17(2) pp. 113–126.

Higginbottom, T. P., Collar, N. J., Symeonakis, E. and Marsden, S. J. (2019) 'Deforestation dynamics in an endemic-rich mountain system: Conservation successes and challenges in West Java 1990–2015.' *Biological Conservation*, 229, January, pp. 152–159.

van der Hoek, Y., Gaona, G. V. and Martin, K. (2017) 'The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world.' *Diversity and Distributions*, 23(10) pp. 1120–1131.

Homberger, D. G. and Beissinger, S. R. (2006) 'Bird trade: conservation strategy or extinction catalyst.' *Acta Zoologica Sinica*, 52 pp. 46–47.

del Hoyo, J. and Collar, N. J. (2014) *HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 1: Non-passerines*. Barcelona, Spain and Cambridge, UK: Lynx Edicions and BirdLife International.

del Hoyo, J. and Collar, N. J. (2016) *HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 2: Passerines*. Barcelona, Spain: Lynx Edicions.

Ihsannudin, I., Hidayat, K., Sukesi, K. and Yuliati, Y. (2020) 'Perception of the local community toward the yellow-crested cockatoo (*Cacatua sulphurea abbotti*), a critically endangered species in Masakambing Island, Indonesia.' *Geografia*, 16(4) pp. 1–14.

Imansyah, M. J., Purwandana, D., Ariefiandy, A., Benu, Y. J., Jessop, T. S. and Trainor, C. R. (2016) 'Valley-floor censuses of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea occidentalis* on Komodo Island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period.' *Forktail*, 32 pp. 66–72.

Inskipp, T., Broad, S. and Luxmoore, R. (1988) *Significant Trade in Wildlife -A Review of Selected Species in CITES Appendix II, Volume 3: Birds*. Cambridge, UK: IUCN Conservation Monitoring Centre.

IUCN (2021) *The IUCN Red List of Threatened Species. Version 2021-3*. Gland, Switzerland: IUCN. [Online] [Accessed on 12th February 2022] https://www.iucnredlist.org/species /22684777/131874695#population.

Jones, C. and Duffy, K. (1993) ‘Conservation management of the echo parakeet Psittacula eques echo.’ *Dodo*, 29 pp. 126–148.

Jones, C. G., Malham, J., Reuleaux, A., Richards, H. A., Raisin, C., Tollington, S., Zuel, N., Chowrimootoo, A. and Tatayah, V. (2013) ‘Echo parakeet *Psittacula eques* Perruche de Maurice.’ *In* Safford, R. and Hawkins, F. (eds) *The Birds of Africa: Volume VIII: The Malagasy Region: Madagascar, Seychelles, Comoros, Mascarenes*. A&C Black, pp. 433–438.

Jones, M. J., Linsley, M. D. and Marsden, S. J. (1995) ‘Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia.’ *Bird Conservation International*, 5(01) pp. 21–52.

Juniper, T. and Parr, M. (2003) *Parrots: a guide to parrots of the world*. London, UK: Christopher Helm Publishers, Incorporated.

Keenan, R. J., Reams, G. A., Achard, F., de Freitas, J. V., Grainger, A. and Lindquist, E. (2015) ‘Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015.’ *Forest Ecology and Management*, 352, September, pp. 9–20.

Kelly, D. and Marples, N. M. (2010) ‘Bird populations of the Wakatobi.’ *In* Clifton, J., Unsworth, R. K. F., and Smith, D. J. (eds) *Marine research and conservation in the Coral Triangle: the Wakatobi National Park.* Hauppauge, NY: Nova Science Publishers, pp. 149–170.

Kendall, S. B. (1979) ‘Citron-crested cockatoos in Sumba.’ *Avicultural Magazine*, 85(2) pp. 93–94.

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. and Steffan-Dewenter, I. (2009) ‘Extinction debt: a challenge for biodiversity conservation.’ *Trends in Ecology and Evolution*. Elsevier Current Trends pp. 564–571.

Lawson, P. W. and Lanning, D. V (1981) ‘Nesting and status of the maroon-fronted parrot (Rhinchopsitta terrisi).’ *In* Pasquier, R. F. (ed.) *Conservation of the New World parrots. Proceedings of the ICBP Parrot Working Group Meeting St. Lucia, 1980*. Smithsonian Institution Press for the International Council for Bird Preservation, pp. 385–392.

Leven, M. R. and Corlett, R. T. (2004) ‘Invasive birds in Hong Kong, China.’ *Ornithological Science*, 3(1) pp. 43–55.

Lim, K. S. (1997) ‘Bird biodiversity in the nature reserves of Singapore.’ *In Proceedings of the Nature Reserves Survey Seminar. Garden’s Bull. Singapore*, pp. 225–244.

Loh, J., Green, R. E., Ricketts, T., Lamoreux, J., Jenkins, M., Kapos, V. and Randers, J. (2005) ‘The Living Planet Index: using species population time series to track trends in biodiversity.’ *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1454) p. 289.

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akçakaya, H. R., Leader-Williams, N., Milner-Gulland, E. J. and Stuart, S. N. (2008) ‘Quantification of extinction risk: IUCN’s system for classifying threatened species.’ *Conservation biology*, 22(6) pp. 1424–1442.

Mack, A. L. and Wright, D. D. (1998) ‘The vulturine parrot, Psittrichas fulgidus, a threatened New Guinea endemic: Notes on it biology and conservation.’ *Bird Conserv.Internatn.*, 8 pp. 185–194.

Mackenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A. and Langtimm, C. A. (2002) ‘Estimating site occupancy rates when detection probabilitiies are less than one.’ *Ecology*, 83(8) pp. 2248–2255.

MacKenzie, D. I., Nichols, J. D., Sutton, N., Kawanishi, K. and Bailey, L. L. (2005) ‘Improving inferences in population studies of rare species that are detected imperfectly.’ *Ecology*, 86(5) pp. 1101–1113.

Mallo, F. N. and Setiawan, I. (1996) *Telaah status* Cacatua sulphurea sulphurea *di Sulawesi Tengah*. Bogor, Indonesia.

Manning, A. D., Gibbons, P., Fischer, J., Oliver, D. L. and Lindenmayer, D. B. (2012) ‘Hollow futures? Tree decline, lag effects and hollow-dependent species.’ *Animal Conservation*, 16(4) pp. 395–403.

Marešová, J. and Frynta, D. (2008) ‘Noah’s Ark is full of common species attractive to humans: The case of boid snakes in zoos.’ *Ecological Economics*, 64(3) pp. 554–558.

Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Moretti, D. J., Harris, D. and Tyack, P. L. (2013) ‘Estimating animal population density using passive acoustics.’ *Biological Reviews*, 88(2) pp. 287–309.

Marsden, S. J. (1995) *The ecology and conservation of the parrots of Sumba, Buru and Seram, Indonesia.* PhD-thesis. Manchester Metropolitan University.

Marsden, S. J. (1999) ‘Estimation of parrot and hornbill densities using a point count distance sampling method.’ *Ibis*, 141(3) pp. 327–390.

Marsden, S. J. and Jones, M. J. (1997) ‘The nesting requirements of the parrots and hornbill of Sumba, Indonesia.’ *Biological Conservation*, 82(3) pp. 279–287.

Marsden, S. J. and Royle, K. (2015) ‘Abundance and abundance change in the world’s parrots.’ *Ibis*, 157(2) pp. 219–229.

Marshall, H., Collar, N. J., Lees, A. C., Moss, A., Yuda, P. and Marsden, S. J. (2019) ‘Spatio-temporal dynamics of consumer demand driving the Asian Songbird Crisis.’ *Biological Conservation*, September, p. 108237.

Martin, R. B. (2000) ‘When CITES works and when it does not.’ *In* Hutton, J. and Dickson, B. (eds) *Endangered Species Threatened Convention: The Past, Present and Future of CITES*. London, UK: Earthscan, pp. 29–37.

Martin, T. E., Kelly, D. J., Keogh, N. T., Heriyadi, D., Singer, H. A. and Blackburn, G. A. (2012) ‘The avifauna of Lambusango Forest Reserve, Buton Island, south-east Sulawesi, with additional sightings from southern Buton.’ *Forktail*, 28 pp. 107–112.

Masello, J. F. and Quillfeldt, P. (2002) ‘Chick growth and breeding success of the Burrowing Parrot.’ *The Condor*, 104(3) pp. 574–586.

Mátyás, C. (2010) ‘Forecasts needed for retreating forests.’ *Nature 2010 464:7293*, 464(7293) pp. 1271–1271.

McCormack, G. and Künzlé, J. (1996) ‘The ’Ura or Rimatara Lorikeet Vini kuhlii: its former range, present status, and conservation priorities.’ *Bird Conserv.Internatn.*, 6 pp. 325–334.

McDonald, L. L. (2004) ‘Sampling rare populations.’ *In* Thompson, W. L. (ed.) *Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters*. Island Press Washington, DC, USA, pp. 11–42.

McGowan, J., Beaumont, L. J., Smith, R. J., Chauvenet, A. L. M., Harcourt, R., Atkinson, S. C., Mittermeier, J. C., Esperon-Rodriguez, M., Baumgartner, J. B., Beattie, A., Dudaniec, R. Y., Grenyer, R., Nipperess, D. A., Stow, A. and Possingham, H. P. (2020) ‘Conservation prioritization can resolve the flagship species conundrum.’ *Nature Communications 2020 11:1*, 11(1) pp. 1–7.

McKirdy, E., Smith-Spark, L. and Tampubolon, T. (2015) ‘Endangered cockatoos found crammed into plastic bottles | CNN.’ *CNN*. [Accessed on 4th January 2023] https://edition.cnn.com/2015/05/06/asia/indonesia-cockatoo-smuggling/index.html.

Meijaard, E. and Nijman, V. (2014) ‘Secrecy considerations for conserving Lazarus species.’ *Biological Conservation*. Elsevier BV pp. 21–24.

Meise, W. (1941) ‘Ueber die Vogelwelt von Noesa Penida bei Bali nach einer Sammlung von Baron Viktor von Plessen.’ *Journal für Ornithologie*, 89(4) pp. 345–367.

Metrick, A. and Weitzman, M. L. (1996) ‘Patterns of behavior in endangered species preservation.’ *Land Economics*, 72(1) pp. 1–16.

Miller, D. L., Burt, M. L., Rexstad, E. A. and Thomas, L. (2013) ‘Spatial models for distance sampling data: Recent developments and future directions.’ Gimenez, O. (ed.) *Methods in Ecology and Evolution*, 4(11) pp. 1001–1010.

Miller, J. (2010) ‘Species Distribution Modeling.’ *Geography Compass*, 4(6) pp. 490–509.

Mochtar, D. (1989) ‘Laporan inventarisasi satwa liar kakatua jambul kuning (*Cacatua sulphurea*) dan beo (*Gracula religiosa*) di Kabupaten Flores Timur.’ *Perlindungan Hutan dan Pelestarian Alam, Kupang*.

Monk, K., De Fretes, Y. and Reksodiharjo-Lilley, G. (1997) *Ecology of Nusa Tenggara and Maluku*. 1st ed., Oxford, UK: Oxford University Press.

Myers, N., Mittermeler, R. A., Mittermeler, C. G., Da Fonseca, G. A. B. and Kent, J. (2000) ‘Biodiversity hotspots for conservation priorities.’ *Nature 2000 403:6772*, 403(6772) pp. 853–858.

Nandika, D. and Agustina, D. (2012) ‘Few and far between. Saving the Yellow-crested Cockatoos.’ *PsittaScene*, 24(3) pp. 130–134.

Nandika, D. and Agustina, D. (2018) ‘Ecology Of Lesser Sulphur Creasted Cockatoo Cacatua Sulphurea Sulphurea At Rawa Aopa Watumohai National Park, Southeast Sulawesi.’ *Metamorfosa: Journal of Biological Sciences*, 5(2) p. 188.

Nandika, D., Agustina, D. and Halouate, M. (2012) *Study of population and conservation of Lesser Sulphur-crested Cockatoo Cacatua sulphurea*. Bekasi, Indonesia.

Nandika, D., Agustina, D., Heinsohn, R. and Olah, G. (2021) ‘Wildlife Trade Influencing Natural Parrot Populations on a Biodiverse Indonesian Island.’ *Diversity 2021, Vol. 13, Page 483*, 13(10) p. 483.

Nandika, D., Mulyani, Y. A., Prawiradilaga, D. M. and Agustina, D. (2020) ‘Monitoring of *Cacatua sulphurea abbotti* in Masakambing Island, Indonesia.’ *Biotropia-The Southeast Asian Journal of Tropical Biology*, 27(3) pp. 271–281.

Nelson, A. and Chomitz, K. M. (2009) ‘Protected area effectiveness in reducing tropical deforestation. A global analysis of the impact of protection status’ pp. 1--42.

Neo, M. L. (2012) ‘A review of three alien parrots in Singapore.’ *Nature in Singapore*, 5 pp. 241–248.

Nunes, M. F. C. and Galetti, M. (2007) ‘Use of forest fragments by blue-winged macaws (Primolius maracana) within a fragmented landscape.’ *Biodiversity and Conservation*, 16 pp. 953–967.

Ó Crídáin, C. (2007) *Study on the effectiveness of the EC Wildlife Trade Regulations*. *A TRAFFIC report for the European Commission*. Brussels, Belgium.

Olah, G., Butchart, S. H. M., Symes, A., Guzmán, I. M., Cunningham, R., Brightsmith, D. J. and Heinsohn, R. (2016) ‘Ecological and socio-economic factors affecting extinction risk in parrots.’ *Biodiversity and Conservation*, 25(2) pp. 205–223.

Pain, D. J., Martins, T. L. F., Boussekey, M., Diaz, S. H., Downs, C. T., Ekstrom, J. M. M., Garnett, S., Gilardi, J. D., McNiven, D., Primot, P., Rouys, S., Saoumoé, M., Symes, C. T., Tamungang, S. A., Theuerkauf, J., Villafuerte, D., Verfailles, L., Widmann, P. and Widmann, I. D. (2006) ‘Impact of protection on nest take and nesting success of parrots in Africa, Asia and Australasia.’ *Animal Conservation*, 9(3) pp. 322–330.

Pell, A. S. and Tidemann, C. R. (1997) ‘The impact of two exotic holow-nesting birds on two native parrots in savannah and woodland in Eastern Australia.’ *Biological Conservation*, 79(2–3) pp. 145–153.

Persulessy, Y. E., Djawarai, Y. B. and Marut, R. (2003) *Survei populasi dan distribusi kakatua-kecil jambul-kuning* Cacatua sulphurea citrinocristata *dan empat jenis paruh bengkok lain di Pulau Sumba*. Bogor, Indonesia.

Petersen, I. K., MacKenzie, M. L., Rexstad, E., Wisz, M. S. and Fox, A. D. (2011) *Comparing pre- and post-construction distributions of long-tailed ducks Clangula hyemalis in and around the Nysted offshore wind farm, Denmark : a quasi-designed experiment accounting for imperfect detection, local surface features and autocorrelation*. St Andrews, UK: University of St Andrews.

PHPA, LIPI and BirdLife International-IP (1998) *Species recovery plan Yellow-crested Cockatoo*. Bogor, Indonesia: PHPA/LIPI/BirdLife International - Indonesia Programme.

Pires, S. F. (2012) ‘The illegal parrot trade: a literature review.’ *Global Crime*, 13(3) pp. 176–190.

Pires, S. F., Olah, G., Nandika, D., Agustina, D. and Heinsohn, R. (2021) ‘What drives the illegal parrot trade? Applying a criminological model to market and seizure data in Indonesia.’ *Biological Conservation*, 257, May.

Pires, S. F., Schneider, J. L. and Herrera, M. (2016) ‘Organized crime or crime that is organized? The parrot trade in the neotropics.’ *Trends in Organized Crime*, 19 pp. 4–20.

Port, J. L. and Brewer, G. L. (2004) ‘Use of Monk Parakeet (Myiopsitta monachus) nests by Speckled Teal (Anas flavirostris) in eastern Argentina.’ *Ornitología Neotropical*, 15 pp. 209–218.

Prijono, S. N. (2008) ‘Case Study: *Cacatua sulphurea*.’ *In NDF Workshop*.

Putra, E., Kristianto, I. and Christianto, Y. I. (1999) *Monitoring populasi dan pengamatan aspek ekologi Kakatua-kecil jambul-kuning (*Cacatua sulphurea abbotti*) di Kepulauan Masalembu*. Yogyakarta, Indonesia: Kutilang.

Rensch, B. (1931) ‘Die Vogelwelt von Lombok Sumbawa und Flores.’ *Mitteilungen aus dem Zoolog. Museum Berlin*, 17(4) pp. 451–636.

Renton, K. and Salinas-Melgoza, A. (2004) ‘Climatic variability, nest predation, and reproductive output of Lilac-crowned Parrots (*Amazona finschi*) in tropical dry forest of western Mexico.’ *The Auk*, 121(4) pp. 1214–1225.

Renton, K., Salinas-Melgoza, A., De Labra-Hernandez, M. A. and de la Parra-Martinez, S. M. (2015) ‘Resource Requeriments of parrots: nest site selectivity and dietary plasticity of Psittaciformes.’ *Journal of Ornithology*, 156 pp. 73–90.

Reuleaux, A., Richards, H. A., Payet, T., Villard, P., Waltert, M. and Bunbury, N. (2014) ‘Insights into the feeding ecology of the Seychelles Black Parrot *Coracopsis* (*nigra*) *barklyi* using two monitoring approaches.’ *Ostrich*.

Ribeiro, J., Reino, L., Schindler, S., Strubbe, D., Vall-llosera, M., Araújo, M. B., Capinha, C., Carrete, M., Mazzoni, S., Monteiro, M., Moreira, F., Rocha, R., Tella, J. L., Vaz, A. S., Vicente, J. and Nuno, A. (2019) ‘Trends in legal and illegal trade of wild birds: a global assessment based on expert knowledge.’ *Biodiversity and Conservation*, 28(12) pp. 3343–3369.

Rocamora, G. and Laboudallon, V. (2013) ‘Seychelles Black Parrot *Coracopsis barklyi*.’ *In* Safford, R. and Hawkins, F. (eds) *The Birds of Africa: Volume VIII: The Malagasy Region: Madagascar, Seychelles, Comoros, Mascarenes*. A&C Black, pp. 445–447.

Romero-Vidal, P., Hiraldo, F., Rosseto, F., Blanco, G., Carrete, M. and Tella, J. L. (2020) ‘Opportunistic or Non-Random Wildlife Crime? Attractiveness Rather Than Abundance in the Wild Leads to Selective Parrot Poaching.’ *Diversity 2020, Vol. 12, Page 314*, 12(8) p. 314.

Rowley, I. (1990) *Behavioural ecology of the galah,* Eolophus roseicapillus. Chipping Norton, Australia: Surrey Beatty & Sons.

Rowley, I. and Collar, N. J. (1997) ‘Order psittaciformes.’ *In* del Hoyo, J., Elliott, A., and Sargatal, J. (eds) *Handbook of birds of the world. Vol. 4, Sandgrouse to cuckoos*. Barcelona, Spain: Lynx Editions, pp. 246–477.

Russell-Smith, J., Djoeroemana, S., Maan, J. and Pandanga, P. (2007) ‘Rural livelihoods and burning practices in Savanna landscapes of Nusa Tenggara Timur, Eastern Indonesia.’ *Human Ecology*, 35(3) pp. 345–359.

Şekercioğlu, Ç. H., Primack, R. B. and Wormworth, J. (2012) ‘The effects of climate change on tropical birds.’ *Biological Conservation*, 148(1) pp. 1–18.

Setiawan, I. (1996) *The status of* Cacatua sulphurea parvula *in Nusa Penida, Bali, and Sumbawa*. *PHPA/BirdLife International*. Bogor, Indonesia: PHPA/BirdLife International.

Simberloff, D. (1998) ‘Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era?’ *Biological Conservation*, 83(3) pp. 247–257.

Sitompul, A. F., Kinnaird, M. F. and O’Brien, T. G. (2004) ‘Size matters: The effects of forest fragmentation and resource availability on the endemic Sumba Hornbill *Aceros everetti*.’ *Bird Conservation International*, 14(SPEC. ISS.).

Snyder, N. F. R., McGowan, P., Gilardi, J. and Grajal, A. (2000) *Parrots. Status Survey and Conservation Action Plan 2000-2004*. Oxford, UK: IUCN.

Snyder, N. F. R., Wiley, J. W. and Kepler, C. B. (1987) *The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot*. Los Angeles, CA: Western Foundation of Vertebrate Zoology.

Sodhi, N. S., Posa, M. R. C., Lee, T. M., Bickford, D., Koh, L. P. and Brook, B. W. (2010) ‘The state and conservation of Southeast Asian biodiversity.’ *Biodiversity and conservation*, 19(2) pp. 317–328.

Spoon, T. R. (2006) 'Parrot Reproductive Behavior, or Who Associates, Who Mates, and Who Cares?' *In* Luescher, A. U. (ed.) *Manual of Parrot Behavior*. Ames: Backwell Publishing, pp. 63–77.

Stattersfield, A. J., Crosby, M. J., Long, A. J. and Wege, D. C. (1998) *Endemic bird areas of the world: priorities for biodiversity conservation*. *Endemic bird areas of the world: priorities for biodiversity conservation*.

Tella, J. L., Baños-Villalba, A., Hernández-Brito, D., Rojas, A., Pacífico, E., Díaz-Luque, J. A., Carrete, M., Blanco, G. and Hiraldo, F. (2015) 'Parrots as overlooked seed dispersers.' *Frontiers in Ecology and the Environment*, 13(6) pp. 338–339.

Tella, J. L. and Hiraldo, F. (2014) 'Illegal and legal parrot trade shows a long-term, cross-cultural preference for the most attractive species increasing their risk of extinction.' *PLoS ONE*, 9(9) p. e107546.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B. B., Marques, T. A. and Burnham, K. P. (2010) 'Distance software: design and analysis of distance sampling surveys for estimating population size.' *Journal of Applied Ecology*, 47(1) pp. 5–14.

Thomsen, J. B. and Mulliken, T. A. (1992) 'Trade in neotropical psittacines and its conservation implications.' *In* Beissinger, S. R. and Snyder, N. F. R. (eds) *New world parrots in crisis: solutions from conservation biology.* New York and London: Smithsonian Institution Press, pp. 221–239.

Trainor, C. R., Santana, F., Pinto, P., Xavier, A. F., Safford, R. and Grimmett, R. (2008) 'Birds, birding and conservation in Timor-Leste.' *Birding Asia*, 9(2008) pp. 16–45.

Trainor, C. R., Verbelen, P. and Johnstone, R. E. (2012) 'The avifauna of Alor and Pantar, Lesser Sundas, Indonesia.' *Forktail*, 28 pp. 77–92.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K. and Possingham, H. P. (2003) 'Improving precision and reducing bias in biological surveys: Estimating false-negative error rates.' *Ecological Applications*, 13(6) pp. 1790–1801.

Valle, S., Collar, N. J., Harris, W. E. and Marsden, S. J. (2018) 'Trapping method and quota observance are pivotal to population stability in a harvested parrot.' *Biological Conservation*, 217, January, pp. 428–436.

Vergara-Tabares, D. L., Cordier, J. M., Landi, M. A., Olah, G. and Nori, J. (2020) 'Global trends of habitat destruction and consequences for parrot conservation.' *Global Change Biology*, 26(8) pp. 4251–4262.

Walker, J. S., Cahill, A. J. and Marsden, S. J. (2001) *The nesting ecology of Yellow-crested Cockatoo* Cacatua sulphurea *on Sumba and the potential for using artificial nest sites to increase recruitment. Preliminary report 2001*. Manchester, UK: Manchester Metropolitan University.

Walker, J. S., Cahill, A. J. and Marsden, S. J. (2005) 'Factors influencing nest-site occupancy and low reproductive output in the Critically Endangered Yellow-crested Cockatoo Cacatua sulphurea on Sumba, Indonesia.' *Bird Conservation International*, 15(4) pp. 347–359.

White, K. L., Eason, D. K., Jamieson, I. G. and Robertson, B. C. (2015) 'Evidence of inbreeding depression in the critically endangered parrot, the kakapo.' *Animal Conservation*, 18(4) pp. 341–347.

White, T. H., Abreu-Gonzalez, W., Toledo-Gonzalez, M. and Torres-Baez, P. (2005) 'Artificial nest cavities for Amazona parrots.' *Wildlife Society Bulletin*, 33 pp. 756–760.

Widmann, P. and Lacerna-Widmann, I. D. (2008) ‘The cockatoo and the community: ten years of Philippine Cockatoo Conservation Programme.’ *BirdingASIA*, 10 pp. 23–29.

Winiarski, K. J., Burt, M. L., Rexstad, E., Miller, D. L., Trocki, C. L., Paton, P. W. C. and McWilliams, S. R. (2014) ‘Integrating aerial and ship surveys of marine birds into a combined density surface model: A case study of wintering Common Loons.’ *The Condor: Ornithological Applications*, 116(2) pp. 149–161.

Winiarski, K. J., Miller, D. L., Paton, P. W. C. and McWilliams, S. R. (2013) ‘Spatially explicit model of wintering common loons: conservation implications.’ *Marine Ecology Progress Series*, 492, October, pp. 273–283.

World Bank Group (2020a) *World Development Indicators database*. Country profile Indonesia. [Online] [Accessed on 1st May 2022] https://data.worldbank.org/country/ID.

World Bank Group (2020b) *World Development Indicators database*. Country Profile Timor-Leste. [Online] [Accessed on 1st November 2021] https://data.worldbank.org/indicator/SP.POP.TOTL?locations=TL.

Wright, T. F., Toft, C. A., Enkerlin-Hoeflich, E., Gonzalez-Elizondo, J., Albornoz, M., Rodríguez-Ferraro, A., Rojas-Suárez, F., Sanz, V., Trujillo, A., Beissinger, S. R., A., V. B., A., X. G., Brice, A. T., Joyner, K., Eberhard, J., Gilardi, J., Koenig, S. E., Stoleson, S., Martuscelli, P., Meyers, J. M., Renton, K., Rodríguez, A. M., Sosa-Asanza, A. C., Vilella, F. J. and Wiley, J. W. (2001) ‘Nest poaching in neotropical parrots.’ *Conservation Biology*, 15(3) pp. 710–720.

Wungo, E. (2011) *Laporan survei populasi paruh bengkok terancam punah* Cacatua sulphurea citrinocristata*, Sumba, Nusa Tenggara Timur*. Bogor, Indonesia: Burung Indonesia.

2 Correlates of persistence in remnant populations of two Critically Endangered cockatoos

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Abstract

A challenge with species that have disappeared from most of their range is to identify correlates of local persistence. With species decimated by trade, site-specific trapping risk is hard to capture by remotely accessed predictors. The recently split Yellow-crested Cockatoo *Cacatua sulphurea* and Citron-crested Cockatoo *C. citrinocristata* have undergone catastrophic declines due to habitat loss and especially trapping, and are now extinct in much of their former range across Indonesia. Of 144 sites on 30 islands known to contain the species in 1950, only 76 on 27 islands did so in 2017–19, with many of the other 68 experiencing extinctions between 1985 and 2000. We compared socio-ecological conditions such as forest cover and loss, human population density and infrastructure, and protected area status between the occupied and unoccupied sites, using 'random forests' within decreasing time intervals 1950–2015. Populations on Sulawesi and West Nusa Tenggara were more likely to become extinct than those on Sumba, Timor-Leste and small remote islands. Sites retaining cockatoos had high proportions of tree cover, low road density and low human densities. The relative importance of these factors changed little over time, but road density and human density became respectively more and less important in recent years. Examination of local conditions at 'false negative' sites (where cockatoos survived contrary to model predictions) showed that, particularly in recent years, cockatoo survival has been promoted by site-specific protection due to traditional beliefs, NGO activities, dedicated individual residents and local topographic barriers. Some of these local influences add complexity to the task of conserving cockatoo strongholds, but also offer exciting possibilities for low-cost conservation prescriptions tailored to individual sites. Studies combining field and remotely sensed data, and examining false negative sites for beneficial location-specific conditions, have broad application for the conservation of taxa with once-large ranges.

2.1 Introduction

Habitat loss and deterioration have rendered almost one in ten tropical bird species at risk of extinction (Sodhi et al., 2010; BirdLife International, 2018, 2021a). Attractive, relatively easy-to-keep species such as parrots face the additional impact of unsustainable direct exploitation for the pet trade (Bush et al., 2014; Tella and Hiraldo, 2014). As a result of this double pressure, parrots are among the most endangered bird orders in the world (Olah et al., 2016; BirdLife International, 2018), with 175 (43%) of the 404 species either threatened or 'Near Threatened' (BirdLife International, 2021a). Since the establishment of CITES in 1975, the international trade in parrots, of which only four species are not included in its appendices (CITES, 2020), has become increasingly regulated, but evidence of a direct benefit to threatened species is inconclusive (Martin, 2000), not least because of a severe lack of reliable abundance data (Marsden and Royle, 2015). Moreover, CITES does not extend to domestic trade. For species with fragmented remnant populations, understanding why they survive at some sites and die out at others is important for their conservation. While some aspects of trade can be predicted well by factors such as species' characteristics and the effect of distance on supply and demand (Romero-Vidal et al., 2020; Pires et al., 2021), there are many factors affecting local exploitation levels that are site-specific and cannot easily be captured by universally available data, especially for distributions that cross cultural and political boundaries. Local demand varies between cultures, as for Maleo *Macrocephalon maleo* eggs (Froese and Mustari, 2019) and turtle (Chelonioidea) products (Garland and Carthy, 2010), and can variously be influenced by traditional beliefs, political circumstances, enforcement activities and conservation interventions (Veríssimo et al., 2020). Capture methods vary with local cultures and traditions, and can determine the stability of the targeted population (Valle et al., 2018). Identifying the factors correlating with survival at some sites and extinction at others offers important leverage points for conservation policy and management.

The Yellow-crested Cockatoo *Cacatua sulphurea* is endemic to the islands of western Wallacea, (BirdLife International, 2021b), with the Citron-crested Cockatoo *C. citrinocristata*, only recently recognised as a separate species from yellow-crested, restricted to Sumba in the south-west of the same region (BirdLife International, 2022a). Like many other parrots the species are negatively affected by habitat loss and trade, as a consequence of which they have disappeared from almost all of their range and been listed as Critically Endangered all this century (Collar et al., 2001; BirdLife International, 2021b). Once the species were so numerous in parts of their ranges that their flocks made trees appear white, and crops had to be guarded against them (Kendall, 1979; Setiawan, 1996; Collar et al., 2001). As obligate hole-nesters the cockatoos are highly vulnerable to trapping when breeding or communally roosting (Marsden and Jones, 1997; Walker et al., 2005; Imansyah et al., 2016). Consequently they were trapped and exported in the thousands for the international pet market (Inskipp et al., 1988; Cahill et al., 2006). Estimated annual exports from Sumba, for example, were as high as 1600 birds in 1992 (Cahill et al., 2006) when a population of only 3200 individuals was estimated to remain (Jones et al., 1995). A number of regional studies were produced (Mallo and Setiawan, 1996; Catterall, 1997; Agista et al., 2001) along with a species recovery plan (PHPA et al., 1998) and a comprehensive status review (Collar et al., 2001). Although export effectively became illegal in 1994 (Cahill et al., 2006), difficulties in enforcement allowed trapping and trade to continue (Collar et al., 2001; CITES, 2002; Persulessy et al., 2003).

Currently, six subspecies of *C. sulphurea* are recognised, all still extant (Collar and Marsden, 2014): the nominate form on Sulawesi and its associated islands, *C. s. occidentalis* on the island chain from Nusa Penida to Alor, *C. s. parvula* on Timor, *C. s. paulandrewi* on the Tukangbesi Islands, *C. s. djampeana* on the Selayar island group, and *C. s. abbotti* on the Masalembo Islands in the Java Sea (this last being the only population presumed native outside of Wallacea). Today, the strongholds of the species are the adjacent islands of Komodo and Rinca (Reuleaux et al., 2020), although Sumba was regarded as holding the most important population when *citrinocristata* was considered conspecific (Jones et al., 1995; Cahill et al., 2006). Conservation efforts should of course encompass all seven taxa involved (Collar and Marsden, 2014), but the split of *C. citrinocristata* inevitably makes the updated status of the newly defined *C. sulphurea* even more serious than previously recognised.

To date, such efforts have mostly been limited to legal protection, including the creation of protected areas and the control of trade, except for *C. s. abbotti* on Masalembo *and C. citrinocristata* on Sumba, where NGOs have carried out public awareness campaigns (Burung Indonesia, 2011; Nandika et al., 2020). Without urgent intervention, however, the long-term viability of the two species, and particularly the tiny relict populations of some subspecies, appears doubtful, and efforts are long overdue to understand the reasons behind the sharp declines in some populations and the relative stability of others. Many plant and animal species find their strongholds in protected areas (Geldmann et al., 2013), the remotest regions (McCauley et al., 2013) or, by contrast, urban refuges (Geary et al., 2021), where they enjoy popular support (Boal, 2018) or the protection of cultural or religious beliefs (Bhagwat and Rutte, 2006; Plieninger et al., 2020).

Although Komodo National Park is known to sustain a currently healthy Yellow-crested Cockatoo population owing to its high level of protection (Reuleaux et al., 2020), little is known about the conditions at other locations that have either maintained or lost their cockatoo populations over the last 2–3 decades. To address this deficiency, we investigate all known sites for the two species across 41 islands in order to determine the main extrinsic factors, such as habitat intactness, human population characteristics, geography and area protection, that promote or prevent the survival of local populations. With this information we review the species' overall conservation status and recommend future management priorities for them.

2.2 Methods

To obtain information on locations of yellow-crested and Citron-crested Cockatoo populations, we collated all location-specific sightings of the two species. A review of extinct and surviving cockatoo populations up to the year 2000 (Collar et al., 2001) formed the base of the dataset. We then checked online platforms such as eBird, Internet Bird Collection and Xeno-Canto, birding trip reports, technical reports and the scientific literature for subsequent geographically referenced records of the species which we used to allocate search effort (Appendix 2.1). Correspondence with other ornithologists, conservation officials, bird guides and local people added further recent information (Appendix 2.1), which we used to plan our fieldwork and exclude certain locations with well-documented population sizes and widely agreed absences. Although all locations with documented cockatoo presence were considered in the planning stage and assessed either by field visits or from reports, the locations for older records were less precise so only those with records after 1950 were used for data analysis. Sites with records in or after 2015 were regarded as holding currently surviving populations. All remaining sites were treated as extinctions for modelling because either the last record was more than a decade old or we had gathered evidence during fieldwork of the population's disappearance.

2.2.1 Local informant interviews

We surveyed known locations in West Nusa Tenggara (March–April 2017), East Nusa Tenggara except Sumba (April–May 2017, November–December 2017, June–August 2018), Timor Leste (July–August 2018), Sulawesi and Buton (March–April 2019), Selayar Islands (November 2018), Tukangbesi Islands (April–May 2019), and, as a component of other work, Sumba in the period October 2016–May 2019. Fieldwork in each area started with enquiries at the local government office in charge of conservation, followed by short interviews with local farmers, trappers, former trappers and other forest users. The total number of interviewees was 1126, the number on each island varying with its size and location (up to 10 per location, mean 7.8). In areas where we could not locate cockatoos, we made particular efforts to interview a range of informed local people. We targeted those who were likely to know and recognise cockatoos from their hunting, farming and forest activities. Although these interviewees were usually not experts, the target species are gregarious, easy to see and identify, and regarded as either crop pests, potential pets or exciting wildlife encounters, so people generally notice cockatoos and recall their observations. There was no formal structure to interviews but multiple standard questions were asked during the conversations. Trappers or former trappers often volunteered valuable information about remaining cockatoo populations, catching techniques and limitations (such as dwindling numbers, lack of demand, deteriorating access to habitat and traders, competition from other trappers, climbing hazards, restricted areas and law enforcement). Promising areas were visited, and leads followed from village to village and into the forest until cockatoo presence or likely absence could be established. When remotely gathered information was inconclusive, we visited the site and presumed absence if no birds could be found and if local interviewees either had not encountered cockatoos in the last decade or clearly remembered when the last individuals disappeared.

2.2.2 Field surveys

The field methods used to detect cockatoo presence and to count birds depended on the nature of the sites themselves. We assessed populations in strongholds on

Komodo and Sumba in separate studies using point-count distance sampling. On Komodo in November and December 2017 we carried out 8-minute point counts at 178 points along 25 randomly located transects in suitable habitat (Reuleaux et al., 2020). On Sumba, to replicate earlier surveys (Jones et al., 1995), from June to October 2017 we carried out 519 10-minute point counts at 328 points along 43 transects in six forested regions distributed in the centre and east of the island (see Chapter 4).

In areas with lower densities we used transects and informal walks with local guides to determine cockatoo presence, and long watches from vantage-points to determine the minimum number of cockatoos present. Wherever possible, we sought communal roosts to attempt to observe and count all individuals in the area simultaneously, taking the resulting number as an absolute minimum population size and using informed judgement to make a best estimate of a realistic local population size. At some sites (n = 28), there was a suitable vantage-point from which most or all cockatoo individuals within the site could be counted at some stage, usually as birds flew to a roost site (n = 15) or travelled between feeding locations. Occasionally roosts were known to local informants (n = 2), otherwise vantage-points (clearings, openings, outcrops, climbable trees, beaches, jetties, stilt houses and boats) were used to follow cockatoo movements at dusk to the roost or to choose another vantage-point closer to the suspected roost on the following evening. Cockatoos were counted as they arrived at the roost and re-counted with binoculars or a spotting scope as they perched high in trees when it was almost dark. For small islands and areas that could be viewed well from a distance (from above or offshore) this method worked well, whereas continuous flat areas without vantage-points were difficult to assess and constrained us to very conservative estimates. At some sites point-count transects were used (n = 22 excluding Sumba and Komodo, see below) but, owing to very low encounter rates, targeted walks with informants were more appropriate (total walked distance across all sites 830 km). Numbers of transects varied by site depending on area and terrain, and transect length averaged 1.8 km (range 1–2.2 km). Transects and walks were not placed randomly at sites, to maximise the likelihood of encountering birds that were present, and thus no encounter rates are presented. In total we spent 1199 hours surveying suitable habitat (forests, savanna woodland, gardens, diverse fields and tree plantations) at times when cockatoos could be expected to be active and best detectable (dusk–10.30 and 15.00–dark, Marsden, 1999).

2.2.3 Environmental factors

To examine the factors that correlate with, and potentially drive, the survival or extinction of individual cockatoo populations, we used random forests—a machine-learning technique for classification and regression (Breiman, 2001; Liaw and Wiener, 2002)—based on remotely available information on environmental, sociological, economic and ecological factors. All layers were obtained or converted to grids of ca. 30 x 30 m resolution, and the data associated with each location were assessed over a 2 km-radius circle around it using QGIS (QGIS Development Team, 2021). To account for suitability for cockatoos, trapping pressure and potential protection we examined seven factors: (1) island group, (2) gross domestic product assuming that trapper's motivation may depend on income, (3) road density as an indicator for accessibility, (4) altitude as the species has rarely been recorded above 1200 m, (5) tree cover indicating suitability for roosting and nesting, (6) human population density relating to trapping pressure, and (7) protected area which could mean less habitat disturbance and direct protection from trapping. (1) Islands were grouped into Sulawesi; West Nusa Tenggara (Bali, Lombok and Sumbawa); Sumba; East Nusa Tenggara (including West Timor) excluding Sumba; Timor-Leste; and small remote islands. (2) Gross domestic product (GDP) per capita in the respective regency is given in constant 2011 international dollars, the unit used by the World Bank for national GDP (Kummu et al., 2018). (3) Road density was calculated from the total length of roads and tracks (all types recorded by OSM, Geofabrik, 2021; OpenStreetMap Contributors, 2021) within each 2 km-radius circle, as a surrogate for accessibility. (4) Altitude was taken at the circle's centre (SRTM Digital elevation model, Van Zyl, 2001). (5) Tree cover is given as percentage of land covered by trees in 2019 (Hansen et al., 2013, 2020). (6) Density of the local human population corresponds to United Nations estimates for 2018 (Worldpop, 2018). (7) Protected area was measured as proportion of land in the 2 km-radius circle located inside a legally protected area equivalent to IUCN categories I–VI (Brun et al., 2015; KLHK and DJ KSDAE, 2018; IUCN, 2021). For protected areas, we explored alternative formats of the predictor, distinguishing between strictly (equivalent to IUCN categories I–II) and weakly (categories III–IV) protected areas (Appendix 2.2). Due to the lack of availability of historical data covering each of the analysis periods, we used the most recent data for each variable. While the environmental predictors have certainly changed over the decades, the relationships between locations are less likely to have changed significantly.

To establish an objective criterion for the separation of locations that tended to match historic site delimitation (Collar et al., 2001) and had some geographical and biological justification, we assigned records of cockatoos to a single site if localities were ≤10 km apart, but to different sites if >10 km apart. This was based on distances of <5 km recorded in cockatoos travelling to roost or forage in several years of fieldwork by AR, RNDL and BAS, mostly on Sumba and Komodo). West Timor was grouped with the rest of East Nusa Tenggara because it shares more social and political characteristics with those Indonesian islands than with Timor-Leste. Bali and its satellite Nusa Penida were grouped with West Nusa Tenggara. Small remote islands comprise three separate archipelagos whose basic common characteristic was their high degree of isolation. For security reasons, to avoid divulging precise site information potentially useful to trappers (Collar et al., 2017), we include small islands under the name of their large neighbours; moreover, we avoid reference to specific sites as far as possible.

2.2.4 Statistical analysis

We used QGIS (QGIS Development Team, 2021) for spatial analysis and R (R Core Team, 2021) for all other analyses and plots: randomForest (Liaw and Wiener, 2002), vegan (Oksanen et al., 2013), viridis (Garnier, 2018), and ggplot2 (Wickham et al., 2021). Our random forest classifiers contained 500 tree structures, and the number of factors to try at each step was optimised based on lowest 'out-of-bag' error. To translate probabilities from the random forest prediction to cockatoo presences or absences, we interpreted cases with 40–60% of tree votes for survival as marginal cases, i.e. undecided, while higher probabilities (>60%) were interpreted as sites with predicted survival and lower probabilities (<40%) as predicted extinctions. We examined false positive and false negative classifications post-hoc to investigate possible causes of survival or extinction not predicted by the models. To examine temporal shifts in factors contributing to extinctions, we created random forests based on eleven subsets of sites with a shift in the starting year (sites regarded as occupied initially) from 1950 to 2000 in five-year intervals. Ideally, we would have split the extinction periods into equal windows; however, the majority of last records were aggregated in a single decade (Figure 2.1), meaning that sample sizes in adjacent decades were too small to build robust models on their own.

2.3 Results

Locations where yellow-crested and Citron-crested Cockatoos were recorded between 1856 and 2019 totalled 375 (data filed with BirdLife International; availability restricted) but, under the definition provided above, grouped into 188 separate sites. Of these, 144 were confirmed as supporting cockatoos in 1950 or later and were therefore included in the analysis. In just over half these sites (76) cockatoos persisted in 2015 (Figure 2.1). Populations at individual sites ranged from a single pair to 300 birds, but the large majority of populations are concentrated in just three strongholds, and only 28% elsewhere. Taking the two species together, the majority of the still occupied sites are located in Nusa Tenggara, Timor-Leste and Sumba. Sulawesi has lost 77%, West Nusa Tenggara 67%, East Nusa Tenggara 66%, Timor-Leste 26% and Sumba 25% of cockatoo sites since 1950 (Figure 2.1). No extinctions are known from the small remote islands after 1950 (although three individual remote island sites have had no cockatoos recorded since 1901, 1907 and 1927). Extinctions appear to have peaked in the 1990s, as representatives of the majority of extinct subpopulations (62%) were last seen in that decade (Figure 2.1).

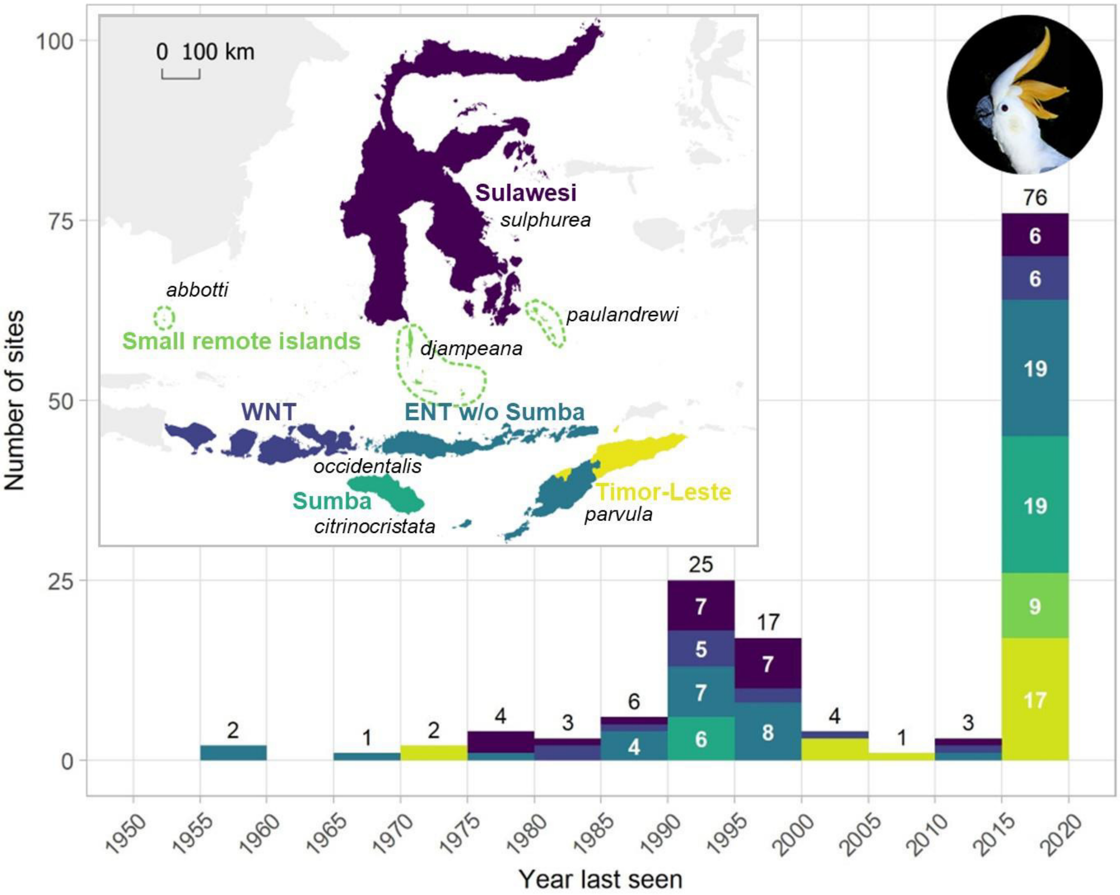

Figure 2.1: Study area, island grouping and timing of last record at sites with historic and extant Yellow-crested Cockatoo *Cacatua sulphurea* and Citron-crested Cockatoo *C. citrinocristata* populations. As a precaution against aiding illegal trapping, we do not show precise location information of extant populations. Sites with records in or after 2015 are regarded as currently surviving. 'Small isolated islands' comprise three separate archipelagos that are geographically separate but share remoteness. WNT = West Nusa Tenggara with Bali (as Bali had too few data to be considered separately), ENT w/o Sumba = East Nusa Tenggara excluding Sumba. Black numbers above the columns specify the column total, i.e. the number of sites with records in the respective five-year period. White numbers give the size of the column sections they are within, i.e. the number of sites with last records in the respective island group and five-year period.

2.3.1 Modelled predictors of survival

The best predictor of survival was the island or group of islands in which each site was located (Table 2.1, Figure 2.2). Populations on Sulawesi and West Nusa Tenggara were most likely to become extinct, whereas those on Sumba, Timor-Leste and small remote islands were most likely to survive. Among the environmental and socio-economic predictors, more extensive tree cover (above a threshold of 20% of the area), lower human densities and lower road densities were all associated with elevated probability of cockatoo population persistence. Altitude, percentage of land allocated to protected areas, and GDP per capita played only minor roles. The relationship between GDP and cockatoo survival showed a negative effect for initial economic development, but turned into a positive effect for very high GDP values (Figure 2.3). In models based on shorter time-intervals for assessing survival (temporal subsets of the data) there was initially little change in the relative importance of the predictors while moving the baseline for inclusion in the dataset from presence in 1950 towards 1990 (Figure 2.2); however, when examining only extinctions between 1995 and 2015 or 2000 and 2015, the relative and absolute importance of the predictors changed considerably. Tree cover and island group appear to become more important, while human density and area protection lose influence, but for these smaller subsets error rates for extinctions rose and model accuracy decreased (Table 2.1, Figure 2.2).

Table 2.1: Accuracy of a series of random forest models examining survival and extinction of Yellow-crested Cockatoos *Cacatua sulphurea* and Citron-crested Cockatoos *C. citrinocristata* with varying start dates of the baseline presence data and importance of predictors in each model (measured by the decrease in model accuracy when the predictor is removed). **n** $_{\textbf{extinct}}$ = number of sites where cockatoos have become extinct (last record between the respective year and 2014). **n** $_{\textbf{survived}}$ = number of sites where cockatoos have survived (at least until 2015). **+** indicates a positive relationship between the predictor and survival. **−** a negative relationship. **+ −** a positive influence for small values of the predictor and a negative one for larger values as displayed in Figure 2.3 and **− +** a negative influence for small values of the predictor and a positive one for larger values as displayed in Figure 2.3. **AUC** = Area under the Receiver Operating Characteristics curve, an indicator of the model's ability to distinguish between classes. 'Road density' = length of road within each 2 km-radius circle.

	1950	**1955**	**1960**	**1965**	**1970**	**1975**	**1980**	**1985**	**1990**	**1995**	**2000**
n $_{\text{extinct}}$	68	68	67	66	65	63	59	57	51	37	11
n $_{\text{survived}}$	76	76	76	76	76	76	76	76	76	76	76
error rate total	0.229	0.229	0.224	0.225	0.227	0.223	0.215	0.211	0.228	0.239	0.161
error rate $_{\text{extinct}}$	0.221	0.221	0.254	0.242	0.262	0.270	0.288	0.316	0.373	0.486	0.727
error rate $_{\text{survived}}$	0.237	0.237	0.197	0.211	0.197	0.184	0.158	0.132	0.132	0.118	0.079
AUC	0.872	0.872	0.870	0.864	0.862	0.855	0.857	0.864	0.840	0.780	0.758
Island group	22.28	22.28	17.78	18.87	18.46	18.23	17.57	16.83	15.09	14.47	8.37
Tree cover	21.29^{+-}	21.29^{+-}	17.69^{+-}	20.99^{+-}	17.18^{+-}	15.74^{+-}	15.80^{+-}	17.78^{+-}	16.11^{+-}	12.55^{+-}	4.32^{+-}
Pop. density	16.23^{-}	16.23^{-}	15.90^{-}	14.60^{-}	13.91^{-}	12.52^{-}	11.09^{-}	13.23^{-}	9.42^{-}	6.25^{-}	-0.54^{-}
Road density	14.11^{-}	14.11^{-}	14.26^{-}	13.95^{-}	13.77^{-}	14.69^{-}	12.88^{-}	13.38^{-}	13.60^{-}	10.61^{-}	8.02^{-}
Altitude	12.86^{+-}	12.86^{+-}	10.81^{+-}	12.39^{+-}	9.90^{+-}	12.34^{+-}	11.10^{+-}	11.88^{+-}	9.12^{+-}	9.82^{+-}	2.34^{+-}
Protected area	11.44^{+}	11.44^{+}	12.16^{+}	11.86^{+}	11.07^{+}	9.67^{+}	9.91^{+}	11.04^{+}	7.56^{+}	2.81^{+}	-0.72^{+}
GDP per capita	8.35^{-+}	8.35^{-+}	8.84^{-+}	7.76^{-+}	8.68^{-+}	7.83^{-+}	8.67^{-+}	10.58^{-+}	12.85^{-+}	8.50^{-+}	2.83^{-+}

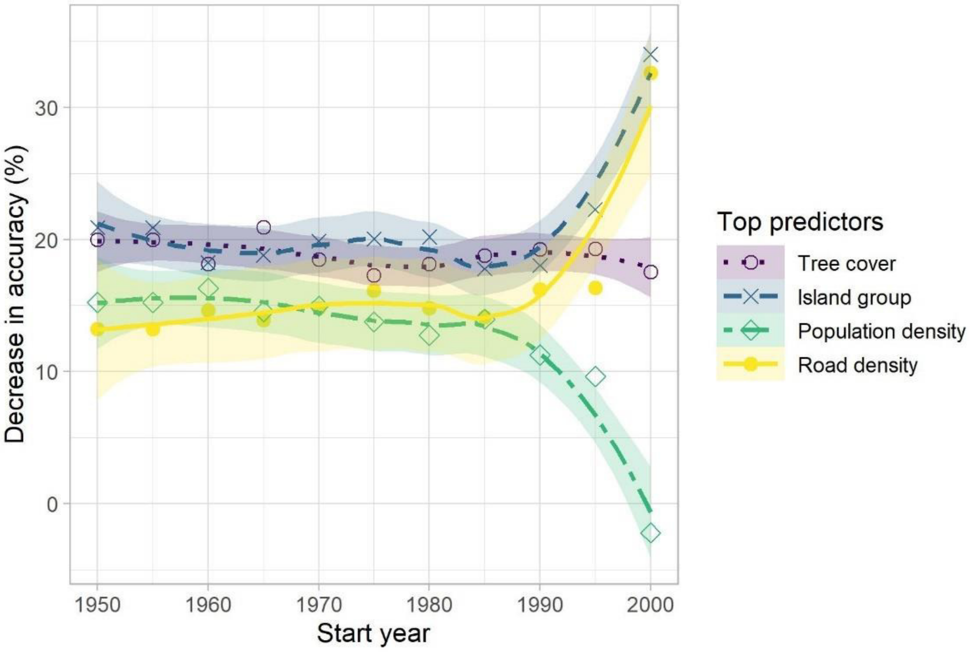

Figure 2.2: Change of predictor importance in random forest models for different time intervals. Importance is measured in decrease of model accuracy when the respective predictor is removed from the model (i.e. more important predictors would cause a larger decrease in model accuracy when removed). Only the four top predictors are shown for clarity. The x-axis represents the baseline year (of sites regarded as occupied initially) for 11 decreasing time intervals (all lasting to 2015).

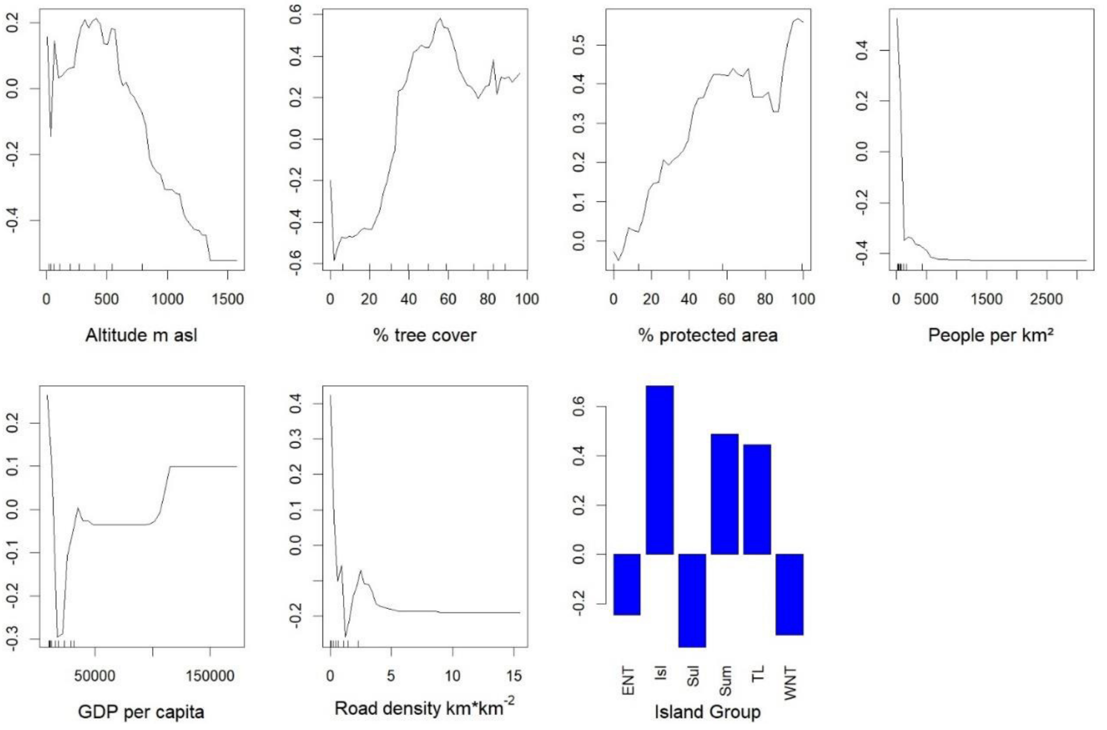

Figure 2.3: Partial importance of seven predictors for survival of Yellow-crested Cockatoo and Citron-crested Cockatoo at 144 sites from 1950 to 2015. ENT = East Nusa Tenggara without Sumba; Isl = small remote islands(see text); Sul = Sulawesi and satellites; Sum = Sumba; TL = Timor-Leste; WNT = West Nusa Tenggara (incl. Bali to Sumbawa).

Unmodelled conditions and examination of prediction errors

At the 76 sites with cockatoos still present in 2015 we found a variety of (often overlapping) site-specific circumstances contributing to their protection which were not considered in the model. At 42 of the sites, highly motivated individuals championed conservation principles, and ten of these and four others had activities by NGOs focused on conservation (12 sites by four NGOs) or humanitarian aims (two sites, two NGOs). In addition to the 28 sites containing formally protected land under the conditions of our model, 18 were visited regularly by governmental conservation staff, despite being located outside protected areas. Traditional beliefs in ‘sacred groves’ kept cockatoos safe at six sites. Poor access to markets with demand for cockatoos hampered trapping at 19 sites (17 in Timor-Leste), while 48 were so remote that they were inaccessible or unknown to outsiders. For cockatoo extinctions and persistence between 1950 and 2015, our random forest model misclassified eight sites as having lost populations when they had actually survived (false negatives), and ten sites as occupied when they had no recent records (false positives; Appendix 2.3). All sites with unexpected survival showed one (two sites) or more (six sites) of the unmodelled site-specific beneficial conditions listed above. A notable false negative was a site on Sulawesi where cockatoos have recently become re-established after decades of almost certain absence. Among the false positives, two types of site dominated: those with good habitat in relatively remote areas but with known (past or present) intense trapping pressure, and those where the current status of cockatoos is not entirely certain, and more search effort is needed.

2.3.2 Population estimates

We recorded a total of 1824 Yellow-crested Cockatoos over the six subpopulations, and our best estimates of the populations on each island add up to 3000-3500 individuals (Table 2.2). We identified two strongholds for this species: Komodo National Park and Timor-Leste, which together may harbour around 61% of the global population. Despite the size of Sulawesi and the formerly huge range of its endemic subspecies *C. s. sulphurea*, the densities (<1 individual 1000 km^{-2}), current range and total numbers are extremely low (Table 2.2). Our best estimate of the global population derives from a range of field methods, some of which are informal or unstandardised in nature. However, 34% of our estimated maximum number come from formal surveys on Komodo using tailored distance sampling, an accepted population estimation method (Buckland et al. 2001). An additional 1091 or 35% of the estimated population were actually directly counted, so we can at least be confident of the size of our minimum population estimate. There is, of course, uncertainty in population sizes at several sites, so it may be best to adopt a precautionary population estimate of 2191 (1100 from our formal survey on Komodo plus 1091 from our minimum estimates from elsewhere). For Citron-crested Cockatoos on Sumba we could confidently separate 256 individuals from direct sightings, but numbers are more likely around 1400. A formal population estimate for the island with associated confidence intervals will be given in Reuleaux (see Chapter 4).

Table 2.2: Estimated Yellow-crested Cockatoo *Cacatua sulphurea* and Citron-crested Cockatoo *C. citrinocristata* population sizes per subspecies and per island group. ENT = East Nusa Tenggara, w/o = without, WNT = West Nusa Tenggara (Bali to Sumbawa). **Minimum estimate** is derived from the sum of maximum flock sizes seen/reported in separate locations. **Estimated** number is the best estimate including suitable habitat that was only partly surveyed. **Sites survived** is the number of sites with extant cockatoo populations in 2015 versus **total** of all sites with cockatoo reports since 1950. **Density on island** is the number of individuals divided by the whole land area of the island(s) in the subspecies' range or in the island group. **% of island area occupied** is the area of occupied forest patches divided by the area of the island(s).

Subspecies/ species	Minimum estimate	Estimated	Sites survived/total	Density on island (ind*km^{-2})	% of island area occupied
C. s. occidentalis	1207	1711	22/47	0.09	3.5%
C. s. parvula	431	985	20/37	0.03	5.9%
C. s. paulandrewi	81	172	4/4	1.27	10.7%
C. s. djampeana	61	156	4/4	0.45	14.7%
C. s. sulphurea	27	105	6/26	0.001	0.3%
C. s. abbotti	17	22	1/1	7.33	11.2%
C. citrinocristata	286	1400	19/25	0.11	11.0%
Island Groups					
ENT w/o Sumba	1210	1716	19/43	0.29	4.8%
Timor-Leste	309	830	17/23	0.03	5.6%
Remote Islands	159	350	9/9	0.72	13.4%
WNT	119	150	6/18	0.01	2.9%
Sulawesi	27	105	6/26	0.001	0.3%
Sumba	286	1400	19/25	0.11	11.0%
Total	**2110**	**4551**	**76/144**	**0.02**	**2.2%**

2.4 Discussion

The once abundant Yellow-crested Cockatoo has declined precipitously across its large original range because of loss of habitat and decades of exploitation for the pet trade; the Citron-crested Cockatoo has also undergone a sharp contraction in numbers and range on Sumba. This first comprehensive assessment of status in 20 years covered almost the entire range of the two species and found a combined minimum 2110 individuals at 76 sites. These numbers warrant concern, as the great majority of birds are concentrated in just three strongholds that are far from constituting a collective barrier against extinction: *C. citrinocristata* is confined to a single island, Sumba, and neither of the two strongholds of *C. sulphurea* is secure (see penultimate paragraph below). The main factors associated with survival are island group, high tree cover and low human densities, but local circumstances such as sacred groves or a highly motivated NGO, community leader or government official can arguably be at least as beneficial, and conservationists should actively seek to engage communities in cockatoo protection by fostering collective local identities and goodwill. Similar patterns of persistence can be expected in other parrots in Indonesia (Pires et al., 2021) and have been observed in the region's other exploited threatened species, such as Tenggara Hill Myna *Gracula venerata* (Reuleaux et al., 2018) and megapodes Megapodiidae (Argeloo and Dekker, 1996; Froese and Mustari, 2019). Although the types of informal protection and cultural determinants may differ in other geographic and taxonomic contexts, this site-by-site review of predictors of persistence represents a novel approach to identifying the most effective bespoke measures for conserving fragmented populations of exploited species.

Our random forest model predicted extinction and survival well. Island group as the most important factor reflects geographical nestedness, but these groups also have other significant common factors including colonisation history, traditions, current dominant religion (Monk et al., 1997; Badan Pusat Statistik, 2016), political affiliation and economic development (Samudro et al., 2015), some of which clearly influence the intensity of habitat loss and trade, the two major threats to cockatoos. Protected areas, whose benefits for biodiversity are well documented (Douglas-Hamilton et al., 2005; Pain et al., 2006; Cazalis et al., 2020; Liévano-Latorre et al., 2021), also increase the survival chances of cockatoo populations, but some were created expressly to conserve Yellow-crested Cockatoo populations (such as national parks on Sumba and in south-east Sulawesi), potentially inverting cause and effect. As is common in parrot (Pires, 2012) and other wildlife trade (Robinson and Bodmer, 1999; Peres and Lake, 2003), trapping occurred first at easily accessible locations and only later at remote sites with poorer infrastructure (Cahill et al., 2006; Eaton et al., 2015), after the initial targets had become scarce (as on South Sulawesi or Lombok) or been protected by better law enforcement (as on Komodo). The cockatoos' requirement of large trees (Walker et al., 2005) or palms (Imansyah et al., 2016) for nesting and tracts of woodland or forest for foraging (Rowley et al., 2017) fits with our finding that their survival is associated with high proportions of tree cover. Human population density, road density and GDP per capita are a measure of geographical remoteness and level of economic development, and reflect the accessibility of both sites and markets (Wilkie et al., 2005; Pires and Clarke, 2011; Fa et al., 2015; Indraswari et al., 2020). However, these relationships are not linear, and cockatoo survival may be influenced by processes that are sometimes recognised as environmental Kuznet's curves (McPherson and Nieswiadomy, 2005; Mills and Waite, 2009): rising GDP brings motorised transport links and mobile phone connections which initially increase trapping, trading effort and efficiency (Stearman, 2000; Pires, 2012), but with their further wealth local people rely less on illegal activities or forest use to survive or boost their incomes (Lunstrum and Givá, 2020), and cockatoo survival then increases. Direct and indirect negative effects of roads on mammal and bird population densities are well documented for many species globally (Benítez-López et al., 2010; Kociolek et al., 2011); in the case of the cockatoos, the effect is most likely a consequence of the access that roads give for trapping and trade (Harris et al., 2017).

The model's misclassifications are arguably as valuable as the correctly classified locations, since false positives highlight sites for potential re-introductions or where the species might persist undetected while false negatives can reveal unmodelled favourable conditions that might be replicated elsewhere. In the present case, sites predicted to retain cockatoos but which actually lacked recent cockatoo sightings (false positives) were all recent extinctions or lacked search effort. Confirming absences is a classic problem in ecology (Diamond, 1987; Butchart et al., 2006; Mortelliti and Boitani, 2007), as detectability has an inverse relationship with rarity. We used a last-seen-date cut-off to separate extinctions from presences, which allowed older extinctions (64 of 68 sites, extinction > 10 years previously) to be presumed with reasonable certainty, but sites with recent records were more likely to involve false absences. We therefore particularly targeted such sites with fieldwork to increase certainty of population status, and soon discovered that, because cockatoos are gregarious large white birds, commonly coveted for trapping or reviled as crop pests, residents in rural areas gave dependable information on their local status. This allowed us to presume extinctions, again with reasonable certainty, when (a) locals reported the disappearance of recently and regularly seen cockatoos and (b) we ourselves could not find the birds despite thorough searches. Consequently, we judge that errors in model inputs were likely only in five sites (3–6% of all sites depending on time period). Even so, we examined classification errors from the random forest model and found that these five cases were among those misclassified or classified as marginals. They are therefore in need of further fieldwork to check their status, although any birds remaining will certainly be few in number. Priority sites for future survey include these five doubtful sites and others where persistence was reported but information about population size and reasons for survival is missing due to lack of fieldwork effort, such as areas in Central Sulawesi, where research was not permitted due to a recent tsunami, and Timor-Leste, where the unexpectedly wide distribution and locally high densities of cockatoos relegated some of the smaller remnant populations to low priorities in search effort.

Examination of the eight false negatives from our model shows in every case some tangible local reason for cockatoo persistence. Topographic barriers abetting cockatoo population persistence include steep slopes, volcanoes and rocky coasts. Sacred groves (Bhagwat and Rutte, 2006; Rutte, 2011) appear to offer informal protection for the cockatoos, notably in remoter areas where animistic religions still influence daily life (Webb, 1986; Snodgrass and Tiedje, 2008; Sopian, 2015). Committed individuals acting as champions for particular populations commonly explain the false negatives and marginal classifications in our model. In one case, a former trapper used traditional beliefs to persuade his community to stop bird persecution, so that the cockatoo population in his village rose from four in 1986 to 34 in 2018, one of only two remaining subpopulations within hundreds of kilometres. NGOs working with local communities to raise awareness for cockatoos and biodiversity have managed to preserve the species at sites on Sumba, Flores and Masalembo (Burung Indonesia, 2011; Nandika et al., 2020). Although mining is well known for its negative effects on wildlife throughout the world (Gould, 2011; Sonter et al., 2018) and in East Nusa Tenggara itself (Erb, 2016), the security measures associated with such operations can reduce bushmeat consumption (Randriamamonjy et al., 2015) or bird trapping (Devenish et al., 2021). A mining operation with its associated security, local economic benefits and an enthusiastic ecologist has contributed to the survival of the only known population on Sumbawa (Yusuf, 2014). In one unfortunate case a trapper’s fatal fall deterred a whole community from climbing cockatoo nest trees.

On our evidence, numbers of Yellow-crested Cockatoo quoted by BirdLife prior to this fieldwork are similar to our estimates when considered without Sumba (for the species pair 2373–2683 individuals of which 2000 considered mature; without the Citron-crested Cockatoo 1810–2120 individuals of which 1380–1675 considered mature; BirdLife International, 2021b) . However, there have undoubtedly been severe declines across the species' range over the last 40 years (three generations, BirdLife International, 2022b). Although we can only guess the extent of losses before 1950, local extinctions were particularly prominent in the 1990s and 2000s when both trade records and field surveys (Inskipp et al., 1988; PHPA et al., 1998; Cahill et al., 2006) showed that market prices of birds had already risen and remnant populations had fallen victim to further trapping. Considerable time-lags between the onset of population decline and extinction are known in long-lived species (Diamond, 1972; Kuussaari et al., 2009), particularly when trappers only target nestlings (Valle et al., 2018). In addition to gauging population changes over long periods, Red List reassessment of the cockatoos is complicated by several other considerations. The recent split of Citron-crested Cockatoo leaves the resultant two species at higher risk of extinction than when combined, as the population on Sumba remains under pressure from illegal trapping and appears to have low productivity (Reuleaux et al., 2022). The subspecies *occidentalis* and *parvula* may seem relatively safe with one stronghold each (Komodo for *occidentalis*, Timor-Leste for *parvula*), but the Komodo population depends on intense patrolling and local goodwill, both of which will be under threat if the recently proposed drastic reduction in visitor numbers to Komodo National Park (CNN Travel, 2019) is implemented, or if international travel is curtailed due to unforeseen issues such the current Covid-19 pandemic (Caraka et al., 2020; Jeon and Yang, 2021). Conservation infrastructure in Timor-Leste (subspecies *parvula*) is still being established, and the probable softening of the currently highly controlled border with Indonesia (Thu, 2012) could increase illegal wildlife trade, as seen elsewhere (Shepherd and Nijman, 2008; Zhang et al., 2008). The other subspecies all survive in very low numbers and their status remains precarious. Currently *C. s. sulphurea* is of greatest concern: a national park formerly considered its last stronghold (Cahyadin et al., 1994; Agista et al., 2001) harbours a much smaller population than previously believed (12–50 individuals), in only a small area, and its staff urgently need support to liaise better with local communities and tackle the ongoing illegal establishment of new plantations in its core. A possible additional remnant population in Central Sulawesi needs urgent investigation. The populations of *djampeana* and *paulandrewi* have a realistic chance of survival only if there is legal protection for their habitat and enforced protection for the birds themselves.

There is an instructive parallel and contrast in the circumstances and management of the Yellow-crested Cockatoo and the Philippine cockatoo *Cacatua haematuropygia*. Both species were once widespread and common in their respective archipelagos—Wallacea and the Philippines—but have been reduced by forest clearance and trapping to scattered remnant populations (Collar et al. 2001). However, while the monotypic Philippine cockatoo has benefited from one major programme (Katala Foundation) focusing almost entirely on one island group (Palawan) (Widmann and Lacerna-Widmann, 2008), the Yellow-crested Cockatoo requires action in multiple parts of its range if it is to retain its complex taxonomic identity, which doubtless reflects important local adaptations (Collar and Marsden, 2014) as seen in tiger *Panthera tigris* subspecies (Ryder, 1986; Luo et al., 2004) and the morphotypes of Aldabra giant tortoises *Aldabrachelys gigantea* (Turnbull et al., 2015). In this respect, the particularity of the factors behind the species' local population persistence underlines the value of tailoring conservation efforts to each site and case. Some of these factors can be turned to advantage in differing local contexts, and represent exciting opportunities to recover crucial populations through relatively low-cost management interventions. This insight is important not only for the conservation of the yellow-crested and Citron-crested Cockatoos and other Asian hole-nesters (such as Tenggara hill myna, parrots and hornbills) but also for species in other parts of the world threatened by persecution (brown bears *Ursus arctos*, Naves et al., 2003; jaguars *Panthera onca*, De Angelo et al., 2013 and other large carnivores under hunting pressure). The models themselves may yield relevant information, such as the importance of human occupation and infrastructure patterns or the role of protected areas in influencing species persistence. However, the approach of looking beyond the model and examining location-specific factors could be applied to many other species with wide but now fragmented ranges for a better understanding of—and stronger measures against—extinction risk. A network of 'cockatoo advocates' (at least one committed individual from each site, such as local residents, protected areas staff, NGO members) would greatly help build local support for the birds' conservation, reducing trapping and upgrading legal protection. The most urgent conservation actions include improving the conditions for law enforcement in south-east Sulawesi, a mobile awareness campaign aimed at communities near remnant populations in Nusa Tenggara, and detailed study of the status and cultural treatment of the species in

Timor-Leste. Without these interventions, the future of the two species, regardless of their Red List status, will remain in the balance.

References

Agista, D., Sumardin, Hamid, A., Mallo, F. N., Alam, S., Harjun and Mamengko, C. (2001) *Status Kakatua-kecil Jambul-kuning di Sulawesi Tenggara dan Sulawesi Tengah*. Bogor, Indonesia: Birdlife International - Indonesia Programme.

De Angelo, C., Paviolo, A., Wiegand, T., Kanagaraj, R. and Di Bitetti, M. S. (2013) 'Understanding species persistence for defining conservation actions: A management landscape for jaguars in the Atlantic Forest.' *Biological Conservation*, 159, March, pp. 422–433.

Argeloo, M. and Dekker, R. W. R. J. (1996) 'Exploitation of megapode eggs in Indonesia: The role of traditional methods in the conservation of megapodes.' *ORYX*, 30(1) pp. 59–64.

Badan Pusat Statistik (2016) *Statistical yearbook of Indonesia*. [Online] [Accessed on 17th October 2017] www.bps.go.id.

Benítez-López, A., Alkemade, R. and Verweij, P. A. (2010) 'The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis.' *Biological Conservation*, 143(6) pp. 1307–1316.

Bhagwat, S. A. and Rutte, C. (2006) 'Sacred groves: potential for biodiversity management.' *Frontiers in Ecology and the Environment*, 4(10) pp. 519–524.

BirdLife International (2018) *State of the world's birds: taking the pulse of the planet*. Cambridge, UK: BirdLife International.

BirdLife International (2021a) *Datazone*. [Online] [Accessed on 11th March 2021] http://datazone.birdlife.org/.

BirdLife International (2021b) *Species factsheet* Cacatua sulphurea. [Online] [Accessed on 16th July 2021] http://www.birdlife.org.

BirdLife International (2022a) *Species Factsheet* Cacatua citrinocristata. [Online] [Accessed on 6th January 2022] http://www.birdlife.org.

BirdLife International (2022b) *Species Factsheet* Cacatua sulphurea. [Online] [Accessed on 6th January 2022] http://www.birdlife.org.

Boal, C. W. (2018) *Urban raptors: ecology and conservation of birds of prey in cities*. Island Press.

Breiman, L. (2001) 'Random forests.' *Machine learning*, 45(1) pp. 5–32.

Brun, C., Cook, A. R., Lee, J. S. H., Wich, S. A., Koh, L. P. and Carrasco, L. R. (2015) 'Analysis of deforestation and protected area effectiveness in Indonesia: A comparison of Bayesian spatial models.' *Global Environmental Change*, 31, March, pp. 285–295.

Burung Indonesia (2011) *The behavioural ecology of Breeding the Yellow-crested Cockatoo in Manupeu Tanahdaru National Park, Sumba Island*. Bogor, Indonesia: Burung Indonesia.

Bush, E. R., Baker, S. E. and Macdonald, D. W. (2014) 'Global trade in exotic pets 2006–2012.' *Conservation Biology*, 28(3) pp. 663–676.

Butchart, S. H. M., Stattersfield, A. J. and Brooks, T. M. (2006) 'Going or gone: defining "Possibly Extinct" species to give a truer picture of recent extinctions.' *Bulletin of the British Ornithologists' Club*, (126A) pp. 7–24.

Cahill, A. J., Walker, J. S. and Marsden, S. J. (2006) 'Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea citrinocristata* in Indonesia after 10 years of international trade control.' *Oryx*, 40(2) pp. 161–167.

Cahyadin, Y., Jepson, P. and Syarief, M. (1994) *A rapid status assessment of* Cacatua sulphurea sulphurea *in South Sulawesi Province*. Bogor, Indonesia: PHPA/BirdLife International - Indonesia Programme.

Caraka, R. E., Lee, Y., Kurniawan, R., Herliansyah, R., Kaban, P. A., Nasution, B. I., Gio, P. U., Chen, R. C., Toharudin, T. and Pardamean, B. (2020) 'Impact of COVID-19 large scale restriction on environment and economy in Indonesia.' *Global Journal of Environmental Science and Management*, 6(Special Issue) pp. 65–84.

Catterall, M. (1997) *Results of the 1996 bird survey of Buton Island, Sulawesi, Indonesia*. Spilsby, UK: Operation Wallacea.

Cazalis, V., Princé, K., Mihoub, J. B., Kelly, J., Butchart, S. H. M. and Rodrigues, A. S. L. (2020) 'Effectiveness of protected areas in conserving tropical forest birds.' *Nature Communications*, 11(1) pp. 1–8.

CITES (2002) *Cacatua sulphurea - Consideration of proposals for amendment of appendices I and II - CoP13 Prop. 11*. [Online] https://cites.org/sites/default/files/eng/cop/13/prop/E13-P11.pdf.

CITES (2020) *Convention on International Trade in Endangered Species of Wild Fauna and Flora - Appendices*. [Online] [Accessed on 10th February 2021] https://cites.org/eng/app/appendices.php.

CNN Travel (2019) *Indonesia cancels plan to ban tourists from Komodo Island*. CNN Travel. [Online] [Accessed on 27th November 2019] https://edition.cnn.com/travel/article/indonesia-komodo-islands-reverse-tourist-ban-intl-hnk/index.html.

Collar, N. J., Andreev, A. V, Chan, S., Crosby, M. J., Subramanya, S. and Tobias, J. A. (2001) *Threatened birds of Asia: The BirdLife International Red Data Book*. Cambridge, UK: BirdLife International.

Collar, N. J., Eaton, J. A. and Sykes, B. (2017) 'Conservation and the redaction of locality data.' *BirdingASIA*, 28 pp. 3–4.

Collar, N. J. and Marsden, S. J. (2014) 'The subspecies of Yellow-crested Cockatoo Cacatua sulphurea.' *Forktail*, (30) pp. 23–27.

Devenish, C., Junaid, A. R., Saryanthi, R., van Balen, S. B., Kaprawi, F., Aprianto, G. C., Stanley, R., Poole, O., Owen, A., Collar, N. J. and Marsden, S. J. (2021) 'Biological richness of Gunung Slamet, Central Java, and the need for its protection.' *Oryx*, in press.

Diamond, J. M. (1972) 'Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands.' *Proceedings of the National Academy of Sciences*, 69(11) pp. 3199–3203.

Diamond, J. M. (1987) 'Extant Unless Proven Extinct? Or, Extinct Unless Proven Extant?' *Conservation Biology*, 1(1) pp. 77–79.

Douglas-Hamilton, I., Krink, T. and Vollrath, F. (2005) 'Movements and corridors of African elephants in relation to protected areas.' *Naturwissenschaften*, 92(4) pp. 158–163.

Eaton, J. A., Shepherd, C. R., Rheindt, F. E., Harris, J. B. C., van Balen, S. B., Wilcove, D. S. and Collar, N. J. (2015) 'Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia.' *Forktail*, 31 pp. 1–12.

Erb, M. (2016) ‘Mining and the conflict over values in Nusa Tenggara Timur province, eastern Indonesia.’ *The Extractive Industries and Society*, 3(2) pp. 370–382.

Fa, J. E., Olivero, J., Farfán, M. Á., Márquez, A. L., Duarte, J., Nackoney, J., Hall, A., Dupain, J., Seymour, S., Johnson, P. J., Macdonald, D. W., Real, R. and Vargas, J. M. (2015) ‘Correlates of bushmeat in markets and depletion of wildlife.’ *Conservation Biology*, 29(3) pp. 805–815.

Froese, G. Z. L. and Mustari, A. H. (2019) ‘Assessments of Maleo Macrocephalon maleo nesting grounds in South-east Sulawesi reveal severely threatened populations.’ *Bird Conservation International*, 29 pp. 497–502.

Garland, K. A. and Carthy, R. R. (2010) ‘Changing taste preferences, market demands and traditions in Pearl Lagoon, Nicaragua: A community reliant on green turtles for income and nutrition.’ *Conservation and Society*, 8(1) pp. 55–72.

Garnier, S. (2018) *viridis: Default Color Maps from ‘matplotlib’. R package version 0.5.1.* [Online] https://cran.r-project.org/package=viridis.

Geary, M., Brailsford, C. J., Hough, L. I., Baker, F., Guerrero, S., Leon, Y. M., Collar, N. J. and Marsden, S. J. (2021) ‘Street-level green spaces support a key urban population of the threatened Hispaniolan parakeet *Psittacara chloropterus*.’ *Urban Ecosystems*, April, pp. 1–8.

Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M. and Burgess, N. D. (2013) ‘Effectiveness of terrestrial protected areas in reducing habitat loss and population declines.’ *Biological Conservation*, 161 pp. 230–238.

Geofabrik (2021) *OpenStreetMap data for Indonesia (with East Timor)*. Geofabrik Download Server. [Online] [Accessed on 5th October 2021] https://download.geofabrik.de/asia/indonesia.html.

Gould, S. F. (2011) ‘Does post-mining rehabilitation restore habitat equivalent to that removed by mining? A case study from the monsoonal tropics of northern Australia.’ *Wildlife Research*, 38 pp. 482–490.

Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, Sa., Tyukavina, A., Thau, D., Stehman, S. V, Goetz, S. J. and Loveland, T. R. (2013) ‘High-resolution global maps of 21st-century forest cover change.’ *Science*, 342 pp. 850–853.

Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, Sa., Tyukavina, A., Thau, D., Stehman, S. V, Goetz, S. J. and Loveland, T. R. (2020) *Global Forest Change 2000–2019 Dataset Hansen/UMD/Google/USGS/NASA*. [Online] [Accessed on 7th February 2020] http://earthenginepartners.appspot.com/science-2013-global-forest.

Harris, J. B. C., Tingley, M. W., Hua, F., Yong, D. L., Adeney, J. M., Lee, T. M., Marthy, W., Prawiradilaga, D. M., Sekercioglu, C. H., Suyadi, C. H., Winarni, N., Wilcove, D. S., Suyadi, Winarni, N. and Wilcove, D. S. (2017) ‘Measuring the impact of the pet trade on Indonesian birds.’ *Conservation Biology*, 31(2) pp. 394–405.

Imansyah, M. J., Purwandana, D., Ariefiandy, A., Benu, Y. J., Jessop, T. S. and Trainor, C. R. (2016) ‘Valley-floor censuses of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea occidentalis* on Komodo Island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period.’ *Forktail*, 32 pp. 66–72.

Indraswari, K., Friedman, R. S., Noske, R., Shepherd, C. R., Biggs, D., Susilawati, C. and Wilson, C. (2020) ‘It’s in the news: Characterising Indonesia’s wild bird trade network from media-reported seizure incidents.’ *Biological Conservation*, 243, March, p. 108431.

Inskipp, T., Broad, S. and Luxmoore, R. (1988) *Significant Trade in Wildlife -A Review of Selected Species in CITES Appendix II, Volume 3: Birds*. Cambridge, UK: IUCN Conservation Monitoring Centre.

IUCN (2021) *Protected Area Categories*. [Online] [Accessed on 19th April 2021] https://www.iucn.org/theme/protected-areas/about/protected-area-categories.

Jeon, C.-Y. and Yang, H.-W. (2021) 'The structural changes of a local tourism network: comparison of before and after COVID-19.' *Current Issues in Tourism*, January, pp. 1–15.

Jones, M. J., Linsley, M. D. and Marsden, S. J. (1995) 'Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia.' *Bird Conservation International*, 5(01) pp. 21–52.

Kendall, S. B. (1979) 'Citron-crested cockatoos in Sumba.' *Avicultural Magazine*, 85(2) pp. 93–94.

KLHK and DJ KSDAE (2018) *Statistik Direktorat Jenderal Konservasi Sumbar Daya Alam dan Ekosistem Tahun 2017*. Jakarta, Indonesia: Kementerian Lingkungan Hidup dan Kehutanan.

Kociolek, A. V., Clevenger, A. P., St. Clair, C. C. and Proppe, D. S. (2011) 'Effects of road networks on bird populations.' *Conservation Biology*, 25(2) pp. 241–249.

Kummu, M., Taka, M. and Guillaume, J. H. A. (2018) 'Gridded global datasets for Gross Domestic Product and Human Development Index over 1990-2015.' *Scientific Data*, 5(1) pp. 1–15.

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. and Steffan-Dewenter, I. (2009) 'Extinction debt: a challenge for biodiversity conservation.' *Trends in Ecology and Evolution*. Elsevier Current Trends pp. 564–571.

Liaw, A. and Wiener, M. (2002) 'Classification and Regression by randomForest.' *R news*, 2(3) pp. 18–22.

Liévano-Latorre, L. F., Brum, F. T. and Loyola, R. (2021) 'How effective have been guerrilla occupation and protected areas in avoiding deforestation in Colombia?' *Biological Conservation*, 253, January, p. 108916.

Lunstrum, E. and Givá, N. (2020) 'What drives commercial poaching? From poverty to economic inequality.' *Biological Conservation*, 245, May, p. 108505.

Luo, S. J., Kim, J. H., Johnson, W. E., Van Der Walt, J., Martenson, J., Yuhki, N., Miquelle, D. G., Uphyrkina, O., Goodrich, J. M., Quigley, H. B., Tilson, R., Brady, G., Martelli, P., Subramaniam, V., McDougal, C., Hean, S., Huang, S. Q., Pan, W., Karanth, U. K., Sunquist, M., Smith, J. L. D. and O'Brien, S. J. (2004) 'Phylogeography and genetic ancestry of tigers (*Panthera tigris*).' *PLoS Biology*, 2(12) p. e442.

Mallo, F. N. and Setiawan, I. (1996) *Telaah status* Cacatua sulphurea sulphurea *di Sulawesi Tengah*. Bogor, Indonesia.

Marsden, S. J. (1999) 'Estimation of parrot and hornbill densities using a point count distance sampling method.' *Ibis*, 141(3) pp. 327–390.

Marsden, S. J. and Jones, M. J. (1997) 'The nesting requirements of the parrots and hornbill of Sumba, Indonesia.' *Biological Conservation*, 82(3) pp. 279–287.

Marsden, S. J. and Royle, K. (2015) 'Abundance and abundance change in the world's parrots.' *Ibis*, 157(2) pp. 219–229.

Martin, R. B. (2000) 'When CITES works and when it does not.' *In* Hutton, J. and Dickson, B. (eds) *Endangered Species Threatened Convention: The Past, Present and Future of CITES*. London, UK: Earthscan, pp. 29–37.

McCauley, D. J., Power, E. A., Bird, D. W., McInturff, A., Dunbar, R. B., Durham, W. H., Micheli, F. and Young, H. S. (2013) ‘Conservation at the edges of the world.’ *Biological Conservation*, 165 pp. 139–145.

McPherson, M. A. and Nieswiadomy, M. L. (2005) ‘Environmental Kuznets curve: Threatened species and spatial effects.’ *Ecological Economics*, 55(3) pp. 395–407.

Mills, J. H. and Waite, T. A. (2009) ‘Economic prosperity, biodiversity conservation, and the environmental Kuznets curve.’ *Ecological Economics*, 68(7) pp. 2087–2095.

Monk, K., De Fretes, Y. and Reksodiharjo-Lilley, G. (1997) *Ecology of Nusa Tenggara and Maluku*. 1st ed., Oxford, UK: Oxford University Press.

Mortelliti, A. and Boitani, L. (2007) ‘Estimating species’ absence, colonization and local extinction in patchy landscapes: an application of occupancy models with rodents.’ *Journal of Zoology*, 273(3) pp. 244–248.

Nandika, D., Mulyani, Y. A., Prawiradilaga, D. M. and Agustina, D. (2020) ‘Monitoring of *Cacatua sulphurea abbotti* in Masakambing Island, Indonesia.’ *Biotropia-The Southeast Asian Journal of Tropical Biology*, 27(3) pp. 271–281.

Naves, J., Wiegand, T., Revilla, E. and Delibes, M. (2003) ‘Endangered Species Constrained by Natural and Human Factors: the Case of Brown Bears in Northern Spain.’ *Conservation Biology*, 17(5) pp. 1276–1289.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Mininchin, P. R., O’Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. and Wagner, H. (2013) ‘vegan: Community Ecology Package. R package version 2.0-8.’

Olah, G., Butchart, S. H. M., Symes, A., Guzmán, I. M., Cunningham, R., Brightsmith, D. J. and Heinsohn, R. (2016) ‘Ecological and socio-economic factors affecting extinction risk in parrots.’ *Biodiversity and Conservation*, 25(2) pp. 205–223.

OpenStreetMap Contributors (2021) *OpenStreetMap data*. [Online] [Accessed on 5th October 2021] https://www.openstreetmap.org/copyright.

Pain, D. J., Martins, T. L. F., Boussekey, M., Diaz, S. H., Downs, C. T., Ekstrom, J. M. M., Garnett, S., Gilardi, J. D., McNiven, D. and Primot, P. (2006) ‘Impact of protection on nest take and nesting success of parrots in Africa, Asia and Australasia.’ *Animal Conservation*, 9(3) pp. 322–330.

Peres, C. A. and Lake, I. R. (2003) ‘Extent of nontimber resource extraction in tropical forests: Accessibility to game vertebrates by hunters in the Amazon Basin.’ *Conservation Biology*, 17(2) pp. 521–535.

Persulessy, Y. E., Djawarai, Y. B. and Marut, R. (2003) *Survei populasi dan distribusi kakatua-kecil jambul-kuning* Cacatua sulphurea citrinocristata *dan empat jenis paruh bengkok lain di Pulau Sumba*. Bogor, Indonesia.

PHPA, LIPI and BirdLife International-IP (1998) *Species recovery plan Yellow-crested Cockatoo*. Bogor, Indonesia: PHPA/LIPI/BirdLife International - Indonesia Programme.

Pires, S. F. (2012) ‘The illegal parrot trade: a literature review.’ *Global Crime*, 13(3) pp. 176–190.

Pires, S. F. and Clarke, R. V. (2011) ‘Sequential Foraging, Itinerant Fences and Parrot Poaching in Bolivia.’ *British Journal of Criminology*, 51(2) pp. 314–335.

Pires, S. F., Olah, G., Nandika, D., Agustina, D. and Heinsohn, R. (2021) ‘What drives the illegal parrot trade? Applying a criminological model to market and seizure data in Indonesia.’ *Biological Conservation*, 257, May.

Plieninger, T., Quintas-Soriano, C., Torralba, M., Mohammadi Samani, K. and Shakeri, Z. (2020) ‘Social dynamics of values, taboos and perceived threats around sacred groves in Kurdistan, Iran.’ Palmer, C. (ed.) *People and Nature*, 2(4) pp. 1237–1250.

QGIS Development Team (2021) ‘QGIS Geographic Information System.’ Hannover, Germany: Open Source Geospatial Foundation Project.

R Core Team (2021) ‘R: A language and environment for statistical computing.’ Vienna, Austria: R Foundation for Statistical Computing.

Randriamamonjy, V. C., Keane, A., Razafimanahaka, H. J., Jenkins, R. K. B. and Jones, J. P. G. (2015) ‘Consumption of bushmeat around a major mine, and matched communities, in Madagascar.’ *Biological Conservation*, 186, June, pp. 35–43.

Reuleaux, A., Collar, N. J., Siregar, B. A., Mardiastuti, A. and Marsden, S. J. (2018) ‘Preliminary range-wide surveys of the heavily traded Tenggara Hill Myna Gracula venerata.’ *Forktail*, 34 pp. 29–34.

Reuleaux, A., Siregar, B. A., Collar, N. J., Mardiastuti, A. and Marsden, S. J. (2022) ‘Productivity constraints on Citron-crested Cockatoos in a rich community of large hole-nesting birds.’ *Avian Research*, 13 p. 100015.

Reuleaux, A., Siregar, B. A., Collar, N. J., Panggur, M. R., Mardiastuti, A., Jones, M. J. and Marsden, S. J. (2020) ‘Protected by dragons: Density surface modeling confirms large population of the critically endangered Yellow-crested Cockatoo on Komodo Island.’ *The Condor*, 122(4) p. duaa042.

Robinson, J. G. and Bodmer, R. E. (1999) ‘Towards wildlife management in tropical forests.’ *The Journal of Wildlife Management*, 63(1) pp. 1–13.

Romero-Vidal, P., Hiraldo, F., Rosseto, F., Blanco, G., Carrete, M. and Tella, J. L. (2020) ‘Opportunistic or Non-Random Wildlife Crime? Attractiveness Rather Than Abundance in the Wild Leads to Selective Parrot Poaching.’ *Diversity 2020, Vol. 12, Page 314*, 12(8) p. 314.

Rowley, I., Sharpe, C. and Boesman, P. (2017) ‘Yellow-crested Cockatoo (*Cacatua sulphurea*) | HBW Alive.’ *In* del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., and de Juana, E. (eds) *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions.

Rutte, C. (2011) ‘The sacred commons: Conflicts and solutions of resource management in sacred natural sites.’ *Biological Conservation*, 144(10) pp. 2387–2394.

Ryder, O. A. (1986) ‘Species conservation and systematics: the dilemma of subspecies.’ *Trends in Ecology & Evolution*, 1(1) pp. 9–10.

Samudro, B. R., Bloch, H. and Salim, R. (2015) ‘The uneven regional pattern of ecological capital in Indonesia: a political economy perspective.’ *International Journal of Green Economics*, 9(3–4) pp. 258–272.

Setiawan, I. (1996) *The status of* Cacatua sulphurea parvula *in Nusa Penida, Bali, and Sumbawa*. *PHPA/BirdLife International*. Bogor, Indonesia: PHPA/BirdLife International.

Shepherd, C. R. and Nijman, V. (2008) ‘The trade in bear parts from Myanmar: An illustration of the ineffectiveness of enforcement of international wildlife trade regulations.’ *Biodiversity and Conservation*, 17(1) pp. 35–42.

Snodgrass, J. G. and Tiedje, K. (2008) ‘Indigenous nature reverence and conservation.’ *Journal for the Study of Religion, Nature and Culture*, 2(1) pp. 6–29.

Sodhi, N. S., Posa, M. R. C., Lee, T. M., Bickford, D., Koh, L. P. and Brook, B. W. (2010) ‘The state and conservation of Southeast Asian biodiversity.’ *Biodiversity and conservation*, 19(2) pp. 317–328.

Sonter, L. J., Ali, S. H. and Watson, J. E. M. (2018) ‘Mining and biodiversity: Key issues and research needs in conservation science.’ *Proceedings of the Royal Society B: Biological Sciences*, 285(1892).

Sopian, N. L. (2015) ‘Informal Dispute Resolution Based on Adat Law: A Case Study of Land Dispute in Flores, East Nusa Tenggara, Indonesia.’ *Indon. L. Rev.*, 5 p. 106.

Stearman, A. M. (2000) ‘A pound of flesh: social change and modernization as factors in hunting sustainability among neotropical indigenous societies.’ *In* Robinson, J. and Bennett, E. L. (eds) *Hunting for sustainability in tropical forests*. 1st ed., New York, US: Columbia University Press, p. 243.

Tella, J. L. and Hiraldo, F. (2014) ‘Illegal and legal parrot trade shows a long-term, cross-cultural preference for the most attractive species increasing their risk of extinction.’ *PLoS ONE*, 9(9) p. e107546.

Thu, P. M. (2012) ‘Access to Land and Livelihoods in Post-conflict Timor-Leste.’ *Australian Geographer*, 43(2) pp. 197–214.

Turnbull, L. A., Ozgul, A., Accouche, W., Baxter, R., Chongseng, L., Currie, J. C., Doak, N., Hansen, D. M., Pistorius, P., Richards, H., van de Crommenacker, J., von Brandis, R., Fleischer-Dogley, F. and Bunbury, N. (2015) ‘Persistence of distinctive morphotypes in the native range of the CITES-listed Aldabra giant tortoise.’ *Ecology and Evolution*, 5(23) pp. 5499–5508.

Valle, S., Collar, N. J., Harris, W. E. and Marsden, S. J. (2018) ‘Trapping method and quota observance are pivotal to population stability in a harvested parrot.’ *Biological Conservation*, 217, January, pp. 428–436.

Veríssimo, D., Vieira, S., Monteiro, D., Hancock, J. and Nuno, A. (2020) ‘Audience research as a cornerstone of demand management interventions for illegal wildlife products: Demarketing sea turtle meat and eggs.’ *Conservation Science and Practice*, 2(3) p. e164.

Walker, J. S., Cahill, A. J. and Marsden, S. J. (2005) ‘Factors influencing nest-site occupancy and low reproductive output in the Critically Endangered Yellow-crested Cockatoo Cacatua sulphurea on Sumba, Indonesia.’ *Bird Conservation International*, 15(4) pp. 347–359.

Webb, R. A. F. P. (1986) ‘Adat and Christianity in Nusa Tenggara Timur: Reaction and Counteraction: Traditional custom and modern development in Eastern Indonesia.’ *Philippine quarterly of culture and society*, 14(4) pp. 339–365.

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H. and Dunnington, D. (2021) ‘Package “ggplot2”: Create Elegant Data Visualisations Using the Grammar of Graphics.’

Widmann, P. and Lacerna-Widmann, I. D. (2008) ‘The cockatoo and the community: ten years of Philippine Cockatoo Conservation Programme.’ *BirdingASIA*, 10 pp. 23–29.

Wilkie, D. S., Starkey, M., Abernethy, K., Effa, E. N., Telfer, P. and Godoy, R. (2005) ‘Role of Prices and Wealth in Consumer Demand for Bushmeat in Gabon, Central Africa.’ *Conservation Biology*, 19(1) pp. 268–274.

Worldpop (2018) ‘Global High Resolution Population Denominators Project.’ Southampton, UK: School of Geography and Environmental Science, University of Southampton.

Yusuf, M. S. (2014) *Status of Yellow-crested Cockatoo at Tatar Spang, West Sumbawa, Indonesia*. Maluk, Indonesia: PT Newmont Nusa Tenggara.

Zhang, L., Hua, N. and Sun, S. (2008) ‘Wildlife trade, consumption and conservation awareness in southwest China.’ *Biodiversity and Conservation*, 17(6) pp. 1493–1516.

Van Zyl, J. J. (2001) ‘The Shuttle Radar Topography Mission (SRTM): a breakthrough in remote sensing of topography.’ *Acta Astronautica*, 48(5–12) pp. 559–565.

Appendices

Appendix 2.1: Sources for presence and absence of Yellow-crested Cockatoos and Citron-crested Cockatoos used in this study

Online platforms

obsr1062042, eBird restricted dataset 2019
obsr140275, eBird restricted dataset 2019
obsr17450, eBird restricted dataset 2019
obsr235781, eBird restricted dataset 2019
obsr270507, eBird restricted dataset 2019
obsr290872, eBird restricted dataset 2019
obsr320327, eBird restricted dataset 2019
obsr355303, eBird restricted dataset 2019
obsr420450, eBird restricted dataset 2019
obsr435628, eBird restricted dataset 2019
obsr44754, eBird restricted dataset 2019
obsr450241, eBird restricted dataset 2019
obsr604567, eBird restricted dataset 2019
obsr620927, eBird restricted dataset 2019
obsr633785, eBird restricted dataset 2019
obsr636911, eBird restricted dataset 2019
obsr647392, eBird restricted dataset 2019
obsr751848, eBird restricted dataset 2019
obsr817048, eBird restricted dataset 2019
obsr968457, eBird restricted dataset 2019
Rick & Leonie Jacobsen-Venroij, eBird 2016
Smathi Chong, eBird 2016
Wayne Klockner, eBird 2016
G. A. L. De Haan, eBird 2016
Iwein Mauro, sound recording 2004, Internet Bird collection 2004
Frank Lambert, sound recording 2005, Xeno-canto 2016
Colin Trainor, sound recording 2012, Xeno-canto 2016

Locations from Threatened Birds of Asia (Collar, N.J., Andreev, A. V, Chan, S., Crosby, M.J., Subramanya, S., Tobias, J.A., 2001. Threatened birds of Asia: The BirdLife International Red Data Book. BirdLife International, Cambridge, UK.)

Andrew and Holmes 1990, in Collar et al. 2001
B. F. King verbally 1998, in Collar et al. 2001
B. Gee in litt. 1999, in Collar et al. 2001
Baltzer undated, Catterall undated, 1998, in Collar et al. 2001
Behrens 1995, in Collar et al. 2001
Butchart et al. 1996, in Collar et al. 2001
C. Trainor in litt. 1999, in Collar et al. 2001
Cahyadin verbally 2000, in Collar et al. 2001
Catterall 1998, in Collar et al. 2001
Coomans de Ruiter 1951, in Collar et al. 2001
D. Agista in litt. 2000, in Collar et al. 2001
Dammerman 1926b, in Collar et al. 2001
Dutson 1995, in Collar et al. 2001
Guillemard 1885, in Collar et al. 2001
Hartert 1896c, in Collar et al. 2001

Hartert 1897a, in Collar et al. 2001
Hartert 1897a, in Collar et al. 2001
Hartert 1898a, in Collar et al. 2001
Hartert 1898c, female in AMNH, in Collar et al. 2001
Hartert 1903b, in Collar et al. 2001
Harun per I. Setiawan verbally 2000, in Collar et al. 2001
Hellmayr 1994, in Collar et al. 2001
I. Setiawan and Y. Cahyadin verbally 2000, in Collar et al. 2001
I. Setiawan verbally 2000, in Collar et al. 2001
Meyer and Wiglesworth 1898, in Collar et al. 2001
J. Robinson-Dean in litt. 2000, in Collar et al. 2001
Johnstone et al. 1996, in Collar et al. 2001
K. D. Bishop in litt. 1999, in Collar et al. 2001
Kendall 1979, in Collar et al. 2001
Lesmana et al. 1999, in Collar et al. 2001
R. Drijvers in litt 1999, in Collar et al. 2001
M. F. Kinnaird and T. G. O'Brien in litt. 2000, in Collar et al. 2001
M. J. Jones et al. 1995, in Collar et al. 2001
Mallo and Setiawan 1996, in Collar et al. 2001
Marsden 1993, in Collar et al. 2001
Mayr 1944, in Collar et al. 2001
Meise 1929-1930, in Collar et al. 2001
Meyer 1879, in Collar et al. 2001
Meyer 1879, Meyer and Wiglesworth 1898, in Collar et al. 2001
Meyer and Wiglesworth 1896, 1898, in Collar et al. 2001
Mochtar 1989a, 1989c in Collar et al. 2001
N. Bostock in litt. 1999, in Collar et al. 2001
Noske 1995, in Collar et al. 2001
Noske and Saleh 1996, in Collar et al. 2001
Oberholser 1917, in Collar et al. 2001
Pilgrim et al. 1997, 2000 in Collar et al. 2001
R. Drijvers in litt. 1999, in Collar et al. 2001
Rensch 1931a,b in Collar et al. 2001
Riffel and Bekti 1991, in Collar et al. 2001
Riley 1924, in Collar et al. 2001
Schlegel 1862-1873, in Collar et al. 2001
Schmutz 1977, in Collar et al. 2001
Setiawan 1996, in Collar et al. 2001
Setiawan et al. 2001, in Collar et al. 2001
Sudaryanto verbally 1997, in Collar et al. 2001
Verbelen 1996, in Collar et al. 2001
Verhejen 1976, in Collar et al. 2001
Viney 1995, in Collar et al. 2001
Vorderman 1895b, in Collar et al. 2001
W. Doherty in Hartert 1896b: 543, in Collar et al. 2001
Wallace 1869, in Collar et al. 2001
Wiglesworth 1895a, 1898, in Collar et al. 2001
Forbes 1885, in Collar et al. 2001
H. Thompson per R. Noske in litt. 1999, in Collar et al. 2001
J. McKean and I. Mason per R. Noske in litt. 1999, in Collar et al. 2001
S. Behrens in Johnston et al. 2014, in Collar et al. 2001
egg and specimen in Rijksmuseum voor Natuurlijke Historie, Leiden, NL, in Collar et al. 2001
specimens in Museum of Comparative Zoology, Harvard University, US, in Collar et al. 2001
specimens in Museum Zoologicum Bogoriense, Indonesian Institute of Sciences, Bogor, ID, in

Collar et al. 2001
specimen in Senckenberg Museum Frankfurt, D, in Collar et al. 2001
specimens in Alabama Museum of Natural History, Tuscaloosa, US, in Collar et al. 2001

Verbal communication and correspondence

in litt. Gerardo Angelo, independent photographer, 2018
in litt. Ian Bishop, birdwatcher Central Sulawesi, 2020
in litt. James Eaton, Birdtour Asia, 2018
in litt. Oki Hidayat, University of Western Australia, 2019
in litt. Fachry Nur Mallo, Universitas Muhammadiyah Palu, 2018
in litt. Ihsan Nur Mallo, Universitas Muhammadiyah Palu, 2018
in litt. Tom Martin, Operation Wallacea, 2019
in. litt. Pantiati, Burung Indonesia, 2018
verbal comm. Dian Agista, Burung Indonesia, 2016, 2018
verbal comm. Thomas Arndt, Fonds für bedrohte Papageien, 2018
verbal comm. Akri T. Babys, Bogor Agricultural University, 2018
verbal comm. Dudi Nandika, Konservasi Kakatua, 2016
verbal comm. Maria Panggur, Komodo National Park, 2017
verbal comm. Samuel Rabenak, Burung Indonesia, Flores Bird Watching 2017
verbal comm. Arifson R. M. Sianturi, Matalawa National Park, 2020
verbal comm. A. Ridha Junaid, Burung Indonesia, 2016
verbal comm. Putu Sutarya, Rawa Aopa Watumohai National Park, 2019
verbal comm. Oka Dwi Prihatmoko, World Parrot Trust, 2017
verbal comm. Denis Sapta Yudhi, Burung Indonesia, 2018
verbal comm. M. Salamuddin Yusuf, Aman Mineral Batu Hijau, 2017

Other reports and literature

Agista, D., & Rubyanto, D. (2001). Telaah awal status, penyebaran, dan populasi kakatua kecil jambul kuning, *Cacatua sulphurea parvula*: di Taman Nasional Komodo, Nusa Tenggara Timur. Bogor, Indonesia: Birdlife International Indonesia Programme.

Agista, D., Sumardin, Hamid, A., Mallo, F. N., Alam, S., Harjun, & Mamengko, C. (2001). Status Kakatua-kecil Jambul-kuning di Sulawesi Tenggara dan Sulawesi Tengah. Bogor, Indonesia: Birdlife International - Indonesia Programme.

Andrew, P., & Holmes, D. A. (1976). Sulawesi Bird Report. *Kukila* **5**, 4–26.

Arndt, T. (2017). Gelbwangenkakadus in Timor Leste. *Papageien* **3**, 95–97.

Arndt, T., & Bashari, H. (2016). Zum Status der Papageien auf Jampea. *Papageien* **4**, 137–141.

Ashari, H., Prawiradilaga, D. M., Eaton, J. A., Suparno, S., & Rheindt, F. E. (2018). New records and range extensions of birds from Timor, Alor and Rote. *TREUBIA* **45**, 47–64.

Aziz, F. A. (2012). Telaah awal habitat dan populasi Kakatua-kecil Jambul-kuning di bentang alam Mbeliling Bagian Barat, Manggarai Barat. Bogor, Indonesia: Burung Indonesia.

Bashari, H., & Arndt, T. (2016). Status of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea djampeana* in the Tanahjampea islands, Flores Sea, Indonesia. *FORKTAIL* 62–65.

BBKSDA NTT. (2017a). Statistik 2017 Balai Besar Konservasi Sumber Daya Alam Nusa Tenggara Timur. Kupang, Indonesia: Kementerian Lingkungan Hidup dan Kehutanan.

BBKSDA NTT. (2017b). Inventarisasi Kakatua Jambul Kinung (*Cacatua sulphurea*) di Taman Wisata Alam Menipo. Kupang, Indonesia: Balai Besar KSDA Nusa Tenggara Timur.

BirdLife International. (2019). Species factsheet: *Cacatua sulphurea*. Available from http://www.birdlife.org (accessed 6 September 2019).

BirdLife International. (2021). Datazone. Available from http://datazone.birdlife.org/ (accessed 11 March 2021).

BKDSA NTB. (2017). Laporan tahunan 2016. Mataram, Indonesia: Balai KSDA Nusa Tenggara Barat.

Burung Indonesia. (2011). The behavioural ecology of Breeding the Yellow-crested Cockatoo in Manupeu Tanahdaru National Park, Sumba Island. Bogor, Indonesia: Burung Indonesia.

Butchart, S. H. M., Brooks, T. M., Davies, C. W. N., Dharmaputra, G., Dutson, G. C. L., Lowen, J. C., & Sahu, A. (1993). Preliminary report of the Cambridge Flores/Sumbawa conservation project 1993. Cambridge, UK.

Butchart, S. H. M., Brooks, T. M., Davies, C. W. N., Dharmaputra, G., Dutson, G. C. L., Lowen, J. C., & Sahu, A. (1996). The conservation status of forest birds on Flores and Sumbawa, Indonesia. *Bird Conserv. Int.* **6**, 335–370.

Cahyadin, Y., Jepson, P., & Arif, S. (1994). The status of Cacatua sulphurea abbotti on the Masalembo Islands. Bogor: PHPA/BirdLife International - Indonesia Programme.

Cahyadin, Y., Jepson, P., & Syarief, M. (1994). A rapid status assessment of *Cacatua sulphurea sulphurea* in South Sulawesi Province. Bogor, Indonesia: PHPA/BirdLife International - Indonesia Programme.

Catterall, M. (1997). Results of the 1996 bird survey of Buton Island, Sulawesi, Indonesia. Operation Wallacea.

Dutson, G. (1995). The birds of Salayar and the Flores Sea islands. *Kukila* **7**, 129–141.

Eaton, J. A., Shepherd, C. R., Rheindt, F. E., Harris, J. B. C., van Balen, S. B., Wilcove, D. S., & Collar, N. J. (2015). Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia. *Forktail* **31**, 1–12.

FFI Indonesia Programme. (2011). Community-Based Agroforestry for Upper Watershed Rehabilitation, Lombok Indonesia. Jakarta.

Hadiprayitno, G., Mertha, I. G., & Ilhamdi, M. L. (2016). Species Richness and Birds Conservation Priority in Mount Rinjani Areas, Lombok. *Biosaintifika J. Biol. Biol. Educ.* **8**, 270.

Hidayat, O. (2014). Komposisi, preferensi dan sebaran jenis tumbuhan pakan Kakatua Sumba (*Cacatua sulphurea citrinocristata*) di Taman Nasional Laiwanggi Wanggameti. *J. Penelit. Kehutan. Wallacea* **3**, 25–36.

Ihsannudin, I., Hidayat, K., Sukesi, K., & Yuliati, Y. (2020). Perception of the local community toward the Yellow-crested Cockatoo (*Cacatua sulphurea abbotti*), a critically endangered species in Masakambing Island, Indonesia. *Geogr. J. Soc. Sp.* **16**.

Imansyah, M. J., Anggoro, D. G., Yangpatra, N., Hidayat, A., & Benu, Y. J. (2005). Sebaran dan karakteristik pohon sarang kakatua jambul kuning (*Cacatua sulphurea parvula*) di pulau Komodo, Taman Nasional Komodo. Denpasar, Indonesia: CRES Komodo Project, TN Komodo.

Imansyah, M. J., Purwandana, D., Ariefiandy, A., Benu, Y. J., Jessop, T. S., & Trainor, C. R. (2016). Valley-floor censuses of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea occidentalis* on Komodo Island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period. *Forktail* **32**, 66–72.

Jones, M. J., Linsley, M. D., & Marsden, S. J. (1995). Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia. *Bird Conserv. Int.* **5**, 21–52.

Kelly, D., & Marples, N. (2010). Bird populations of the Wakatobi. In J. Clifton, R. K. F. Unsworth, & D. J. Smith (Eds.), *Marine research and conservation in the Coral Triangle: the Wakatobi National Park.* p. 149–170. Hauppauge, NY: Nova Science Publishers.

KLHK, & DJ KSDAE. (2018). Statistik Direktorat Jenderal Konservasi Sumbar Daya Alam dan Ekosistem Tahun 2017. Jakarta, Indonesia: Kementerian Lingkungan Hidup dan Kehutanan.

Lesmana, D., Trainor, C. R., & Gatur, A. (2000). Arti penting hutan di daratan Timor Bagian Barat: telaah awal informasi keanekaragaman hayati dan sosial-ekonomi di Pulau Timor (Propinsi Nusa Tenggara Timur). Jakarta, Indonesia: Direktorat Jenderal Perlindungan dan Konservasi Alam (PKA), Departemen Kehutanan.

Linsley, M. D., Jones, M. J., & Marsden, S. J. (2011). A review of the Sumba avifauna. *Kukila* **10**, 60–90.

Mallo, F. N., & Setiawan, I. (1996). Telaah status *Cacatua sulphurea sulphurea* di Sulawesi

Tengah. Bogor, Indonesia.

Mardiastuti, A., Kusrini, M. D., Mulyani, Y. A., Manullang, S., & Soehartono, T. (2018). Arahan Strategis Konservasi Spesies Nasional 2008 - 2018. Jakarta, Indonesia: Direktorat Jenderal Perlindungan Hutan dan Konservasi Alam.

Marsden, S., & Fielding, A. (1999). Habitat associations of parrots on the Wallacean islands of Buru, Seram and Sumba. *J. Biogeogr.* **26**, 439–446.

Marsden, S. J., & Pilgrim, J. D. (2003). Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain, PNG. *Ibis (Lond. 1859).* **145**, 45–53.

Martin, T. E., Kelly, D. J., Keogh, N. T., Heriyadi, D., Singer, H. A., & Blackburn, G. A. (2012). The avifauna of Lambusango Forest Reserve, Buton Island, south-east Sulawesi, with additional sightings from southern Buton. *Forktail* **28**, 107–112.

Mayr, E., & Stein, G. H. W. (1944). The birds of Timor and Sumba. *Bull. AMNH* **83**.

Metz, S., Zimmerman, B., Augustina, D., & Nandika, D. (2009). Mysteries of 'Abbott's Cockatoo.' *AFA Watchb.* **36**, 14–19.

Myers, S. D., & Bishop, K. D. (2005). A review of historic and recent bird records from Lombok, Indonesia. *Forktail* **21**, 147–160.

Nandika, D. (2006). Recent observations of the critically endangered *Cacatua sulphurea* subspecies of Yellow-crested Cockatoo: Rawa Aopa Watumohai National Park SE Sulawesi, Indonesia. *PsittaScene* **18**, 10–11.

Nandika, D., & Agustina, D. (2012). Few and far between. Saving the Yellow-crested Cockatoos. *PsittaScene* **24(3)**, 130–134.

Nandika, D., & Agustina, D. (2018). Ecology Of Lesser Sulphur Creasted Cockatoo Cacatua Sulphurea Sulphurea At Rawa Aopa Watumohai National Park, Southeast Sulawesi. *Metamorf. J. Biol. Sci.* **5**, 188.

Nandika, D., Mulyani, Y. A., Prawiradilaga, D. M., & Agustina, D. (2020). Monitoring of *Cacatua sulphurea abbotti* in Masakambing Island, Indonesia. *Biotropia-The Southeast Asian J. Trop. Biol.* **27**, 271–281.

O'Connell, D. P., Kelly, D. J., Kelly, S., Analuddin, K., Karya, A., Marples, N. M., Rheindt, F. E., & Martin, T. E. (2020). An assessment of the avifauna of the Wakatobi Islands, South-east Sulawesi, Indonesia: species recorded and taxonomic considerations. *Raffles Bull. Zool.* **68**.

O'Connell, D. P., Marcraigh, F. Ó., O'Neill, A., Griffin, R., & Karya, A. (2019). The avifauna of Muna and Wawonii Islands, with additional records from mainland South-east Sulawesi, Indonesia. *Forktail* **35**, 50–56.

Oberholser, H. C. (1917). Birds Collected by Dr. W. L. Abbott on Various Islands in the Java Sea. *Proc. United States Natl. Museum*. Vol. 54.

Persulessy, Y. E., Djawarai, Y. B., & Marut, R. (2003). Survei populasi dan distribusi kakatua-kecil jambul-kuning *Cacatua sulphurea citrinocristata* dan empat jenis paruh bengkok lain di Pulau Sumba. Bogor, Indonesia.

PHPA, LIPI, & BirdLife International-IP. (1998). Species recovery plan Yellow-crested Cockatoo. Bogor, Indonesia: PHPA/LIPI/BirdLife International - Indonesia Programme.

Putra, E., Kristianto, I., & Christianto, Y. I. (1999). Monitoring populasi dan pengamatan aspek ekologi Kakatua-kecil jambul-kuning (*Cacatua sulphurea abbotti*) di Kepulauan Masalembu. Yogyakarta, Indonesia: Kutilang.

Ramdhani, N. (2011). Nilai Ekonomi Taman Nasional Gunung Rinjani: Studi Kasus di Obyek Wisata Otak Kokok Gading dan Desa Perian, Kecamatan Montong Gading, Nusa Tenggara Barat. Bogor Agricultural University (IPB).

Rensch, B. (1931). Die Vogelwelt von Lombok Sumbawa und Flores. *Mitteilungen aus dem Zool. Museum Berlin* **17**, 451–636.

Riley, E. P. (2010). The endemic seven: Four decades of research on the Sulawesi macaques. *Evol. Anthropol. Issues, News, Rev.* **19**, 22–36.

Sayogo, A., Rachmansah, A., Afnan, E. M., Jihad, Yansyah, M., & Prasetyo, P. N. (2012). Survey Biodiversity DAS Renggung, Pulau Lombok.

Schellekens, M., Trainor, C. R., & Duhan, G. U. U. B. (2011). New and significant bird records for Solor, Adonara, and Lembata (Lomblen) islands, Lesser Sundas. *Kukila* **15**, 31–49.

Setiana, T., Masy'ud, B., Jarwadi, D., Hernowo, B., & Pascasarjana. (2018). Faktor penentu keberhasilan teknis penangkaran kakatua kecil jambul kuning (*Cacatua sulphurea sulphurea*) (Determinant factors of technical success on captive breeding of Yellow-crested Cockatoo). *Media Konserv.* Vol. 23.

Setiawan, I. (1996). The status of Cacatua sulphurea parvula in Nusa Penida, Bali, and Sumbawa. *PHPA/BirdLife Int.* Vol. 6. Bogor, Indonesia: PHPA/BirdLife International.

Setiawan, I., Jati, A., Lesmana, D., Trainor, C. R., & Agista, D. (2000). Telaah awal status dan penyebaran Kakatua-kecil Jambul-kuning (*Cacatua sulphurea parvula*) di Pulau Alor, Pantar, Timor Barat, Flores dan Moyo. Bogor, Indonesia: PKA, BirdLife International-IP.

Setiawan, I., Yudha, E. P. P., Basuki, O. P., Purwandana, D., Suryakusumah, A., & Agista, D. (2001). Telaah status bio ekologi dan upaya pelestarian di Pulau Masakambing, Jawa Timur dan Pulau Nusa Penida, Bali. Bogor, Indonesia: PHPA/BirdLife International - Indonesia Programme.

Trainor, C. R. (2002a). Status and habitat associations of birds on Lembata Island, Wallacea, Indonesia, with reference to a simple technique for avifaunal survey on small islands. *Bird Conserv. Int.* **12**, 365–381.

Trainor, C. R. (2002b). The birds of Adonara, Lesser Sundas, Indonesia. *Forktail* **18**, 93–100.

Trainor, C. R. (2005). Birds of Tapuafu Peninsula, Roti Island, Lesser Sundas, Indonesia. *Forktail* **21**, 121.

Trainor, C. R. (2003). The birds of Lembata (Lomblen), Lesser Sundas, Indonesia. *Kukila* **12**, 39–53.

Trainor, C. R., Benstead, P. J., Martin, K., Lesman, D., Agista, D., Benstead, M. C., Drijvers, R., & Setiawan, I. (2006). New Bird Records for Nusa Tenggara Islands: Sumbawa, Moyo, Sumba, Flores, Pulau Besar and Timor. *Kukila* **13**, 6–22.

Trainor, C. R., Coates, B. J., Bishop, K. D., & Gardner, D. (2007). As Aves de Timor-Leste: Birds of Timor Leste. BirdLife International and Dove Publications.

Trainor, C. R., Imanuddin, A., Verbelen, P., & Walker, J. S. (2009). The birds of Wetar, Banda Sea: one of Indonesia's forgotten islands. *BirdingASIA* **10**, 78–93.

Trainor, C. R., Santana, F., Pinto, P., Xavier, A. F., Safford, R., & Grimmett, R. (2008). Birds, birding and conservation in Timor-Leste. *Bird. Asia* **9**, 16–45.

Trainor, C. R., & Soares, T. (2004). Birds of Atauro Island, Timor-Leste (East Timor). *Forktail* **20**, 41–48.

Trainor, C. R., Verbelen, P., & Johnstone, R. E. (2012). The avifauna of Alor and Pantar, Lesser Sundas, Indonesia. *Forktail* **28**, 77–92.

United Nations Office for Drug and Crime. (2015). Independent project evaluation of Strengthening Land Border Control in Timor Leste. Vienna: United Nations.

Wakatobi National Park. (2007). Peta Zonasi Taman Nasional Wakatobi. Bau-Bau, Indonesia: WWF Indonesia.

Wardill, J. C., Fox, P. S., Hoare, D. J., Marthy, W., & Anggraini, K. (2011). Birds of the Rawa Aopa Watumohai National Park, South-East Sulawesi. *Kukila* **10**, 91–114.

Widodo, W. (2009). Population status of *Cacatua sulphurea parvula* and *Trichoglossus euteles* in Alor, East Nusa Tenggara. *Biodiversitas J. Biol. Divers.* **10**, 81–87.

Wungo, E. (2011). Laporan survei populasi paruh bengkok terancam punah *Cacatua sulphurea citrinocristata*, Sumba, Nusa Tenggara Timur. Bogor, Indonesia: Burung Indonesia.

Yusuf, M. S. (2014). Status of Yellow-crested Cockatoo at Tatar Spang, West Sumbawa, Indonesia. Maluk, Indonesia: PT Newmont Nusa Tenggara.

Appendix 2.2: Accuracy and variable importance (measured in decrease in model accuracy when the predictor is removed) compared between three different measures of area protection as predictors of yellow-crested and Citron-crested Cockatoo site-specific survival from 1950 to 2015 in a random forest model**. % of area with any legal protection** = the percentage of a 5 km circle around the site that is legally protected under Indonesian protection categories equivalent to IUCN categories I–VI. **% of area strictly protected** = percentage of area protected as national park or conservation area equivalent to IUCN category III. **Area protection category (strict, weak, none)** = categorical variable with three protection levels: IUCN categories I–II = strict, III–VI = weak, or none; **n_{extinct}** = number of sites where cockatoos have become extinct (last record between the respective year and 2014). **n_{survived}** = number of sites where cockatoos have survived (at least until 2015). **+** indicates a positive relationship between the predictor and survival, **–** a negative relationship and **+ –** a positive influence for small values of the predictor and a negative one for larger values and **– +** a negative influence for small values of the predictor and a positive one for larger values. **AUC** = Area under the Receiver Operating Characteristics curve, an indicator of the model's ability to distinguish between classes. **Road density** = density of all types of roads and tracks calculated from total length of road within each 2 km-radius circle. Rows in bold were used as criteria to select best measure of area protection for prediction.

	% of area with any legal protection	**% of area strictly protected**	**Area protection category (strict, weak, none)**
Error rate total	0.229	0.201	0.201
Error rate $_{\text{extinct}}$	0.221	0.250	0.221
Error rate $_{\text{survived}}$	0.237	0.158	0.184
AUC	**0.872**	**0.860**	**0.871**
Island group	22.28	15.61	17.51
Tree cover	21.29^{+-}	16.57^{+-}	18.91^{+-}
Human density	16.23^{-}	14.74^{-}	12.69^{-}
Road density	14.11^{-}	13.66^{-}	15.62^{-}
Altitude	12.86^{+-}	13.17^{+-}	13.70^{+-}
Protected area	**11.44^{+}**	**10.89^{+}**	**7.20**
GDP per capita	8.37^{-+}	6.76^{-+}	9.93^{+-}

Appendix 2.3: Broad locations with surviving cockatoo populations despite random forest model predictions of extinction between 1950 and 2015. These false negative classifications exemplify mechanisms by which subpopulations survived due to individual circumstances, which are impossible to capture with one model for all. Predicted survival is the proportion of tree votes for survival; marginal predictions (0.4−0.6) are not included. OpWall = Operation Wallacea, a commercial volunteer organisation carrying out conservation research on Buton; ENT = East Nusa Tenggara, WNT = West Nusa Tenggara (with Bali).

Site	Predicted survival	Year last seen	Type of location	Protection	Status	Source*	Visited by AR
False negatives (surviving, predicted to be extinct)							
Masalembo 1	0.08	2017	Remote island with highly modified habitat	Protection by NGO	At risk from stochastic events	a, b	n
Sulawesi 1	0.12	2015	Connection between forested hills and mangrove roosting area	OpWall raised awareness in one local community	Last remnant birds disappeared in 2016	c, d	y
Sulawesi 2	0.16	2019	Garden area, cockatoos only passing by daily, source population not known	None yet	Probably disappeared for decades, now re-colonised	e	n
Sumba 1	0.23	2017	Outskirts of a forest population but already in highly modified habitat	Regular birdwatching activity using the road, proximity to birding lodge	Only dispersers	c	y
ENT 1	0.24	2016	Outskirts of a forest but already in modified habitat close to humans	None known, maybe birders	Possibly already extinct, no other recent sightings	c	n
ENT 2	0.28	2018	Island surrounded by mangroves	Tourism reserve, with permanent presence	Safe at roost, at risk foraging on mainland	f	y
ENT 3	0.30	2017	Outskirts of a forest population but already in modified habitat close to humans	Near tourism reserve but without actual protection, intensely trapped	Disappearing	g	y
ENT 4	0.39	2017	Good forest affected by trapping, logging and conversion to gardens	Traditional belief: small area (1 ha) of sacred forest	One family chosen as area guardians for generations	h	y

Site	Predicted survival	Year last seen	Type of location	Protection	Status	Source*	Visited by AR
False positives (extinct, predicted to survive)							
WNT 1	0.60	1998	Connected to large forest but easily accessible from market and harbour	None	Gone for at least a decade	h	y
ENT 5	0.66	1998	Connected to large forest but easily accessible	Protection forest	No recent sightings	i	y
Sulawesi 3	0.69	1995	Mainland near small cockatoo-populated offshore island	None	Lacks search effort	i, j	n
ENT 6	0.74	1997	Poor habitat far from known surviving populations	Border of nature reserve	No recent sightings	i, f	n
Timor-Leste 1	0.75	2003	Forested mountain-top, good habitat	Conservation area	No recent confirmed sightings but lacks search effort	i, k, l, m	n
ENT 7	0.77	1998	Between 2 surviving sites in degraded scarce forest	Wildlife reserve	May support dispersers from other site but no recent sightings	i, n	y
Timor-Leste 2	0.79	2004	River valley surrounded by sparse forest	None	Lacks search effort, might survive	c, m	n
WNT 2	0.85	1999	Tip of cockatoo-populated island connecting to larger island	Hunting reserve but not patrolled	No recent sightings	i, f	y
Sumba 2	0.90	1995	Isolated forest block, far from known populations	None	No recent sightings despite visits by nearby national park staff	i, o	y
Timor-Leste 3	0.94	2005	Good forest at border Timor-Leste and Indonesia	Conservation area	Lacks search effort, might survive	c	n

*sources: **a** D. Nandika verbal comm. 2017, **b** Nandika et al., 2020, **c** eBird 2019, **d** P. Sekdes verbal comm. 2019, **e** I. Bishop *in litt*. 2019, **f** BBKSDA NTT 2017, **g** local trapper verbal comm. 2017, **h** local residents verbal comm. 2017, **i** Collar et al., 2001, **j** I. N. Mallo & F. N Mallo *in litt*. 2019, **k** IBC, 2019, **l** Trainor et al., 2008, **m** PP verbal obs., **n** local residents verbal comm. 2018, **o** A. R. M. Sianturi *in litt*. 2019

3 Protected by dragons: density surface modelling confirms large population of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea* on Komodo Island

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At the time of publication, the Yellow-crested and Citron-crested Cockatoo were still regarded as a single species.

Abstract

Intense trapping of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea* for the International pet trade has devastated its populations across Indonesia such that populations >100 individuals remain at only a handful of sites. We combined distance sampling with density surface modelling (DSM) to predict local densities and estimate total population size for one of these areas, Komodo Island, part of Komodo National Park (KNP) in Indonesia. We modelled local density based on topography (topographic wetness index) and habitat types (percentage of palm savanna and deciduous monsoon forest). Our population estimate of 1,113 (95% CI: 587–2,109) individuals on Komodo Island was considerably larger than previous conservative estimates. Our density surface maps showed cockatoos to be absent over much of the island, but present at high densities in wooded valleys. Coincidence between our DSM and a set of independent cockatoo observations was high (93%). Standardized annual counts by KNP staff in selected areas of the island showed increases in cockatoo records from <400 in 2011 to ~650 in 2017. Taken together, our results indicate that KNP, alongside and indeed because of preserving its iconic Komodo Dragons *Varanus komodoensis*, is succeeding in protecting a significant population of Indonesia’s rarest cockatoo species. To our knowledge this is the first time DSM has been applied to a Critically Endangered species. Our findings highlight the potential of DSM for locating abundance hotspots, identifying habitat associations, and estimating global population size in a range of threatened taxa, especially if independent datasets can be used to validate model predictions.

Indonesian title: Terlindungi oleh komodo: density surface modeling pada Cacatua sulphurea (Kakatua-kecil Jambul-kuning) di Pulau Komodo

Abstrak (Bahasa Indonesia)

Perburuan ilegal untuk perdagangan internasional terhadap burung *Cacatua sulphurea* (Kakatua-kecil Jambul-kuning) - yang telah dikategorikan sebagai Kritis - telah menyebabkan penurunan populasi pada hampir semua lokasi di Indonesia, sehingga populasi dengan jumlah >100 individu hanya tersisa di beberapa tempat saja. Untuk menduga kepadatan dan jumlah populasi burung ini di Pulau Komodo, (salah satu pulau di Taman Nasional Komodo; TNK), dilakukan penelitian dengan menggunakan perpaduan antara *distance sampling* dan *density surface modelling* (DSM). Permodelan kepadatan dilakukan berdasarkan topografi (*topographic wetness index*) dan tipe habitat. Dugaan populasi spesies burung ini di Pulau Komodo adalah 1.113 ekor (95% *CI* 587–2.109), lebih tinggi dari pendugaan populasi sebelumnya. Peta kepadatan (*density surface maps*) menunjukkan bahwa kakatua ini tidak terdapat di sebagian besar pulau, namun dapat ditemukan dengan kepadatan yang tinggi di lembah-lembah berhutan. Kesesuaian antara DSM dan titik pengamatan independen bernilai tinggi (93%). Penghitungan populasi tahunan oleh staf Balai TNK pada lokasi-lokasi terpilih menunjukkan adanya penambahan populasi dari <400 ekor pada tahun 2011 menjadi sekitar 650 ekor pada tahun 2017. Dengan demikian, selain melindungi satwa komodo *Varanus komodoensis,* TNK juga berhasil melindungi populasi *Cacatua sulphurea* dalam jumlah yang signifikan. Penelitian ini merupakan upaya pertama yang menggunakan DSM untuk spesies dengan status Kritis. Metoda ini berpotensi untuk menentukan pusat-pusat kepadatan populasi, mengidentifikasi asosiasi habitat, serta menduga ukuran populasi secara global bagi taksa-taksa yang terancam punah, terutama jika dataset yang independen dapat dipakai untuk memvalidasi prediksi model.

3.1 Introduction

Estimates of population sizes are cornerstones of conservation science at both the global and local scale and are instrumental in assessing extinction risks, conservation priorities and Red List status (Mace et al., 2008; Collen et al., 2011). These essential data are however lacking for a great many rare and threatened species (MacKenzie et al., 2005), which are often difficult to survey on account of their biology and/or the areas they inhabit (McDonald, 2004). Even for relatively well-known groups such as psittacines (parrots), around 75% of species are lacking abundance estimates (Marsden and Royle, 2015), a worrying statistic given that almost one-third of psittacines are currently threatened (IUCN, 2021). A variety of methods have been used to calculate population size in parrots. For very rare species it may be possible to count every individual. For others, marked or identifiable individuals allow mark-recapture or mark re-sighting methods, but these conditions are not the norm. For most species, roost counts, flyway counts and distance sampling have been used more or less effectively (Casagrande and Beissinger, 1997; Marsden and Royle, 2015). Distance sampling, despite difficulties in meeting method assumptions, has become a well-established method for estimating sizes of animal populations generally (Thomas et al., 2010) and parrots in particular (Marsden and Royle, 2015).

Local densities are a key driver of population sizes and are usually assessed as the first step before extrapolating to the whole population (e.g. Bibby et al., 2000). Estimates derived from distance sampling have become the most commonly used method, involving 84% of published parrot abundance estimates (Marsden and Royle, 2015), despite question marks over reliability related to lack of records in rare species, and idiosyncrasies of parrot behaviour (Marsden, 1999; Dénes et al., 2018). Alternative methods fail to measure absolute bird abundance (Bibby et al., 2000), face the same (and additional) challenges (Casagrande and Beissinger, 1997) or remain largely untested (Dénes et al., 2018).

While there has been considerable work on optimizing distance sampling design, field protocol, and analysis phases (Marsden, 1999; Buckland, 2006; Bächler and Liechti, 2007; Marques et al., 2007; Buckland et al., 2008; Oedekoven et al., 2015), far less attention has been paid to the process of estimating site-based or total population sizes through extrapolation of local abundances at sampled sites to larger areas or even whole ranges of threatened birds. Several extrapolation methods have been used, including simple multiplication of average density by area of study site or range (e.g. Guix et al., 1999; Marques et al., 2007), stratification by habitat type (e.g. Jones et al., 1995; Casagrande and Beissinger, 1997), and interpolation across unvisited sites (Koshkin et al., 2016). The best accepted methods are those which model local density against habitat and other relevant features (Buckland, 2006), sometimes along with spatial information, to predict densities in unvisited areas (e.g. Williamson and Homes, 1964; Somershoe et al., 2006). Apart from predicting spatial distributions and producing realistic abundance estimates, spatial modelling can also identify factors that affect abundance (Hedley and Buckland, 2004), knowledge which can then inform conservation management decisions. The spatial input for the model can either originate from covariates with a spatial distribution (e.g. habitat, elevation, distance from coast) or include the location coordinates directly (usually latitude and longitude). The functional relationships between these covariates and the response variable are rarely linear in reality, and generalized additive models (GAMs) allow this to be reflected in complex non-linear functions in the modelling process (Zuur et al., 2014).

Density surface modelling (DSM) uses GAMs (Wood, 2017) to model the point-specific density at the sampling points (or segment-specific for line transects) in a two-step approach: first it accounts for detectability using the distance sampling method; second it incorporates spatial and/or environmental covariates to explain the variation between sampling points (Hedley and Buckland, 2004; Miller et al., 2013). The resultant model can then be used to map predicted population densities within the sampling area and also, with caution, for new unsampled areas (Miller et al., 2013). DSMs are not widely used for population estimates at present but have been successfully applied to marine birds (Petersen et al., 2011; Winiarski et al., 2013, 2014; Bradbury et al., 2014), a peatland bird community (Leivits and Leivits 2016), marine mammals (de Segura et al., 2007; Gilles et al., 2011; Williams et al., 2011; Miller et al., 2013; Bravington et al., 2019) and ungulates (Harihar et al., 2014; Schroeder et al., 2014; La Morgia et al., 2015; Valente et al., 2016). Several of these studies have conservation objectives, e.g. identifying priority areas for protection (Winiarski et al., 2013) or assessment of endangered species (Ibouroi et al., 2019). While the method has been recommended as suitable for parrots (Dénes et al., 2018), we know of no application of DSMs to any parrot, or indeed to any Critically Endangered species.

The Yellow-crested Cockatoo *Cacatua sulphurea* used to occur commonly across the Lesser Sunda Islands, parts of Sulawesi and its satellites (Figure 3.1), but habitat alteration and especially excessive trapping for the international pet trade from the 1970s through the 1990s caused severe declines and local extinctions across much of its range. Thus, populations >100 individuals remain at only a handful of sites, rendering the species Critically Endangered (Broch, 1981; Cahyadin, Jepson and Arif, 1994; Cahyadin, Jepson and Syarief, 1994; Jones et al., 1995; PHPA et al., 1998; Agista et al., 2001; Collar, 2001; Eaton et al., 2015). Some 560–4,000 of the very distinctive subspecies *citrinocristata* are thought to exist in several forest patches on Sumba (Bashari and Wungo, 2011; Wungo, 2011; AR unpublished data, Figure 3.1). The population of Yellow-crested Cockatoos of the subspecies *occidentalis* in Komodo National Park (KNP, Figure 3.1), in the Lesser Sunda Islands, is also believed to be relatively large, although a survey in 2006 (Imansyah et al., 2016) diagnosed a sharp decline since 2000 (Agista et al., 2001). Both these surveys obtained minimum numbers for selected coastal valleys by direct sightings from vantage points, which cover <10% of the island's area. Here we use density surface modelling to predict local cockatoo densities across Komodo Island. We validate the models using independent sightings, investigate correlates of local abundance, and estimate the island-wide population size.

3.2 Methods

3.2.1 Study Area

Komodo Island (8°24'S-8°50'S, 119°21'E-119°49'E) is situated between Flores and Sumbawa in the Lesser Sunda Islands, Nusa Tenggara Timur, Indonesia (Figure 3.1). With an area of 340 km² and a maximum elevation of 824 meters above sea level it is the largest and highest of the islands of KNP, which was established in 1980 to protect the Komodo Dragon *Varanus komodoensis* and the terrestrial and marine biodiversity of the islands (UNESCO World Heritage Committee 1991, Lilley 1997). It now harbours one of the most important remnant populations of Yellow-crested Cockatoos, and the most important population of subspecies *C. s. occidentalis* (Collar and Marsden, 2014). Komodo is situated in one of the driest areas of Indonesia; streams do not run for most of the year and natural water sources rare (Monk et al., 1997). Large areas of the island are covered by open grassland (Auffenberg 1980) interspersed with scrubland, palm savanna, small stands of broadleaved trees and gallery forests along watercourses (Monk et al., 1997). Where larger streams meet the sea, deciduous monsoon forests cover the valley floors (Figure 3.2; Auffenberg, 1980; Monk et al., 1997). Higher altitudes (>500 m) support denser closed-canopy forest (Figure 3.2), which is often dominated by bamboo or rattan and referred to as 'quasi cloud forest' (Auffenberg 1980) or 'mossy forest' (Monk et al., 1997); this transitions downhill via sparse forest into scrubland. Following recommendations on conservation considerations (Collar et al., 2017), to avoid supplying information to potential trappers, we do not include complete maps of our results here. The complete maps of the whole island are available for bona-fide researchers or conservation purposes from the authors. They are replaced here by out of context cutouts of exemplary locations.

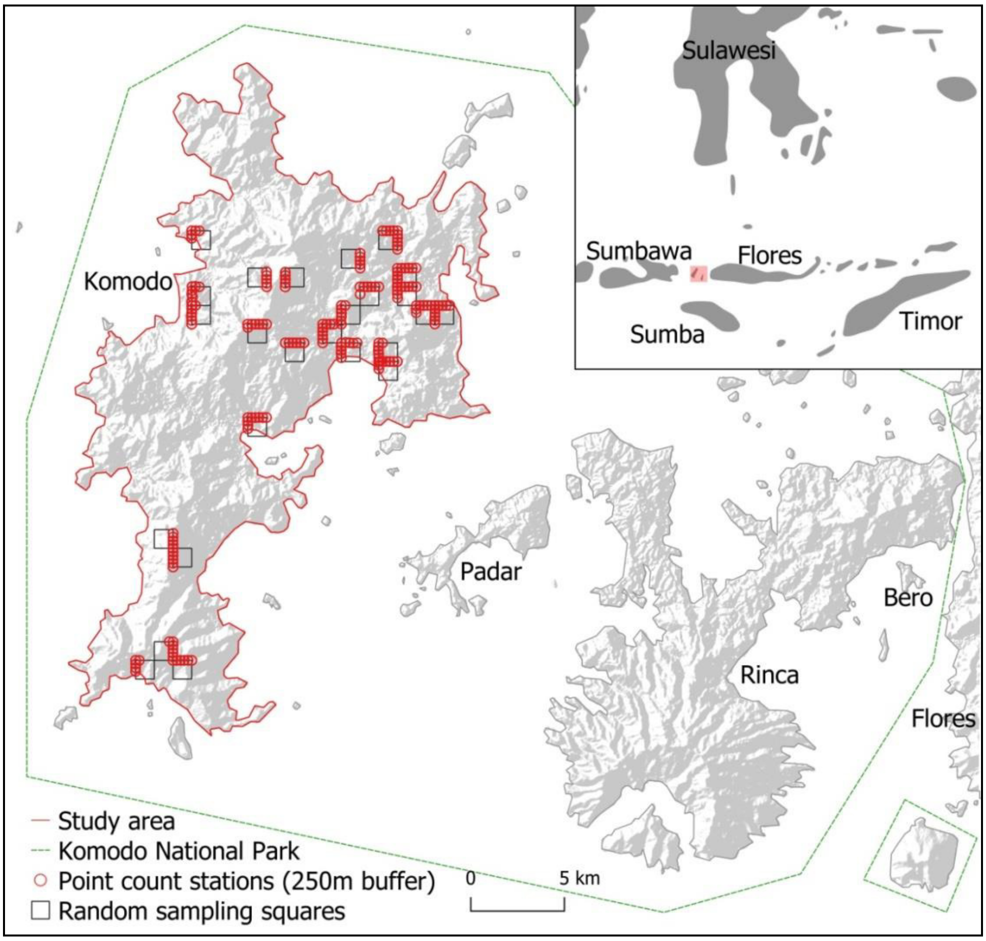


Figure 3.1: Study area Komodo Island situated in Komodo National Park, Indonesia, showing 178 point count stations, nested within 25 sampling squares, with their 250 m radius buffers.

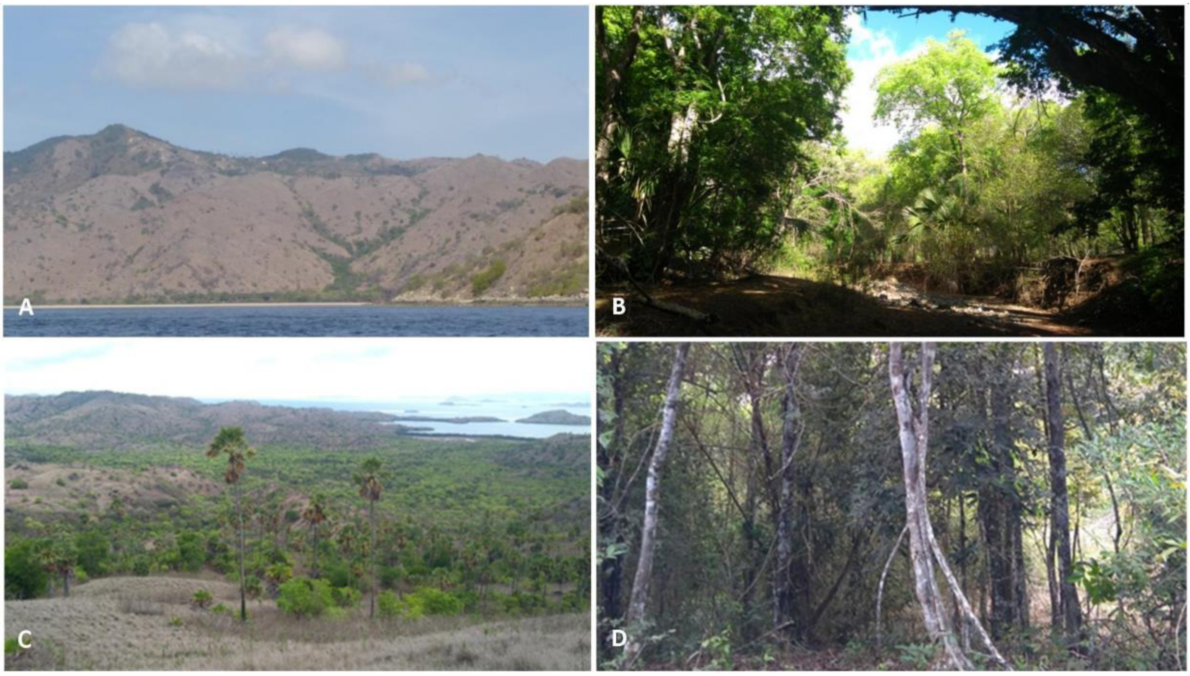


Figure 3.2: Habitat types on Komodo Island: (**A**) gallery forest among open grassland; (**B**) gallery forest; (**C**) palm savanna in front of deciduous monsoon forest; (**D**) quasi cloud forest (mossy forest, >500 m a.s.l.).

3.2.2 Point Count Distance Sampling

Komodo Island has a surface area of 340 km². We first excluded all 1x1 km² pixels that contained >50% bare grassland or sea (landcover map by Ministry of Environment and Forestry Indonesia, KLHK 2017), habitat types deemed unsuitable for cockatoos. From the remaining 152 potentially suitable pixels we randomly selected 25 for our point count distance sampling. The survey stations were located 200 m apart on the perimeter of each of these pixels (navigation by GPS). From November 6–December 14 2017 one of two experienced observers (first and second author) carried out one distance sampling point count at each of 178 stations between 06h00 and 10h00. Both observers had experience in studying cockatoos (22 and 36 months respectively) and distance sampling of cockatoos (each three months, earlier in 2017). The number of survey stations per pixel varied from 5–10 (mean = 7) depending on how many point counts could be finished within the survey time-frame. Slow walking speed in rough terrain and large distances from the nearest permitted campsite often hindered maximization of survey effort. We followed standard methods for point count distance sampling (Buckland et al., 2001, 2008; Thomas et al., 2010). Specifically we adapted the field protocol described by Marsden (1999): (a) 10-minute count durations but without a settling-down period, (b) exclusion of encounters in flight, (c) recording of flocks as clusters including the number of their individuals and (d) replacement of group sizes for purely aural detections with the average size of known groups. Given the openness of the habitat, double counting and undetected movement into the plot was not considered to be a serious risk. Nevertheless, we minimized the likelihood of double counting by only recording the second call as a new cluster if calls from the first location could still be heard or undetected movement would have been impossible due to an open topography and a good view. This was made possible by the two observers' extensive experience with the behaviour of the target species (see above). As a high proportion of aural-only contacts was expected and cockatoos tend to have gaps of several minutes between vocalizations we used a 10-minute interval which is slightly longer than the 8 minutes recommended for canopy frugivores by Lee and Marsden (2008). The minute of detection was recorded for each contact, which allowed us to assess the influence of count duration during data exploration. To minimize errors in assessing distances we used laser rangefinders (Nikon Forestry Pro) and followed protocols suggested by Buckland (2006), and Buckland et al. (2008). For example, this included measuring distances to other objects at a similar distance if the target was not directly visible. Our survey period fell in the early part of the breeding season (Agista and Rubyanto, 2001). Although all pairs observed near cavities were still prospecting, we checked the surrounding of each survey station for cavities with incubating adults. Analysis followed standard methods recommended in Buckland et al. (2001) and used a truncation distance of 350 m and open versus enclosed habitat as a two-level covariate for the detection function. We defined stations as open habitat if palm savanna, scrubland and grassland made up ≥60% of landcover within a 50 m radius). We carried out distance sampling analysis in R using package *distance* (Miller et al., 2016; R Core Team, 2019). We used ungrouped distances as recorded without manual binning. Cluster size as a covariate was very unstable against truncation distances and did not improve AIC, so no cluster size bias regression was used. Results are reported as means ± SE.

3.2.3 Environmental Variables

We used the SAGA wetness index, a topographic index predicting the soil moisture based solely on a digital elevation grid (Böhner and Selige, 2006; Conrad et al., 2015), in our case an SRTM Digital Elevation Model with ~30 x 30 m resolution. We generated a contemporary raster habitat map based on LANDSAT 8 imagery from September and October 2015–2017 (Appendix 3.1). After cloud removal and adjustment of burnt areas to the survey period, we used our field observations and Google Maps to generate training data for land-cover classification in QGIS with the semi-automatic classification plug-in (Congedo, 2016; QGIS Development Team, 2019).

We tailored the classification for use as a predictor of cockatoo detectability and density, and distinguished six habitat types (Appendix 3.2) following Auffenberg (1980) and Monk *et al.* (1997): open grassland and scrubland; palm savanna; deciduous monsoon forest including gallery forests and monsoon forests of the coastal plains; mangrove forest; quasi cloud forest >500 m; and sparse forest as a transition zone between quasi cloud forest and open habitat types. After inspection of spectral signature plots of the training units, cut-off values for critical bands were set manually to improve separation of overlapping categories (Congedo, 2016); grassland and scrubland were classified separately and pooled afterwards. Mangrove forest was not recognized properly by the classification method, so the Indonesian Ministry of Forestry's landcover data (KLHK, 2017) were used instead to correct the extent of this locally rare habitat type. We used the resulting fine-resolution habitat map to calculate percentage cover for each 250 m radius buffer around sampling stations and for each 0.25 km² prediction pixel. The two classes with the highest cockatoo encounter rates were termed 'suitable habitat' and their combined percentages were used as covariate in the DSM.

For model building we summarized the environmental covariates at the point count locations by averaging the gridded values within overlapping 250 m radius circles (sampling buffers) centred at each location. For our prediction surface, we divided each 1 km² pixel of the island into four, resulting in 1,457 prediction grid-pixels containing land. The environmental covariate values obtained at a smaller resolution were averaged within each of these 0.25 km² prediction pixels (Figure 3.3).

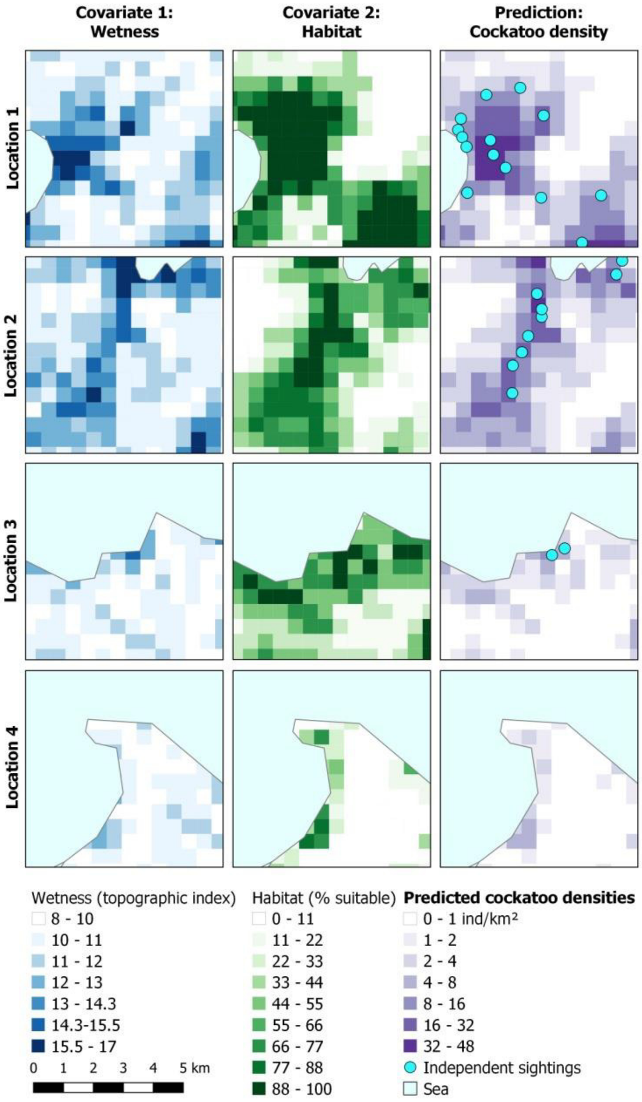


Figure 3.3: Exemplary map details of predictor values (Topographic wetness index and percentage of suitable habitat) and densities of Yellow-crested Cockatoos (individuals km^{-2}) predicted by the density surface model, on a 0.25 km² grid of Komodo Island; cross-validated with independent sightings of the species (Agista and Rubyanto 2001, Imansyah et al. 2003, 2016; Taman Nasional Komodo 2016, eBird Basic Dataset 2019). To avoid supplying information to potential trappers, locations are provided out of context, with smoothed coastlines and random orientation. The complete maps of the whole island are available for research or conservation purposes from the authors.

3.2.4 Density Surface Modelling (DSM) and Prediction

We used density surface modelling (Miller et al., 2013) to estimate population density within each 0.25 km² pixel across the island, involving the distance-based abundance estimates and the two environmental covariates. The ‘dsm’ function in R (Miller et al., 2019) is based on generalized additive models (Wood, 2017, 2019) and a detection function (Miller et al., 2016), and allows for the uncertainty of detection probability when estimating the variance of this two-step modelling process. Our full generalized additive mixed model (GAMM) included the explicit spatial term s(x,y) (a smooth function for interaction of latitude and longitude), smooth functions of the log-transformed SAGA wetness index and the arcsine transformed percentage of suitable habitat, as well as an autocorrelation structure (AR1 structure with form = ~1|sampling square) to account for the nestedness of point count stations within the sampling squares. After confirming the presence of residual autocorrelation between neighbouring stations using the 'dsm.cor' function in the *dsm* package (Miller et al., 2019), we included the random effect in all subsequent models. For the spatial term, we used a Duchon spline (Duchon, 1977) as recommended for areas with complex borders where misidentification of population hotspots is a potential problem (Miller and Wood, 2014). Smooth functions for interactions of these environmental variables were also explored but did not improve model fit. We compared Gaussian, Tweedie and quasi-Poisson distributions by inspection of residual plots. The power of the Tweedie function was estimated during fitting (Miller et al., 2013, Wood 2019). After dropping non-significant terms, we selected the best combination of the remaining terms using AIC minimization (Appendix 3.3). As a comparison of GAMMs is not straightforward, indicators are still in development (Wood, 2017) and the AIC of the lme component of the GAMM is not recommended as an indicator for model selection (Wood, 2019), we used the AIC of the equivalent GAM for this step. With the GAM component of the chosen GAMM we predicted cockatoo density and coefficient of variation (CV) for each pixel of the prediction grid. To obtain the overall variance and confidence intervals we combined the variance of the detection function and that of the GAM using the Delta method via the 'dsm.var.gam' function (Seber, 1982; Miller et al., 2019).

3.2.5 Validating DSM Predictions Using Independent Cockatoo Sightings

We used three independent sources of cockatoo observations that were not included in our DSM analysis to validate the spatial predictions of our DSM. The first source was: annual monitoring by KNP staff on flight paths and roosts (2012–2017, 16 locations, KNP unpublished data). The second source was citizen science observations from eBird (eBird Basic Dataset, 2019), from which we selected those records where the observer had specified a precise location on the map instead of allocating it to a pre-defined hotspot, the national park or the island in general (2004–2017, seven locations). The third source was cockatoo records from survey reports, involving nine locations from valley-floor surveys in 2000 (Agista and Rubyanto, 2001) and ten locations from a general fauna survey in 2002 (Imansyah et al., 2003), which were partly confirmed again by cockatoo valley-floor surveys in 2005 and 2006 (Imansyah et al., 2005, 2016). We used only one independent sighting location per prediction pixel. We checked coincidence of the model's local density predictions against these known positives (regarding densities ≥1 individual km^{-2} as predicted presence).

3.3 Results

Cockatoo groups were observed at 48 of the 178 point count locations, with an encounter rate of 0.38 groups per point count (after exclusion of flying individuals and truncation). Encounter rates were highest in deciduous monsoon forest (0.91 ± 0.17, *n*=22) and palm savanna (0.62 ± 0.11, *n*=86) and lowest in the remaining habitat types (0.19 ± 0.10, *n*=26 in grass- and scrubland, 0.06 ± 0.04, *n*=32 in sparse forest, 0.00, *n*=12 in quasi cloud forest, and no data in mangrove forest). The average number of individuals in each group seen was 2.61 individuals (SE=0.49, *n*=31, before truncation). Detection probabilities were described best by a hazard-rate detection function with habitat openness as a covariate (Table 3.1; Appendix 3.4).

Table 3.1: Comparison of half-normal and hazard-rate detection functions with and without habitat openness as a covariate. ΔAIC between the two top models was small but visual inspection of the detection function confirmed the choice of a hazard-rate key detection function with openness as two-level covariate, although resulting confidence intervals were slightly larger than with the equivalent half-normal model. (C-vM: Cramér-von Mises goodness-of-fit test, ΔAIC: difference in Akaike Information Criterion to best model)

Key function	Formula	df	C-vM *p*-value	Average detectability	SE(average detectability)	ΔAIC
Hazard-rate	**~openness**	**3**	**0.98**	**0.247**	**0.050**	**0**
Half-normal	~openness	2	0.77	0.224	0.030	1.0
Half-normal	~1	1	0.63	0.252	0.031	8.4
Hazard-rate	~1	2	0.76	0.248	0.055	9.0

The DSM with the best fit contained two smooth terms with thin plate regression splines of two environmental covariates: SAGA wetness index (log-transformed, edf=1, *F*=8.08, *p*=0.005, Appendix 3.3) and percentage cover by suitable habitat (palm savanna and deciduous monsoon forest combined and arcsine transformed, edf=1, *F*=7.70, *p*=0.006; Figure 3.3, supplemental material Appendix 3.5). The spatial term was excluded as it was not significant ($p > 0.3$ regardless of spline base, as long as the model accounted for the autocorrelation structure of the points within sampling squares). This best model predicted high cockatoo densities (>8 individuals km^{-2}, locally up to 48 individuals km^{-2}) for two forested valleys (Figure 3.3) where cockatoos are known to be common and where we had high encounter rates at point counts (2.77 ± 0.49 individuals per station, *n*=35, presence at 32, up to six groups at one station) and flock sizes up to 60 individuals in incidental observations. High densities were also predicted for a dry river valley and a coastal valley which we did not sample, along with moderate densities for several other unsampled locations (Figure 3.3). Cross-checking these locations with the independent sightings showed that the model had predicted almost all known cockatoo hotspots, and 93% of the 42 independent presence points. The three false negatives were very close (<85 m) to pixels with predicted cockatoo presence. The mapped coefficient of variation showed that CV was high in areas with predicted low densities and low in high-density areas. Totalling the modelled population densities over the whole island resulted in a population estimate for Komodo Island of 1,113 individuals (95% CI: 587–2,109; Figure 3.3).

3.4 Discussion

We used density surface modelling (Miller et al., 2013) of local abundance estimates from distance sampling to estimate the population of the Critically Endangered Yellow-crested Cockatoo on the 340 km^2 island of Komodo. Our estimated population size of 1,113 individuals and the spatial density predictions are in line with independent KNP Authority monitoring, which recorded direct sightings of over 600 individuals (KLHK and DJ KSDAE, 2018) when selectively covering <10% (albeit the most suitable areas) of the island. In their preference for palm savanna and deciduous monsoon forest Komodo's cockatoos resemble conspecifics on other islands, whereas their near-complete absence from quasi cloud forest is unexpected, as similar habitat types and altitudes are readily used on other islands (e.g. Jones et al., 1995; Trainor et al., 2008). While the absence from quasi cloud forest could be seasonal, there are no incidental sightings reported for other times of the year. Mangrove forest—an important roosting habitat for cockatoos on Komodo (Agista and Rubyanto, 2001)—did not feature in our samples or encounters because our survey times were deliberately chosen to avoid daily periods of high cockatoo mobility and commenced after the cockatoos had travelled away from their roosts early in the morning. Although the numbers are not directly comparable we calculated a local abundance estimate for the pixels overlapping the valley-floor study areas used by Imansyah et al. (2016). For these valleys our model predicts a population size of 397 individuals, which is more than double the number of direct sightings in September and October 2005/2006 (Imansyah et al., 2016) but not far above the 340 individuals sighted in September–October 2000 in those areas (Agista and Rubyanto, 2001).

Table 3.2: Minimum estimate of Yellow-crested Cockatoo numbers from annual monitoring by Komodo National Park authorities derived by summing direct encounters from simultaneous valley-floor counts (Taman Nasional Komodo 2016, A. Kefi *in litt.* 2019, KLHK and DJ KSDAE 2018).

Island(s)	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**
Komodo	382	406	500	524	547	522	641	660	733
Rinca & Bero	111	136	149	122	148	160	141	151	150
Total	**493**	**542**	**649**	**646**	**695**	**682**	**782**	**811**	**883**

Our results strongly suggest that the population on Komodo Island is substantial, and we found no evidence that the steep decline reported for the early 2000s has continued (Imansyah et al., 2016). Direct counts collected annually by experienced KNP rangers from vantage points overlooking six coastal valleys show an increase from <400 recorded cockatoos for Komodo Island in 2011 to 641 in 2017 (Table 3.2; Taman Nasional Komodo, 2016; unpublished data KNP). This is evidence that the population has certainly been stable and probably increasing over the last six years. As such, in addition to providing protection to the iconic Komodo Dragon (Purwandana et al., 2014), KNP appears to be working as a long-term stronghold for the cockatoo. This park's population is by far the largest of the subspecies *occidentalis* and became the largest for the entire species when the distinctive *C. s. citrinocristata* was accorded species rank (BirdLife International, 2022). The remoteness and topography of Komodo Island and its fear-inducing dragon appear to provide some natural protection from habitat destruction (e.g. fires and conversion to agriculture) and illegal trapping, but enforcement of legal protection for the cockatoo by park authorities has undoubtedly played an important role in the current situation. Poor soils, steep terrain and lack of water mean that there has never been much incentive for the single community on the island, which traditionally relied almost exclusively on fishing, to convert land for agriculture (Singleton et al., 2002; Pannell, 2013). The Komodo Dragons attract a stream of paying visitors (~180,000 in 2018, CNN Travel, 2019) and therefore KNP is relatively well resourced (Hakim, 2017; KLHK and DJ KSDAE, 2018). It has twelve field stations, 120 staff (including a permanent presence of ca. 30 rangers on the islands), several speedboats, and provision for regular patrols and ecological monitoring (Taman Nasional Komodo, 2016). Although patrols discover a few poaching incidents every year, these mainly concern marine life, and occasionally deer (two cases of deer 2009 – 2015, Taman Nasional Komodo, 2016). When over 40 young Komodo Dragons were discovered in trade in 2019, they indicatively turned out to originate from the species' scarce populations outside KNP's borders (Gokkon, 2019). The park has the support of local communities (Walpole and Goodwin, 2001), which largely depend economically on tourism (Walpole and Goodwin, 2000, 2001; Nurilma et al., 2019). Although KNP's fame, protection, visitors, income and acceptance are mainly owed to Komodo Dragons and marine life (UNESCO World Heritage Committee, 1991), the cockatoos clearly benefit from the protection as well. KNP's success could be used to apply similar methods and resources in other protected areas where formal protection has yet to increase cockatoo numbers.

Based on just five weeks of fieldwork, and despite the poor accessibility of most of the island and a complex mosaic of habitats, we succeeded in modelling the population of this difficult-to-count species with a distribution map, suitable for conservation practitioners, local parrot densities that correspond to those of other parrots for the respective habitat types (Marsden and Royle, 2015) and confidence intervals narrow enough to be used for assessing conservation status and viability. An independent dataset of cockatoo sightings gave us the opportunity to validate our predictions. During the modelling process this validation process in fact prevented us from accepting a candidate model which neglected residual spatial autocorrelation and instead included the spatial term as a predictor (Gaspard et al., 2019). This model, although favoured according to information theoretic criteria, scored very poor hit-rates on the independent sightings dataset, as it was dominated by the spatial term. This might be important for other researchers, as >80% of ecological and biogeographical modelling studies do not account for spatial autocorrelation (Gaspard et al., 2019), which can lead to estimation-errors of coefficients of 25% on average

(Dormann, 2007). Accounting for autocorrelation was particularly important for our clustered sampling design as opposed to studies where sampling is able to cover the whole prediction surface well. However, for parrot species and other rare, highly mobile birds in fragmented rugged habitats, sampling each inhabited patch will often be impractical.

As a two-step modelling process, the DSM required that we combine the variances of both models (detection function and GAM) to obtain a realistic measure of the variance of our prediction. We used the Delta method (Seber, 1982; Miller et al., 2019) for this purpose, ignoring a potential lack of independence between the two steps (stemming from the covariate in the detection function), because the more advanced variance propagation method (Williams et al., 2011) is not available for mixed models, and bootstrapping (Hedley and Buckland, 2004) should not be used if smooth functions are involved in the model formula (Miller et al., 2013; Bravington et al., 2019). In general, we were forced by the combination of point transects, a covariate in the detection function and an autocorrelation structure in the DSM to use mixed models (GAMMs instead of GAMs), for which more recent developments in the statistical software have yet to be incorporated. Optimizing adjustments (e.g. use of variance propagation or restricted maximum likelihood) might have increased the precision of our estimates, but spatial density predictions and estimated total population size were so stable across models and modelling engines that final results are unlikely to have differed.

Red List assessments of extinction risk currently rely heavily on population sizes and areas of occupancy (SSC IUCN, 2001), but estimating these indicators for threatened species is often problematic as available resources limit precision and reliability of results. DSMs have the potential to provide these data based on limited sampling effort (La Morgia et al., 2015), because they cope well with non-random sampling designs (Miller et al., 2013), and can still predict absolute abundances and distributions (Hedley and Buckland, 2004). They account for detection probability and utilize spatial environmental information which is often available remotely. DSMs can also identify habitat associations or other ecological dependencies and predict population hotspots and range limits which can be cross-validated with independent opportunistic datasets. However, despite their broad applicability for population estimates, DSMs have limitations as well: survey designs still need to cover the study area sufficiently (geographical extent, full range of densities including absence, all relevant habitat types and altitudes; Miller et al., 2013) and reach the minimum number of contacts for reliably estimating a detection function (Buckland et al., 2001). DSM can only make useful predictions if the population's limiting factors can be captured directly or indirectly by spatially referenced covariates, and the method only develops its full potential if these data are available remotely. Interpolated densities for unsampled areas between samples are predicted with confidence whereas extrapolation to new areas outside the sample range require more caution (Miller et al., 2013). Consequently, predictions across islands (or functional islands such as protected areas or areas which span biogeographical boundaries) that are not included at the modelling stage are risky, as new areas might be subject to unconsidered influences. In our case we decided against using the model from Komodo Island to estimate the neighbouring cockatoo subpopulation on Rinca Island because additional factors such as introduced predators and accessibility for potential trappers from Flores could not be accounted for.

Cockatoos in KNP are a showcase for the potential of a two-level monitoring approach, where annual trend assessment with relatively simple methods could be used to indicate optimal timing of high-effort abundance surveys like distance sampling with DSM. In future large gaps in published abundance data, coinciding with suspected population declines as in the decades before our study (Imansyah et al., 2016), could be prevented if annual monitoring data are accessible to conservation practitioners who can then trigger more intensive research as soon as a decline becomes apparent and in time for potential mitigations. We found DSM to be an efficient and effective estimator of population size and distribution in the Yellow-crested Cockatoo, and suggest its use for larger populations of the species (e.g. on Sumba and in Timor Leste), provided that region-specific limiting factors such as trapping pressure can be accounted for. The useful predictions and broad applicability of DSM give it an edge over alternative methods with similar survey effort and make it a powerful tool for estimating population sizes of threatened island species.

References

Agista, D. and Rubyanto, D. (2001) *Telaah awal status, penyebaran, dan populasi kakatua kecil jambul kuning,* Cacatua sulphurea parvula*: di Taman Nasional Komodo, Nusa Tenggara Timur*. Bogor, Indonesia: Birdlife International Indonesia Programme.

Agista, D., Sumardin, Hamid, A., Mallo, F. N., Alam, S., Harjun and Mamengko, C. (2001) *Status Kakatua-kecil Jambul-kuning di Sulawesi Tenggara dan Sulawesi Tengah*. Bogor, Indonesia: Birdlife International - Indonesia Programme.

Auffenberg, W. (1980) 'The herpetofauna of Komodo with notes on adjacent areas.' *Bulletin of Florida State Museum, Biological Sciences*, 25(2) pp. 39–156.

Bächler, E. and Liechti, F. (2007) 'On the importance of g (0) for estimating bird population densities with standard distance sampling: implications from a telemetry study and a literature review.' *Ibis*, 149(4) pp. 693–700.

Bashari, H. and Wungo, E. (2011) *Survey burung di Taman Nasional Manupeu Tanah Daru, Sumba, Indonesia*. Borgor, Indonesia.

Bibby, C. J., Burgess, N. D., Hill, D. A. and Mustoe, S. (2000) *Bird census techniques*. 2nd ed., Amsterdam, Netherlands: Academic Press.

BirdLife International (2022) *Species Factsheet* Cacatua sulphurea. [Online] [Accessed on 6th January 2022] http://www.birdlife.org.

Böhner, J. and Selige, T. (2006) 'Spatial prediction of soil attributes using terrain analysis and climate regionalisation.' *In* Böhner, J., McCloy, K. R., and Strobl, J. (eds) *SAGA - Analysis and Modelling Applications*. Göttingen, Germany: Göttinger Geographische Abhandlungen, pp. 13–28.

Bradbury, G., Trinder, M., Furness, B., Banks, A. N., Caldow, R. W. G. and Hume, D. (2014) 'Mapping seabird sensitivity to offshore wind farms.' Magar, V. (ed.) *PLoS ONE*, 9(9) p. e106366.

Bravington, M. V, Miller, D. L. and Hedley, S. L. (2019) 'Reliable variance propagation for spatial density surface models,' July.

Broch, H. B. (1981) 'Cultural variation on the islands in the sea of Flores.' *Archipel*, 22(1) pp. 43–53.

Buckland, S. T. (2006) 'Point-transect surveys for songbirds: robust methodologies.' *The Auk*, 123(2) pp. 345–357.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. (2001) *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.

Buckland, S. T., Marsden, S. J. and Green, R. E. (2008) 'Estimating bird abundance: making methods work.' *Bird Conservation International*, 18 pp. 91–108.

Cahyadin, Y., Jepson, P. and Arif, S. (1994) *The status of* Cacatua sulphurea abbotti *on the Masalembo Islands*. Bogor: PHPA/BirdLife International - Indonesia Programme.

Cahyadin, Y., Jepson, P. and Syarief, M. (1994) *A rapid status assessment of* Cacatua sulphurea sulphurea *in South Sulawesi Province*. Bogor, Indonesia: PHPA/BirdLife International - Indonesia Programme.

Casagrande, D. G. and Beissinger, S. R. (1997) ‘Evaluation of four methods for estimating parrot population size.’ *The Condor*, 99(2) pp. 445–457.

CNN Travel (2019) *Indonesia cancels plan to ban tourists from Komodo Island*. CNN Travel. [Online] [Accessed on 27th November 2019] https://edition.cnn.com/travel/article/indonesia-komodo-islands-reverse-tourist-ban-intl-hnk/index.html.

Collar, N. J. (2001) ‘Yellow-crested Cockatoo *Cacatua sulphurea*.’ *In* Collar, N. J., Andreev, A. V, Chan, S., Crosby, M. J., Subramanya, S., and Tobias, J. A. (eds) *Threatened birds of Asia: the BirdLife International Red Data Book*. Cambridge: BirdLife International, pp. 1643–1661.

Collar, N. J., Eaton, J. A. and Sykes, B. (2017) ‘Conservation and the redaction of locality data.’ *BirdingASIA*, 28 pp. 3–4.

Collar, N. J. and Marsden, S. J. (2014) ‘The subspecies of Yellow-crested Cockatoo *Cacatua sulphurea*.’ *Forktail*, (30) pp. 23–27.

Collen, B., McRae, L., Deinet, S., De Palma, A., Carranza, T., Cooper, N., Loh, J. and Baillie, J. E. M. (2011) ‘Predicting how populations decline to extinction.’ *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1577) pp. 2577–2586.

Congedo, L. (2016) ‘Semi-automatic classification plugin documentation.’ *QGIS-plugin* p. 29.

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V. and Böhner, J. (2015) ‘System for Automated Geoscientific Analyses (SAGA) v. 2.1.4.’ *Geoscientific Model Development*, 8(7) pp. 1991–2007.

Dénes, F. V, Tella, J. L. and Beissinger, S. R. (2018) ‘Revisiting methods for estimating parrot abundance and population size.’ *Emu-Austral Ornithology*, 118(1) pp. 67–79.

Dormann, C. F. (2007) ‘Effects of incorporating spatial autocorrelation into the analysis of species distribution data.’ *Global Ecology and Biogeography*, 16(2) pp. 129–138.

Duchon, J. (1977) ‘Splines minimizing rotation-invariant semi-norms in Sobolev spaces.’ *In Constructive theory of functions of several variables*. Berlin, Germany: Springer, pp. 85–100.

Eaton, J. A., Shepherd, C. R., Rheindt, F. E., Harris, J. B. C., van Balen, S. B., Wilcove, D. S. and Collar, N. J. (2015) ‘Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia.’ *Forktail*, 31 pp. 1–12.

eBird Basic Dataset (2019) ‘Version: EBD_relMay-2019.’ Ithaca, New York: Cornell Lab of Ornithology.

Gaspard, G., Kim, D. and Chun, Y. (2019) ‘Residual spatial autocorrelation in macroecological and biogeographical modeling: A review.’ *Journal of Ecology and Environment*, 43(1).

Gilles, A., Adler, S., Kaschner, K., Scheidat, M. and Siebert, U. (2011) ‘Modelling harbour porpoise seasonal density as a function of the German Bight environment: implications for management.’ *Endangered Species Research*, 14(2) pp. 157–169.

Gokkon, B. (2019) *Indonesia arrests 7 for allegedly selling Komodo dragons over Facebook*. Mongaby. Jakarta. [Online] [Accessed on 27th November 2019] https://news.mongabay.com/2019/04/indonesia-arrests-7-for-allegedly-selling-komodo-dragons-over-facebook/.

Guix, J. C., Martín, M. and Mañosa, S. (1999) ‘Conservation status of parrot populations in an Atlantic rainforest area of southeastern Brazil.’ *Biodiversity and Conservation*, 8(8) pp. 1079–1088.

Hakim, L. (2017) 'Managing biodiversity for a competitive ecotourism industry in tropical developing countries: New opportunities in biological fields.' *In AIP Conference Proceedings*. American Institute of Physics Inc., p. 030008.

Harihar, A., Pandav, B. and MacMillan, D. C. (2014) 'Identifying realistic recovery targets and conservation actions for tigers in a human-dominated landscape using spatially explicit densities of wild prey and their determinants.' Robertson, M. (ed.) *Diversity and Distributions*, 20(5) pp. 567–578.

Hedley, S. L. and Buckland, S. T. (2004) 'Spatial models for line transect sampling.' *Journal of Agricultural, Biological, and Environmental Statistics*, 9(2) pp. 181–199.

Ibouroi, M. T., Hassane, N. A., Moindjié, S., Ombade, M., Mohamed, N., Saidou, M. H., Abderemane, K., Cheha, A. and Chiffard, J. (2019) 'The first comprehensive survey of habitat suitability and population size for the endangered Grande Comoro Scops Owl (*Otus pauliani*): implications for its conservation.' *Journal of Ornithology*, 160(4) pp. 1121–1132.

Imansyah, M. J., Anggoro, D. G., Yangpatra, N., Hidayat, A. and Benu, Y. J. (2005) *Sebaran dan karakteristik pohon sarang kakatua jambul kuning (*Cacatua sulphurea parvula*) di pulau Komodo, Taman Nasional Komodo*. Denpasar, Indonesia: CRES Komodo Project, TN Komodo.

Imansyah, M. J., Purwandana, D., Ariefiandy, A., Benu, Y. J., Jessop, T. S. and Trainor, C. R. (2016) 'Valley-floor censuses of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea occidentalis* on Komodo Island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period.' *Forktail*, 32 pp. 66–72.

Imansyah, M. J., Purwandana, D., Rudiharto, H. and Jessop, T. S. (2003) *Survey potensi hidupan liar terestrial di Pulau Komodo, Taman Nasional Komodo 2002*. Labuan Bajo, Indonesia: Zoological Society of San Diego, Taman Nasional Komodo, The Nature Conservancy.

IUCN (2021) *The IUCN Red List of Threatened Species. Version 2021-3*. Gland, Switzerland: IUCN. [Online] [Accessed on 12th February 2022] https://www.iucnredlist.org/species/22684777/131874695#population.

Jones, M. J., Linsley, M. D. and Marsden, S. J. (1995) 'Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia.' *Bird Conservation International*, 5(01) pp. 21–52.

KLHK (2017) *Penutupan lahan Indonesia*. Landcover map Indonesia by WebGIS Ministry of Environment and Forestry. [Online] [Accessed on 15th October 2017] http://webgis.menlhk.go.id:8080/kemenhut.

KLHK and DJ KSDAE (2018) *Statistik Direktorat Jenderal Konservasi Sumbar Daya Alam dan Ekosistem Tahun 2017*. Jakarta, Indonesia: Kementerian Lingkungan Hidup dan Kehutanan.

Koshkin, M. A., Burnside, R. J., Collar, N. J., Guilherme, J. L., Showler, D. A. and Dolman, P. M. (2016) 'Effects of habitat and land use on breeding season density of male Asian Houbara *Chlamydotis macqueenii*.' *Journal of Ornithology*, 157(3) pp. 811–823.

Lee, D. C. and Marsden, S. J. (2008) 'Adjusting count period strategies to improve the accuracy of forest bird abundance estimates from point transect distance sampling surveys.' *Ibis*, 150(2) pp. 315–325.

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akçakaya, H. R., Leader-Williams, N., Milner-Gulland, E. J. and Stuart, S. N. (2008) 'Quantification of extinction risk: IUCN's system for classifying threatened species.' *Conservation biology*, 22(6) pp. 1424–1442.

MacKenzie, D. I., Nichols, J. D., Sutton, N., Kawanishi, K. and Bailey, L. L. (2005) 'Improving inferences in population studies of rare species that are detected imperfectly.' *Ecology*, 86(5) pp. 1101–1113.

Marques, T. A., Thomas, L., Fancy, S. G. and Buckland, S. T. (2007) ‘Improving estimates of bird density using multiple-covariate distance sampling.’ Handel, C. M. (ed.) *The Auk*, 124(4) pp. 1229–1243.

Marsden, S. J. (1999) ‘Estimation of parrot and hornbill densities using a point count distance sampling method.’ *Ibis*, 141(3) pp. 327–390.

Marsden, S. J. and Royle, K. (2015) ‘Abundance and abundance change in the world’s parrots.’ *Ibis*, 157(2) pp. 219–229.

McDonald, L. L. (2004) ‘Sampling rare populations.’ *In* Thompson, W. L. (ed.) *Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters*. Island Press Washington, DC, USA, pp. 11–42.

Miller, D. L., Burt, M. L., Rexstad, E. A. and Thomas, L. (2013) ‘Spatial models for distance sampling data: Recent developments and future directions.’ Gimenez, O. (ed.) *Methods in Ecology and Evolution*, 4(11) pp. 1001–1010.

Miller, D. L., Rexstad, E., Burt, L., Bravington, M. V and Hedley, S. (2019) ‘dsm: Density Surface Modelling of distance sampling data.’

Miller, D. L., Rexstad, E., Thomas, L., Marshall, L. and Laake, J. L. (2016) ‘Distance sampling in R.’ *BioRxiv* p. 63891.

Miller, D. L. and Wood, S. N. (2014) ‘Finite area smoothing with generalized distance splines.’ *Environmental and Ecological Statistics*, 21(4) pp. 715–731.

Monk, K., De Fretes, Y. and Reksodiharjo-Lilley, G. (1997) *Ecology of Nusa Tenggara and Maluku*. 1st ed., Oxford, UK: Oxford University Press.

La Morgia, V., Calmanti, R., Calabrese, A. and Focardi, S. (2015) ‘Cost-effective nocturnal distance sampling for landscape monitoring of ungulate populations.’ *European Journal of Wildlife Research*, 61(2) pp. 285–298.

Nurilma, A. D., Sjarmidi, A. and Yustiana, Y. (2019) ‘Economic valuation of Komodo Dragon (Varanus komodoensis, Ouwens 1912) and its contribution to locally-generated revenue of West Manggarai Regency, East Nusa Tenggara Province.’ *In IOP Conference Series: Earth and Environmental Science*. Bandung, Indonesia, p. 12001.

Oedekoven, C. S., Laake, J. L. and Skaug, H. J. (2015) ‘Distance sampling with a random scale detection function.’ *Environmental and Ecological Statistics*, 22(4) pp. 725–737.

Pannell, S. (2013) ‘Nature and culture in a global context: A case study from World Heritage Listed Komodo National Park, eastern Indonesia.’ *Terra Australis 36* pp. 53–63.

Petersen, I. K., MacKenzie, M. L., Rexstad, E., Wisz, M. S. and Fox, A. D. (2011) *Comparing pre- and post-construction distributions of long-tailed ducks Clangula hyemalis in and around the Nysted offshore wind farm, Denmark : a quasi-designed experiment accounting for imperfect detection, local surface features and autocorrelation*. St Andrews, UK: University of St Andrews.

PHPA, LIPI and BirdLife International-IP (1998) *Species recovery plan Yellow-crested Cockatoo*. Bogor, Indonesia: PHPA/LIPI/BirdLife International - Indonesia Programme.

Purwandana, D., Ariefiandy, A., Imansyah, M. J., Rudiharto, H., Seno, A., Ciofi, C., Fordham, D. A. and Jessop, T. S. (2014) ‘Demographic status of Komodo dragons populations in Komodo National Park.’ *Biological Conservation*, 171, March, pp. 29–35.

QGIS Development Team (2019) ‘QGIS Geographic Information System.’ Zanzibar, Tanzania: Open Source Geospatial Foundation Project.

R Core Team (2019) ‘R: A language and environment for statistical computing.’ Vienna, austria: R Foundation for Statistical Computing.

Schroeder, N. M., Matteucci, S. D., Moreno, P. G., Gregorio, P., Ovejero, R., Taraborelli, P. and Carmanchahi, P. D. (2014) ‘Spatial and seasonal dynamic of abundance and distribution of Guanaco and livestock: insights from using density surface and null models.’ Festa-Bianchet, M. (ed.) *PLoS ONE*, 9(1) p. e85960.

Seber, G. A. F. (1982) *The estimation of animal abundance and related parameters*. 2nd ed., New York: McMillan Pub.Co.

de Segura, A. G., Hammond, P. S., Cañadas, A. and Raga, J. A. (2007) ‘Comparing cetacean abundance estimates derived from spatial models and design-based line transect methods.’ *Marine Ecology Progress Series*, 329, January, pp. 289–299.

Singleton, J., Sulaiman, R. and TNC staff (2002) *Environmental assessment study – Komodo National Park Indonesia*. Bali, Indonesia: The Nature Conservancy-SE Asia Center for Marine Protected Areas.

Somershoe, S. G., Twedt, D. J. and Reid, B. (2006) ‘Combining Breeding Bird Survey and distance sampling to estimate density of migrant and breeding birds.’ *The Condor*, 108(3) pp. 691–699.

SSC IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. Gland, Switzerland and Cambridge, UK: Species Survival Commission. IUCN. [Online] http://www.iucnredlist.org/apps/redlist/static/categories_criteria_3_1.

Taman Nasional Komodo (2016) *Statistik Balai Taman Nasional Komodo tahun 2009-2015*. Labuan-Bajo, Indonesia: Kementerian Lingkungan Hidup dan Kehutanan.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B. B., Marques, T. A. and Burnham, K. P. (2010) ‘Distance software: design and analysis of distance sampling surveys for estimating population size.’ *Journal of Applied Ecology*, 47(1) pp. 5–14.

Trainor, C. R., Santana, F., Pinto, P., Xavier, A. F., Safford, R. and Grimmett, R. (2008) ‘Birds, birding and conservation in Timor-Leste.’ *Birding Asia*, 9(2008) pp. 16–45.

UNESCO World Heritage Committee (1991) *Convention concerning the protection of the world cultural and natural heritage*. [Online] [Accessed on 25th November 2019] https://whc.unesco.org/en/list/609/.

Valente, A. M., Marques, T. A., Fonseca, C. and Torres, R. T. (2016) ‘A new insight for monitoring ungulates: density surface modelling of roe deer in a Mediterranean habitat.’ *European Journal of Wildlife Research*, 62(5) pp. 577–587.

Walpole, M. J. and Goodwin, H. J. (2000) ‘Local economic impacts of dragon tourism in Indonesia.’ *Annals of Tourism Research*, 27(3) pp. 559–576.

Walpole, M. J. and Goodwin, H. J. (2001) ‘Local attitudes towards conservation and tourism around Komodo National Park, Indonesia.’ *Environmental Conservation*, 28(2) pp. 160–166.

Williams, R., Hedley, S. L., Branch, T. A., Bravington, M. V., Zerbini, A. N. and Findlay, K. P. (2011) ‘Chilean Blue Whales as a case study to illustrate methods to estimate abundance and evaluate conservation status of rare species.’ *Conservation Biology*, 25(3) pp. 526–535.

Williamson, K. and Homes, R. C. (1964) ‘Methods and preliminary results of the Common Birds Census, 1962--63.’ *Bird Study*, 11(4) pp. 240–256.

Winiarski, K. J., Burt, M. L., Rexstad, E., Miller, D. L., Trocki, C. L., Paton, P. W. C. and McWilliams, S. R. (2014) ‘Integrating aerial and ship surveys of marine birds into a combined density surface model: A case study of wintering Common Loons.’ *The Condor: Ornithological Applications*, 116(2) pp. 149–161.

Winiarski, K. J., Miller, D. L., Paton, P. W. C. and McWilliams, S. R. (2013) ‘Spatially explicit model of wintering common loons: conservation implications.’ *Marine Ecology Progress Series*, 492, October, pp. 273–283.

Wood, S. (2019) ‘mgcv: Mixed GAM computation vehicle with automatic smoothness estimation.’ R-project.

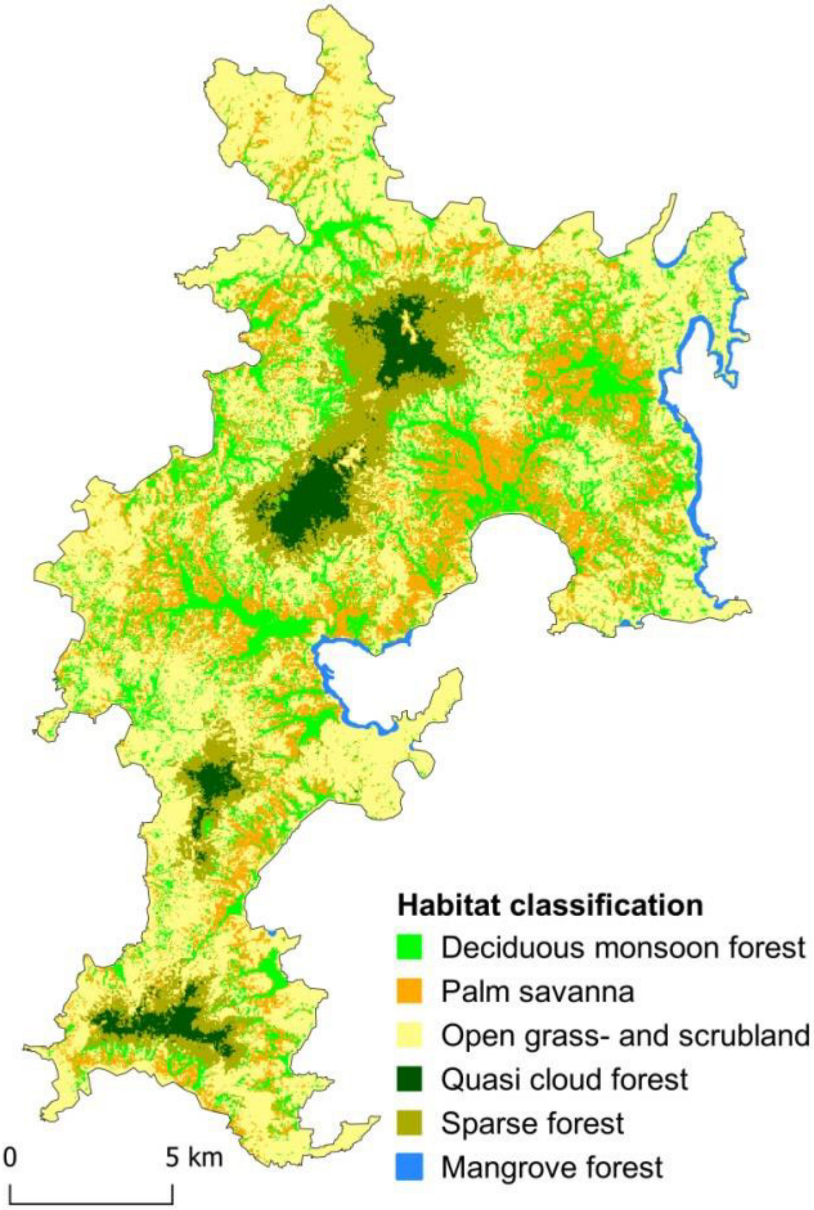
Wood, S. N. (2017) *Generalized additive models: an introduction with R*. 2nd ed., London, UK: Chapman and Hall/CRC.

Wungo, E. (2011) *Laporan survei populasi paruh bengkok terancam punah* Cacatua sulphurea citrinocristata*, Sumba, Nusa Tenggara Timur*. Bogor, Indonesia: Burung Indonesia.

Zuur, A., Ieno, E. N. and Saveliev, A. A. (2014) *A beginner’s guide to Generalized Additive Mixed Models with R*. Newburgh, UK: Highland Statistics Ltd.

Appendices

Appendix 3.1: Komodo Island habitat classification derived from supervised classification of LANDSAT 8 satellite images with training data from Google Maps. Forest types follow Auffenberg (1980) and Monk et al. (1997) with addition of sparse forest as a traditional zone between quasi cloud forest and open habitat types. Mangrove forest was not distinguished in the supervised classification and was added afterwards (KLHK 2017).



Appendix 3.2: Habitat type classification on Komodo Island modified from Auffenberg (1980) and Monk et al. (1997).

Habitat class (this study)	**Class in Auffenberg 1980**	**Class in Monk et al. 1997**	**Location**	**Main characteristics**	**Cockatoo observations at point counts***	**Cover on Komodo Island**
Open grass- & scrubland	steppe	savanna	mostly lowlands	treeless	6)	51.5%
Palm savanna	savanna forest	savanna	large lowland areas and many small fragments	open with tall *Borassus* and *Corypha* palms	37	18.6%
Deciduous monsoon forest	deciduous monsoon forest	gallery forest, dry monsoon forest, moist deciduous monsoon forest	along rivers and in coastal valleys	closed canopy, *Tamarindus*, *Sterculia* and *Bredelia*	25	16.5%
Mangrove forest	mangrove forest	mangrove forest	tidal zone,	mangrove species	0	0.5%
Quasi cloud forest	quasi cloud forest	mossy forest	>500 m	moss and lichen on trees, bamboo, rattan	0	3.7%
Sparse forest	transitional zone to quasi cloud forest	not mentioned	<500 m, transition zone from quasi cloud forest to scrubland	no closed canopy, bamboo groves	0	9.2%

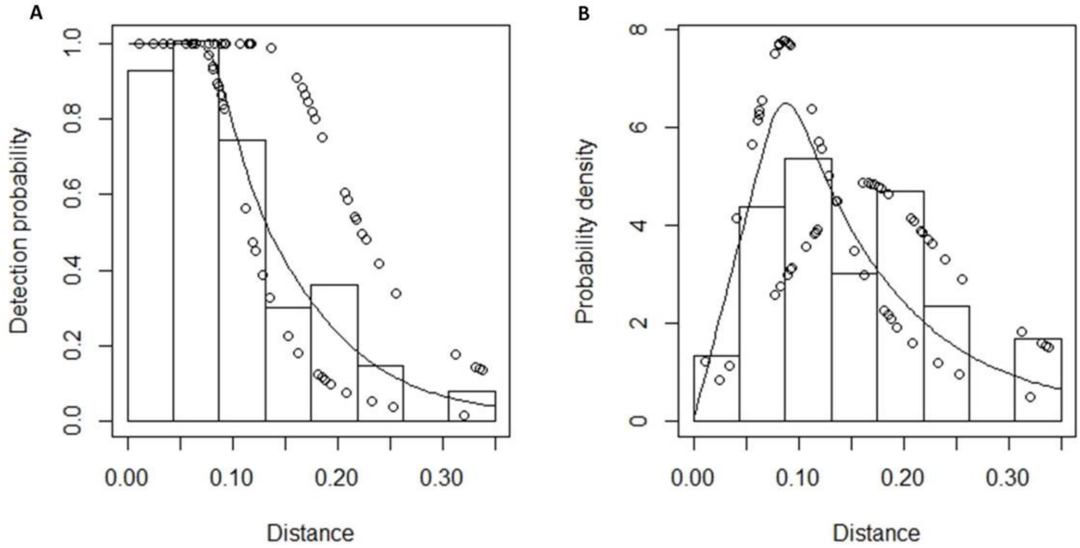
* number of encounters in our distance sampling survey during point counts

Appendix 3.3: Model choice for the density surface model. wetness: topographic wetness index, habitat: percentage of suitable habitat types, edf = effective degrees of freedom, AIC(GAM) = AIC of the equivalent GAM

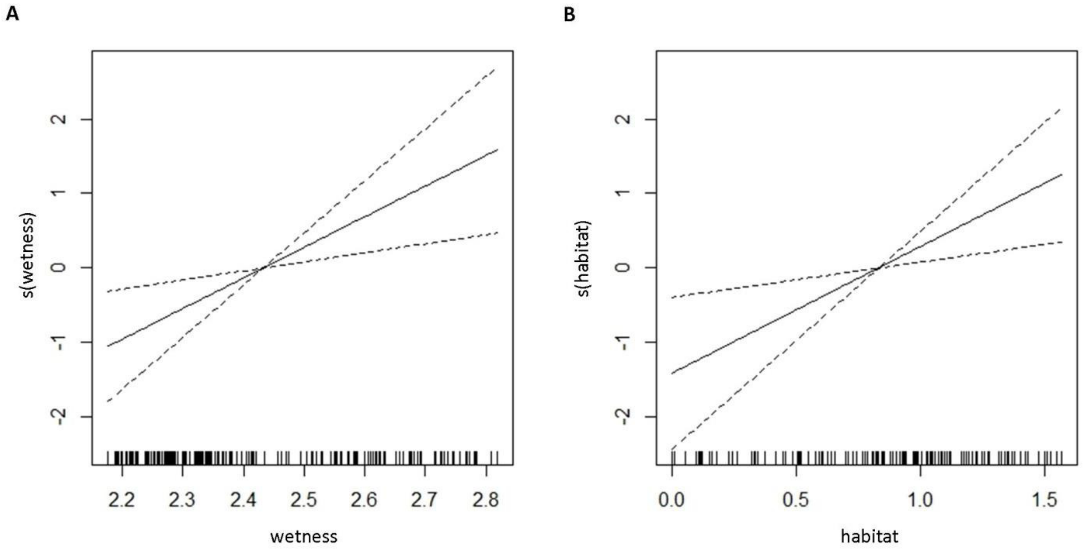
Predictors	edf	CI	*p*	AIC(GAM)
W+H*				**468**
(Intercept)	1.25	0.55 – 1.95	**0.001**	
s(wetness)	1		**0.005**	
s(habitat)	1		**0.006**	
S+W+H				**468**
(Intercept)	1.27	0.58 – 1.96	**<0.001**	
Smooth term (X,Y)	0		0.445	
s(wetness)	1		**0.003**	
s(habitat)	1		**0.005**	
W				**473**
(Intercept)	1.6	1.03 – 2.17	**<0.001**	
s(wetness)	1		**<0.001**	
H				**474**
(Intercept)	1.44	0.75 – 2.13	**<0.001**	
s(habitat)	1		**<0.001**	

*chosen model

Appendix 3.4: Hazard-rate key detection function (**A**) and detection probability density function (**B**) with openness of the habitat as two-level covariate (open/not-open).



Appendix 3.5: Shape of the smooth functions used as environmental predictors for Yellow-crested Cockatoo densities in the GAMM. “Wetness” is the log-transformed SAGA wetness index and “habitat” is the percentage cover by suitable habitat (palm savanna and deciduous monsoon forest combined and arcsine transformed). Ticks on the x-axis indicate the sample distribution.



4 Population changes over 25 years in parrots and hornbills on Sumba

Abstract

Population density and distribution data are essential to assess the status and conservation needs of threatened species. Although the importance of long-term monitoring is widely recognised, very few tropical bird species have been monitored over the span of 25 years. We replicated a multi-species distance sampling survey from 1992 in 2017, matching sampling seasons, locations of transects and methods as closely as possible, and present data on five parrot species and a hornbill, with three threatened island endemics, Citron-crested Cockatoo *Cacatua citrinocristata* (CR), Sumba Eclectus *Eclectus cornelia* (EN) and Sumba Hornbill *Rhyticeros everetti* (EN), two restricted-range species, Great-billed parrot *Tanygnathus megalorynchos* and Marigold Lorikeet *Trichoglossus capistratus*, and one Wallacean-Papuan species, Red-cheeked Parrot *Geoffroyus geoffroyi*. Densities of the three large parrots and the hornbill in 2017 were similar to 1992 but densities of the smaller Red-cheeked Parrot and Marigold Lorikeet declined significantly. This decline coincided with forest loss at two sites but also occurred in the protected sites where forest quantity remained stable. We assess quantity of forest on Sumba for both years using satellite imagery and pair the size of the resulting forest patches with presence data and local density estimates from survey sites to gauge island-wide population sizes. To avoid future long gaps in population estimates, regular monitoring is needed at least every 10 years with combined methodology for comparability to the 1992 and 2017 surveys and additional effort to cover the island's habitat more representatively. This is particularly important for the Marigold Lorikeet, which may need a re-assessment of its global Red List status. The uncertainty in trends for the threatened cockatoo, eclectus and hornbill is of concern as they show no sign of sustainable recovery from the extensive trapping of past decades.

4.1 Introduction

Although the importance of long-term biological monitoring is widely recognised (Snyder et al., 2000; Magurran et al., 2010; Marsden and Royle, 2015; Dénes et al., 2018), very few tropical bird species, have been repeatedly monitored over decades (Thiollay, 2006; Marsden and Royle, 2015). Population densities, sizes and their changes form an integral part of Red List assessments (SSC IUCN, 2001), but recent population estimates are missing for many threatened species and data on population changes are even scarcer. While areas with many local ornithologists such as Europe and North America have several monitoring programmes spanning decades (Gregory et al., 2005; Sauer et al., 2017), both the loss of biodiversity and the lack of data on it are most severe in the tropics (Collen et al., 2008; Beaudrot et al., 2016). Species occurring in low densities in remote and barely accessible habitats can be expected to be even less well covered by research. Although parrots are relatively well known to the public and can even function as flagship species for their communities and habitat, density estimates are only available for about a quarter of parrot species and assessments for abundance change for even fewer (Marsden and Royle, 2015).

Deterioration in forest quantity and quality is a well-known threat to bird species worldwide, and primary forest has been identified as essential for maintaining biodiversity (Gibson et al., 2011; Kormos et al., 2017). As large hole-nesters, most parrots and hornbills rely on old-growth forests for nesting and suffer more than other species from selective logging if old trees are targeted (Collar, 1997). In long-lived, K-selected species – such as large parrots and hornbills – effects of such habitat changes may only become apparent after decades (Collar and Juniper, 1992; Kuussaari et al., 2009). Both groups are also heavily targeted by trappers for commercial purposes (Collar and Juniper, 1992; Snyder et al., 2000; Pires, 2012; Eaton et al., 2015), which can cause unpredictable and often dramatic population declines depending on accessibility, trapping effort and methods (Marsden and Pilgrim, 2003; Valle et al., 2018).

Distance Sampling has become well established as a method for avian density estimates (Buckland et al., 2001, 2008; Thomas et al., 2010). It accounts for detectability and clustering of individuals (Buckland et al., 2001) and therefore deals well with characteristics of parrots and hornbills that produce biases in results generated by other methods such as roost counts, flyway counts, strip transects and mark-resighting studies (Casagrande and Beissinger, 1997; Marsden, 1999). Extrapolating from estimated densities to absolute population numbers requires additional knowledge of the species' ranges and distributions. If the sample was representative for the whole study area, densities can simply be multiplied by the size of the area. For non-representative sampling local densities can be projected on areas with similar characteristics (Buckland et al., 2001, 2008). Which areas are deemed similar to each other can be determined spatially, by site characteristics or using cluster-like models (Jones et al., 1995). More advanced methods such as Density Surface Modelling (Winiarski et al., 2013; Miller et al., 2019) model the influence of local characteristics on local densities and use these characteristics to predict densities for unsurveyed areas.

The island of Sumba in the central 'Wallacea' region of the Indonesian archipelago is a biodiversity hotspot with 15 restricted-range species, including nine island endemics (del Hoyo and Collar, 2014, 2016; Eaton et al., 2016; BirdLife International, 2021). Among our study species the Citron-crested Cockatoo *Cacatua citrinocristata*, recently elevated to species level from a subspecies of Yellow-crested Cockatoo *Cacatua sulphurea*, is Critically Endangered, while Sumba Eclectus *Eclectus cornelia* and Sumba Hornbill *Rhyticeros everetti* are listed as Endangered. Two other restricted-range species, the Great-billed parrot *Tanygnathus megalorynchos* and the Marigold Lorikeet *Trichoglossus capistratus*, are currently listed as Least Concern, as is the much wider-ranging Red-cheeked Parakeet *Geoffroyus geoffroyi*, which is found throughout New Guinea and in northernmost Australia. We refer to the latter two as Sumba's smaller parrot species while the cockatoo, eclectus and Great-billed Parrot are all similar in size and treated here as large parrots. Despite calamitous declines of the sister species Yellow-crested Cockatoo *Cacatua sulphurea* elsewhere, a relatively large population of Citron-crested Cockatoo still exists on Sumba (Reuleaux, Collar, et al., 2022; Reuleaux, Siregar, et al., 2022). This cockatoo population, and those of other cavity-nesting and frugivorous birds, were first surveyed by MMU researchers in 1992 (Jones et al., 1995; Marsden, 1999), and again in 2002 (Cahill et al., 2006). For the cockatoo the 2002 survey detected a population increase which was attributed to a ban of international trade in 1994. An extensive but unpublished survey by Burung Indonesia, an Indonesian NGO dedicated to bird conservation, indicated drastically lower population densities in 2007–2008 (Bashari and Wungo, 2011; Wungo, 2011).

Reliable population numbers comparable to the baseline survey were therefore needed to be able to assess the conservation status of the Critically Endangered cockatoo.

Among the rare long-term monitoring studies of birds in tropical forests, re-surveys are usually carried out by different groups and use new field and analysis methods. In contrast, our current study offered an exceptional opportunity to monitor decadal changes in threatened parrot and hornbill abundance in tropical forest by attempting to replicate as precisely as possible the earlier surveys of the birds of Sumba

4.2 Methods

4.2.1 Study site

The island of Sumba (9.3–10.3°S, 118.9–120.8°E) in East Nusa Tenggara, Indonesia, comprises just over 11,000 km² and has 650,000 inhabitants (Badan Pusat Statistik, 2016). It is dominated by relatively low limestone hills reaching up to 1200 m asl. It has a dry season from May to November and a rainy season from December to April. Sumba is one of the economically weakest islands of Indonesia, with many inhabitants relying on subsistence farming. Pastures for livestock and irrigated rice fields are the most important agricultural land uses (Badan Pusat Statistik, 2016). Many villages still do not have electricity, mobile phone network or a reliable source of water. The study area on Sumba comprises the Matalawa National Park (consisting of the former national parks ‘Manupeu-Tanadaru’ and ‘Laiwangi-Wanggameti’, which were joined together administratively in 2017) and three smaller isolated patches of forest. The central parts of the national parks are the remotest and least accessible areas of the island and contain the largest areas of remaining forest.

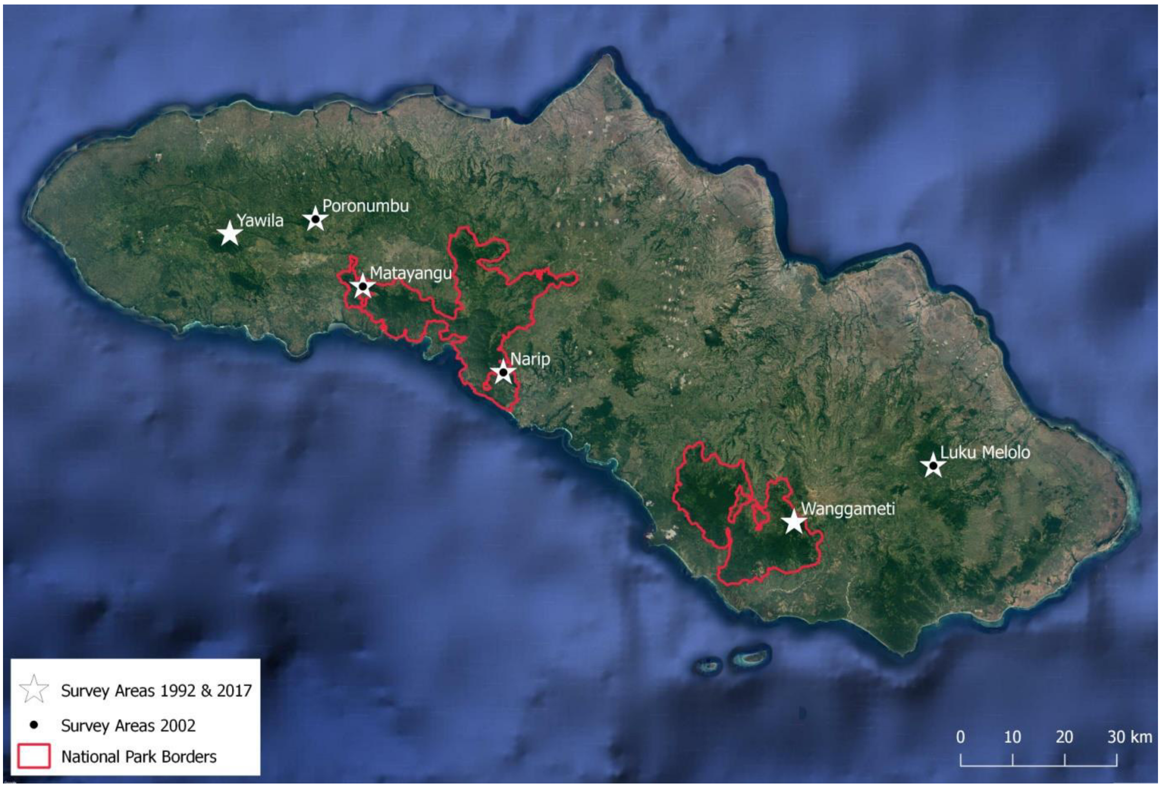


Figure 4.1: Survey locations of the 1992, 2002 and 2017 bird surveys. The original choice of survey locations was based on proposed locations for protected areas. Matayangu was formerly listed as Manupeu and Narip as Nerip or Langgaliru. The locations are identical; only the names have been adapted to current usage. Jones et al. (1995) listed two further locations visited in 1989 but different methods were used there and data from these areas were not included in any of the population estimates.

4.2.2 Point count field methods

In this point-count distance sampling survey we assessed the population of the parrot and hornbill species of Sumba in six forested areas. Methods of the 1992 MMU bird survey (Jones et al., 1995) were replicated as closely as possible to allow direct comparison of results. Jones et al. surveyed six locations all over Sumba between July and September 1992. Part of the 1992 survey was repeated in 2002 by another MMU team covering four of the initial locations (Cahill et al., 2006).

Between July and September 2017, we surveyed 43 transects with 276 points to match the season and sampling design of 1992. We investigated field diaries and photos of the former expeditions and as far as possible used the same guides and camp sites as 25 years before. The exact location of the old transects could be determined with some confidence in about 80% of cases. In the remaining cases habitat type of the point-count locations was the only information available and transects matching these were sought within in the respective survey location. In cases where the habitat type at the original point had changed, an additional point was surveyed in the missing habitat type as close to the original transect as possible. This inflated the total number of points by 52 to 328 and enabled the creation of different subsets of the data that matched the sampling effort in terms of either location or habitat type across years.

Transects followed footpaths, streams and ridges or else used relatively open terrain. Stations for point-counts were located 150 m apart on these routes, which matched the distances originally used by Jones et al. (1995), who measured in steps. Distances between stations were measured with a GPS. Where potential bias by the topography of the route was suspected the stations were placed 50 m perpendicular off the route to alternate sides.

At each station two overlapping sampling intervals were used. The first interval of ten minutes, starting immediately with arrival at the station, follows current best practice recommendations (Lee and Marsden, 2008; Mollon, 2010). The second interval followed Jones et al. (1995), who allowed a two-minute settling-down period before starting a ten-minute count. In practice this meant a twelve-minute count at each point while noting the time of each detection and repetitions from the first two minutes.

The counts followed the usual distance sampling protocol (Buckland et al., 2001, 2008), noting all aural and visual detections accompanied by the distance of the individual/flock (cluster) to the observers, movement and height from the ground. Horizontal distances from the observer to the initial location of the cluster were measured with a Nikon Forestry Pro laser rangefinder. Detections of over-flying or newly arriving birds were noted without distance measurement but were excluded in the analysis. Intensive training in aural and visual species recognition and distance estimates supported by laser rangefinder measurements was carried out before the start and throughout the survey. This included regular practice sessions with playback of calls from measured distances. Further calibration of call location estimates was carried out by searching for the individual after aural encounters to verify the location and measured distance. Two main observers (AR, BS) worked in varying teams with three assistants, approximating the observer team size used in 1992. Teams were mixed regularly and the two main observers worked together at least once per location. The majority of transects were repeated once on a different day, usually by the other main observer. The observers both had experience with distance sampling of parrots and with identifying and monitoring parrot species on Sumba. The local field assistants already had extensive species identification skills, including by sound, from other surveys on Sumba. These identification skills were checked against sound recordings. Recordings were taken of 50% of the point-counts and used to confirm uncertain identifications of aural only contacts.

Habitat data collection

Habitat data were collected at each point following the methods in Jones et al. (1995), where they are described in detail. This included canopy cover at four levels, average slope, number of fallen/felled trees, number of potential cavities in a radius of 30 m around the station as well as characteristics of the ten trees above 20 cm diameter at breast height (dbh) nearest to the counting station: diameter, height, flowering, fruiting, deciduousness and tree architecture (Torquebiau, 1986; Jones et al., 1995). In 1992 the distance to the centre of the plot was measured for each tree, whereas in 2017 we only noted the distance of the furthest of the ten nearest trees, which is sufficient for the calculation of tree density and biomass. These data were used to calculate comparable habitat measures to Jones et al. (1995) and standardise allocation of habitat class across surveys.

Habitat classes

We used random forest classifiers to standardise habitat classes between the 1992 and 2017 surveys. We built a random forest model that predicted habitat class (primary forest, secondary forest or non-forest) based on nine habitat variables derived from field data following Jones et al. (1995): (1) ratio of canopy cover to ground cover; (2) proportion of trees with architecture indicating development under closed canopy (Torquebiau, 1986); (3) canopy cover; (4) ground cover; (5) total biomass in the plot; (6) tree density; (7) average tree girth; (8) proportion of trees with architecture indicating regeneration (Torquebiau, 1986); (9) stratum richness. Random forest classifiers were based on 500 trees and 3 predictors tried at each iteration. We initially assessed error rate for 1992 data alone by retaining half the data for validation, but subsequently a random forest was built on all 1992 data and used to predict 2017 habitat classes (Table 4.1). We also explored using 2017 data to build the model and predict 1992 classes, but discarded this option due to higher error rates. For all further analysis we replaced the habitat class assigned in the field in 2017 with the prediction from the 1992 random forest model.

Classification of stations into three habitat types in the field did not match well between years. Primary and secondary forest in particular had high error rates when random forest classifiers developed for 1992 were applied to predict classes in 2017 based on habitat measurements collected in the field (Table 4.1, Figure 4.2). The most useful characteristic for classifying habitat was the ratio of canopy cover to ground cover and the proportion of trees with architecture, which indicated development under a closed canopy and was therefore a measure of primariness (Figure 4.2).

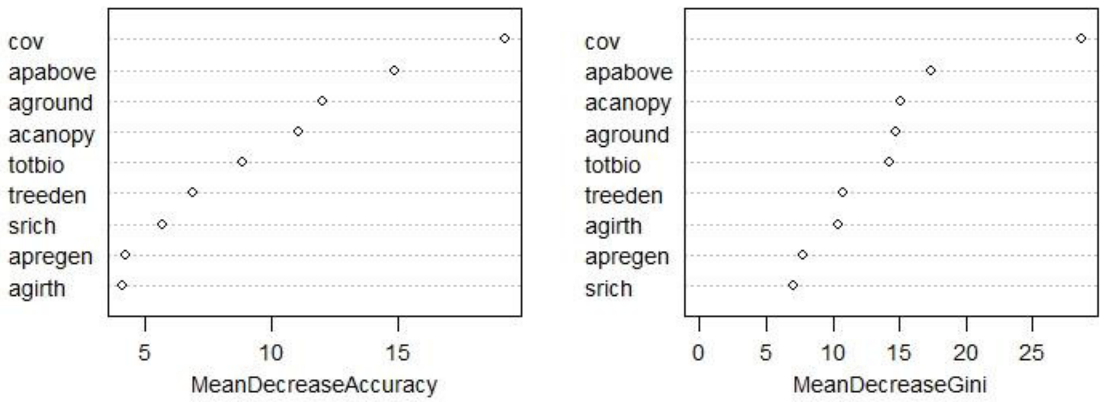


Figure 4.2: Relative importance of nine habitat characteristics in a random forest classifier to distinguish between three habitat classes (primary forest, secondary forest and non-forest). Habitat data were collected in 285 field plots around the point-count sampling stations. Cov = ratio of canopy cover to ground cover; apabove = proportion of trees with architecture indicating development under closed canopy; aground = ground cover; acanopy = canopy cover >15 m; totbio = total biomass (calculated from tree height, tree diameter and plot size); treeden = tree density (trees/ha); srich = stratum richness (number of strata above mode cover density); apregen = proportion of trees with architecture indication development in regenerating forest; agirth = average girth of trees in plot.

Table 4.1: Random Forest Confusion Matrix for classifier based on 1992 field data applied to 2017 habitat (without fire-damaged stations at Luku Melolo) to separate survey plots into three habitat types. Stations correctly classified shaded in green, classification errors in red.

	predicted			
observed	Non-forest	Primary forest	Secondary forest	Class error
Non-forest	52	0	15	0.224
Primary forest	1	79	58	0.428
Secondary forest	6	8	61	0.187

4.2.3 Statistical Analysis

Distance sampling analysis

As detection functions we considered six combinations of three key functions with three adjustment terms (Buckland et al., 2001) and two covariates. After exploitation of different options we used the following covariates: (1) time after sunrise (for better performance hours after sunrise were classed as ‘early’ [<2h after sunrise] versus ‘late’ [>2 hours after sunrise]); and (2) species-specific canopy cover at the two height strata where the species was most often found (proportion arcsine transformed).

We excluded data from non-forest survey plots as these yielded only very few parrot and hornbill observations (usually at forest edges), had too few observations for separate detection functions and, owing to much higher visibility in open habitats, would have biased a global detection function. Observations of flying birds were recorded but not included in the distance analysis. We chose the best models by comparing AIC and averaged results for all those models with ΔAIC<=2 functions, following Bolker (2008). For the Sumba Hornbill we diverted from this method and used visual inspection of detection functions to choose the best model. This was necessary because small sample sizes in this species caused some base-functions to produce models with low AICs but very large variability (CV>1000%) and poor visual fit of the detection function to the data. We calculated habitat- and site-specific densities using encounter rate ratios. To compare densities between survey years we applied two-sided Z-tests following Buckland (2001 p.84–85) and Buckland et al. (2008).

Habitat classification map

To determine the amount of available habitat we carried out supervised classifications of Landsat images from 1992 and 2017 (Landsat 5, Bands 1– 5 and 7 from July–November 1992; and Landsat 8 bands 2–7 from July–November 2017). After conversion of the images to surface reflectance, cloud masking, and creating a mosaic covering the whole of Sumba, we used QGIS (QGIS Development Team, 2021) and the Semi-automatic Classification Plugin (Congedo, 2016, 2021) to carry out a supervised classification. As training data we used subsets of our point-count stations. For 2017 we included 207 stations where habitat class assessed in the field matched the result of the re-classification by the random forest model. As no GPS data were available for 1992 we only included the 166 stations for which the location matched the GPS point taken in 2017 with sufficient certainty (as noted during fieldwork, based on precision of the transect description from 1992). Although we aimed for four macro-classes (water, primary or old growth forest, secondary forest and non-forest) in the outcome we used 20 classes (four types of primary forest, two of secondary forest, nine types of open area and four water classes) throughout the process. Polygons of training areas were drawn by hand around the station on the background of the Landsat images and Bing and Google Earth satellite maps for 1992/1994 and 2017. Training polygons were 0.14–113 ha in size depending on the patch of homogeneous habitat around the station. As these training data were not sufficient for some fragmented types of landcover (e.g. scrubland and cultivations) we added additional ones in known places away from the survey sites. We continued adding training data until extra polygons no longer significantly changed the outcome for each class.

Extrapolation of densities to population numbers

To estimate population numbers from densities we used (1) size of forest areas, (2) additional presence data and (3) population densities from our distance sampling survey sites. (1) The habitat classifications described in the previous section resulted in a map of forested areas for each of our survey years. We selected areas >1 km^2, presuming that smaller patches contain more edge habitat than closed-canopy forest and are of little importance to parrot populations. (2) As parrot and hornbill occupancy of forest patches is not only determined by habitat suitability but also influenced by trapping pressure we used presence data (Marsden, 1995; Collar et al., 2001; Persulessy et al., 2003; Sitompul et al., 2004; Bashari and Wungo, 2011; Djawarai et al., 2014; Hidayat and Kayak, 2014; eBird Basic Dataset, 2019) to filter the forest patch dataset (for 1992 presences after 1982 were used and for 2017 presences after 2007). Forest patches were included if they had sightings of the species within 5 km of any part of the patch. (3) We projected local densities from our survey sites onto these forest patches based on similarity in size, protection status, altitude, proportion of primary forest and proximity.

4.3 Results

4.3.1 Forest change

We detected a net decrease in forest cover at all surveyed forest blocks between 1992 and 2017. Yawila, the westernmost and most disturbed survey site, lost the largest percentage, closely followed by the far eastern Luku Melolo, which was partly devastated by a large forest fire in 2015. Total forest loss on Sumba depends on the size of forest patches considered and was more than a quarter of the area of forest patches >1 km² (Table 4.2). Most forest change was, however, detected in non-survey sites (Figure 4.3) which were typically of poorer quality and more fragmented than the survey sites. Comparing forest quality between the years in our landcover classifications (Figure 4.3) primary forest was more common in 2017 than in 1992, presumably because secondary forest aged into old-growth forest, improving forest quality, especially in protected areas.

Table 4.2: Forest change at survey sites; comparison of continuous area of forest at the six survey sites on Sumba of 1992 and 2017. In the case of Wanggameti only forest above 850 m was included.

Name	**km² 1992**	**km² 2017**	**Change**
Wanggameti	30.5	29.1	−5%
Luku Melolo	34.1	26.5	−22%
Yawila	28.4	21.9	−23%
Poronumbu	13.9	13.1	−6%
Matayangu	116.7	105.3	−10%
Narip	146.6	141.1	−4%
All survey sites	370.3	336.9	−9%
All large forest patches	1,893.8	1,364.8	−28%
All medium–large forest patches	1,903.3	1,641.0	−14%

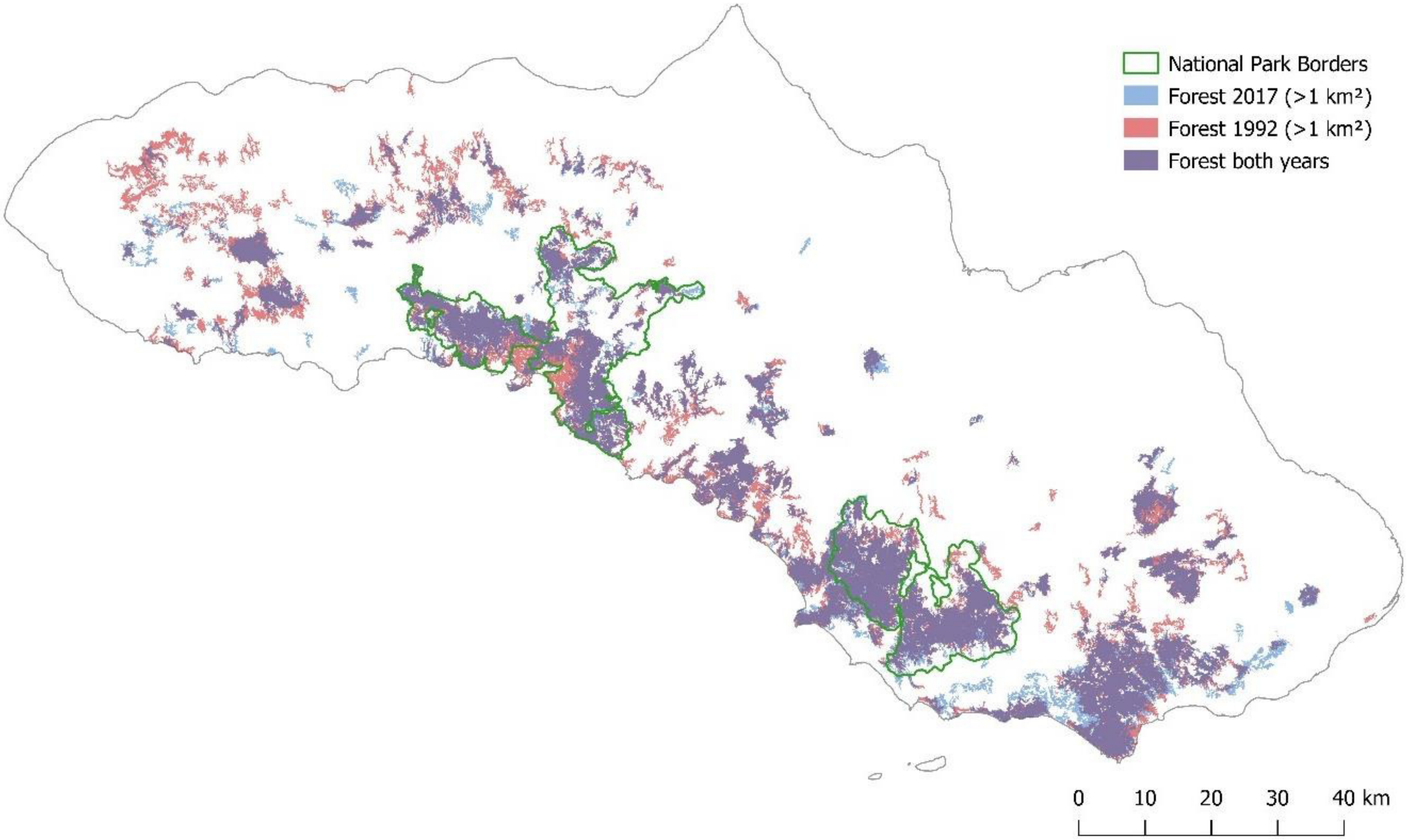


Figure 4.3: Forest cover in 1992 and 2017 from supervised classification of LANDSAT images. The overlap of forest areas in both years is shown in purple. Red areas represent forest loss and blue areas forest gain over the 25-year period. We only considered areas above 1 km² on this map as smaller patches are unlikely to support the study species.

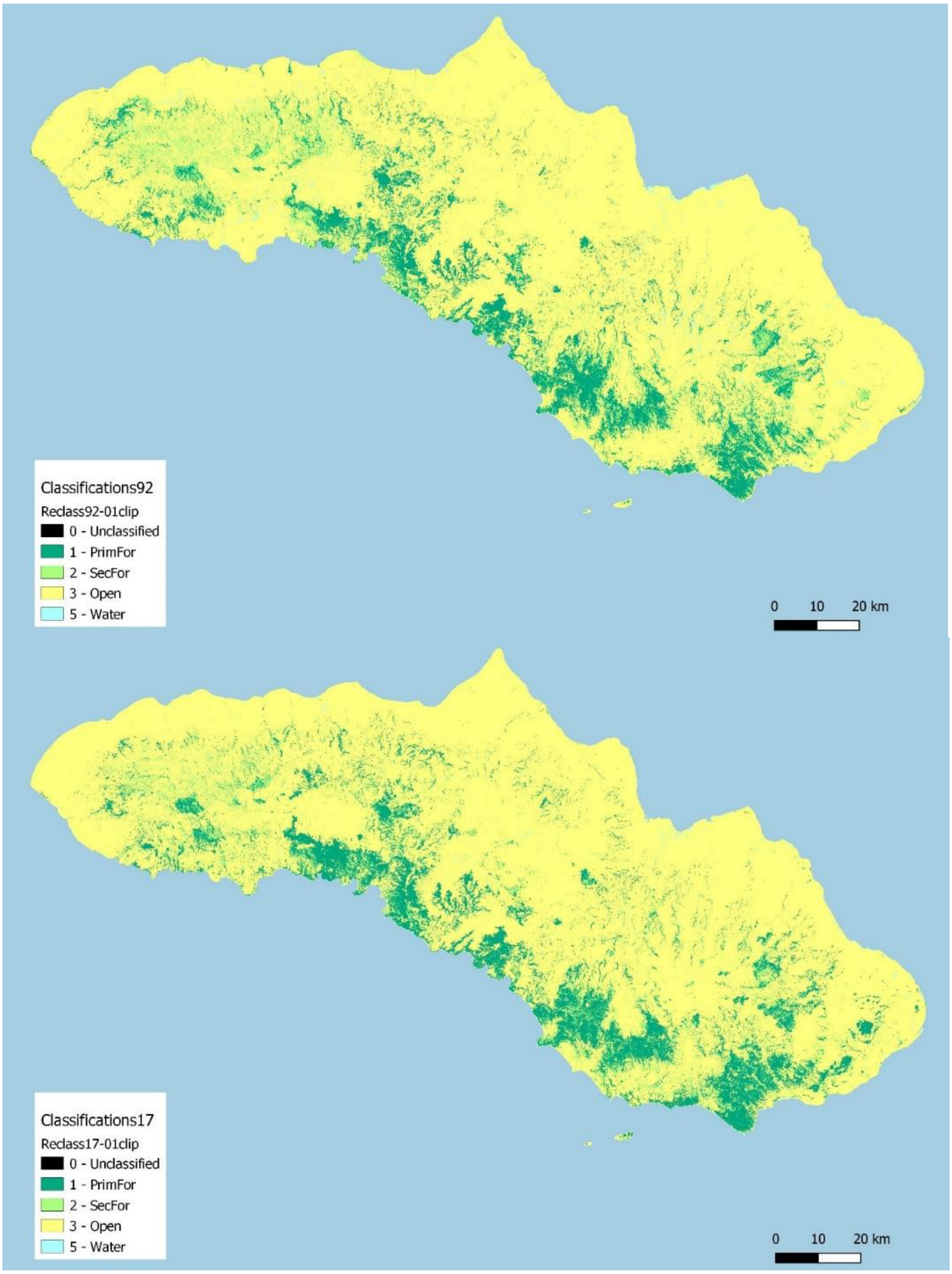


Figure 4.4: Landcover classification of Sumba island using a supervised classification of a mosaic of LANDSAT images. Here forest fragments of all sizes are included, **above for 1992** and **below for 2017**. Secondary forest represented in light green is more prevalent in 1992 than in 2017, which is most likely due to a bias in the training data used for the classification which had sufficient samples for primary forest and open habitat but lacked low-quality secondary forest. To prevent this bias from affecting our consecutive results we grouped primary and secondary forest cover together. In both years flooded rice fields (sawah) were detected as waterbodies. We grouped inland water with other types of open landcover which has little relevance for our study species.

4.3.2 Parrot and hornbill presence

Five of the six study species were found at all six sites in both years, although not necessarily detected during point counts. The Citron-crested Cockatoo was detected at all except one site in 2017, where it was present but already rare in 1992. It was absent from point counts in the higher-altitude site (Wanggameti) in both years and from the highly modified western forest patch of Yawila in 1992. Other absences during point-counts despite detections outside these intervals (indicating low local densities or detectabilities) were found for Sumba Eclectus in both years and Great-billed Parrot in 2017 at Wanggameti, Sumba Hornbills in 2017 at Poronumbu and Great-billed Parrots in 1992 at Matayangu.

4.3.3 Parrot and hornbill densities

Encounter rates and densities varied largely between sites, less so between the two examined forest types (Figure 4.5, Figure 4.6). The three large parrots and the hornbill were all limited by low total number of detections (<30 in at least one of the years, Table 4.3), rendering confidence intervals around the density estimates relatively large in both years, whereas the two smaller parrots were more common and number of encounters was sufficient to reach reasonably precise density estimates (CV<25%), using a global detection function for each species in all habitats and sites (Table 4.3). Population changes in cockatoos were mostly driven by secondary forest, with increases in the two small western forest fragments (Figure 4.5). Eclectus densities declined in three of the sites, and mostly in secondary forest. Great-billed Parrot density increases were due to primary forest, almost exclusively in the western half of the national park (former known as Manupeu Tanadaru). Declines in small parrot densities were drastic and universal for both forest types, at all sites for the Red-cheeked Parrot and three of six sites for the lorikeet (Figure 4.6). Hornbill density changes are masked by very large confidence intervals, particularly in 2017. Figure 6 shows that this is largely due to Matayangu (labelled ‘Td’ in Figure 4.6), a western national park site with primary forest, where large flocks of hornbills (up to 18 individuals per cluster) were detected feeding in a group of fruiting trees close to both transects (only 18 survey stations at this site).

Table 4.3: Population density estimates (in individuals/km² ±SE) and number of detections (n = number of encounters with groups or individuals within truncation distance) for hornbills and parrots recorded in 306 point counts at 217 sampling stations at six sites on Sumba in 1992 (Marsden 1999) and in 387 point counts at 240 stations in the same six sites in 2017.

Species	Year	Estimate ±se (n)	%CV	CI	ER	Average p
Citron-crested Cockatoo	1992	1.17 ±0.47 (17)	40.2	0.54–2.56	0.11	0.46
	2017	1.74 ±0.51 (30)	29.0	0.99–3.07	0.16	0.45
Sumba Eclectus	1992	5.4 ±2.5 (26)	45.5	2.25–12.94	0.13	0.29
	2017	3.26 ±0.60 (41)	18.3	2.28–4.66	0.16	0.61
Great-billed Parrot	1992	2.51 ±1.37 (19)	54.7	1.05–8.19	0.08	0.60
	2017	6.15 ±1.45 (58)	23.5	3.89–9.75	0.20	0.60
Red-cheeked Parrot	1992	39.9 ±5.78 (150)	14.5	30.05–52.97	0.80	0.25
	2017	22.88 ±2.13 (207)	9.3	19.07–27.46	0.88	0.48
Marigold Lorikeet	1992	28.94 ±6.45 (60)	22.3	18.78–44.81	0.47	0.20
	2017	10.43 ±2.19 (48)	21.0	6.92–15.75	0.30	0.37
Sumba Hornbill	1992	6.21 ±3.35 (10)	54.0	2.18–17.82	0.08	0.24
	2017	11.91 ±5.02 (24)	42.1	5.32–26.65	0.17	0.07

Table 4.4: Density comparisons between survey years by Z-tests; **D** Estimated density, **CV** coefficient of variation, **n** number of detections within truncation distance, **Z** Z-statistic (from two sided Z-test, higher density–lower density), **ns** not significant

	1992			**2017**					
	D	**CV**	**n**	**D**	**CV**	**n**	**Z**	**P**	**Change**
Citron-crested Cockatoo	1.17	0.403	17	1.74	0.287	30	-0.828	0.408	
Sumba Eclectus	5.40	0.455	26	3.26	0.183	41	-0.847	0.397	
Red-cheeked Parrot	39.90	0.145	150	22.88	0.093	207	-2.760	**0.006****	decrease
Sumba Hornbill	6.21	0.533	10	11.91	0.421	24	-0.948	0.343	
Great-billed Parrot	2.51	0.555	19	6.15	0.234	58	-1.819	0.067	ns increase
Marigold Lorikeet	28.94	0.223	60	10.43	0.209	48	-2.718	**0.007****	decrease

Investigation of cockatoo density trends could potentially include a published estimate from 2002 (Jones et al., 1995; Marsden, 1995; Cahill et al., 2006), but analysis of the 1992 and 2002 data by Cahill et al. apparently includes multiple repetitions of transects in two protected sites with high cockatoo densities and excluded two sites with low cockatoo densities. Therefore, densities combined for the whole survey of four sites weighted by survey effort are not comparable with our results (Table 4.5). Splitting density estimates by site shows that the increases in 2002 are mainly driven by the sites Matayangu and Poronumbu. The former is a large area of intact primary forest in the national park with only two transects (18 stations), the latter is a small patch of relatively degraded primary forest with a small remnant population. Looking at comparable subsets of the data for 1992 and 2017 (labelled 'This analysis' in Table 4.5) we see a decrease in Matayangu and increase in Poronumbu while there is little change in the other sites (Figure 4.5).

Table 4.5: Density estimates of Citron-crested Cockatoo in four to six selected sites on Sumba Island including only forested habitat. Estimates are given as densities in individuals/km² ±SE with the number of detections in parenthesis (groups of perched birds within truncation distance). Results for 1992 and 2002 by Cahill et al. (2006) include additional repetitions (up to 12 per point) of the same stations on selected transects.

Survey year	**1992**	**1992**	**1992**	**2002**	**2017**
Site ↓ Source→	published 1995[1]	Cahill et al. 2006	This analysis	Cahill et al. 2006	This analysis
Matayangu	3.53 ±1.22	4.2 ±1.4 (20)	4.75 ±2.40 (7)	9.9 ±3.3 (39)	1.99 ±1.28 (3)
Poronumbu	0.88 ±0.49	0.9 ±0.8 (3)	1.58 ±1.10 (4)	7 ±2.5 (20)	4.38 ±1.77 (14)
Narip	1.09 ±0.53	2.1 ±1.1 (12)	1.67 ±1.06 (5)	2.7 ±1 (13)	1.75 ±0.76 (9)
Luku Melolo	0	0.2 ±0.5 (1)	0.17 ±0.25 (1)	0	0.22 ±0.31 (1)
Wanggameti	0	NA	0	NA	0
Yawila	0.21 ±0.20	NA	0	NA	1.41 ±0.81 (3)
Sites combined	**2.2 ±1.1 (38)**	**1.98 ±0.6 (36)[2]**	**1.17 ±0.47 (17)**	**4.3 ±1 (72)[2]**	**1.74 ±0.51 (30)[1]**

[1] estimate for sites combined by Jones et al. 1995, estimates per site from Marsden 1995;

[2] The totals calculated by Cahill et all. 2006 only account for four of the six sites

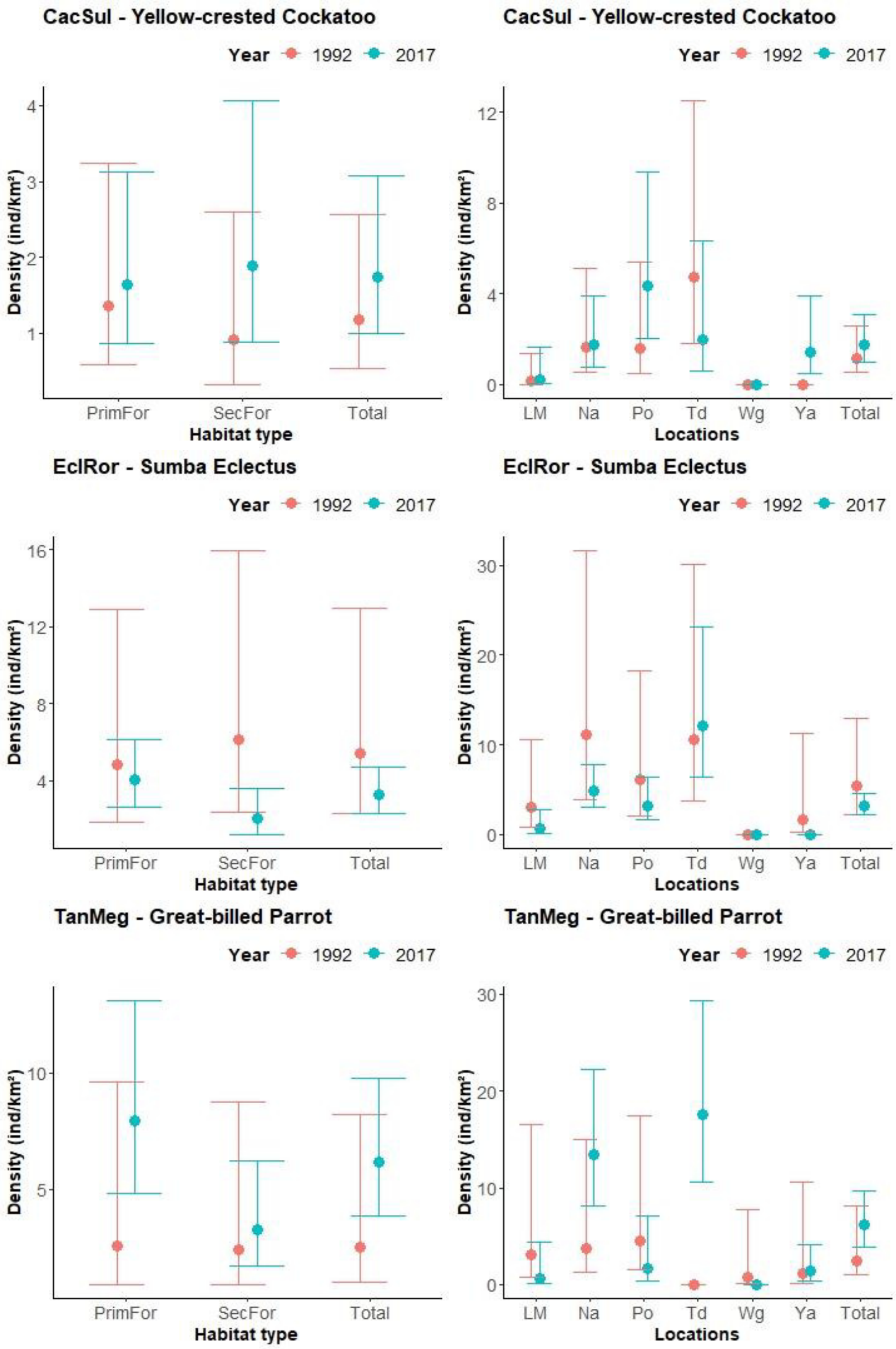
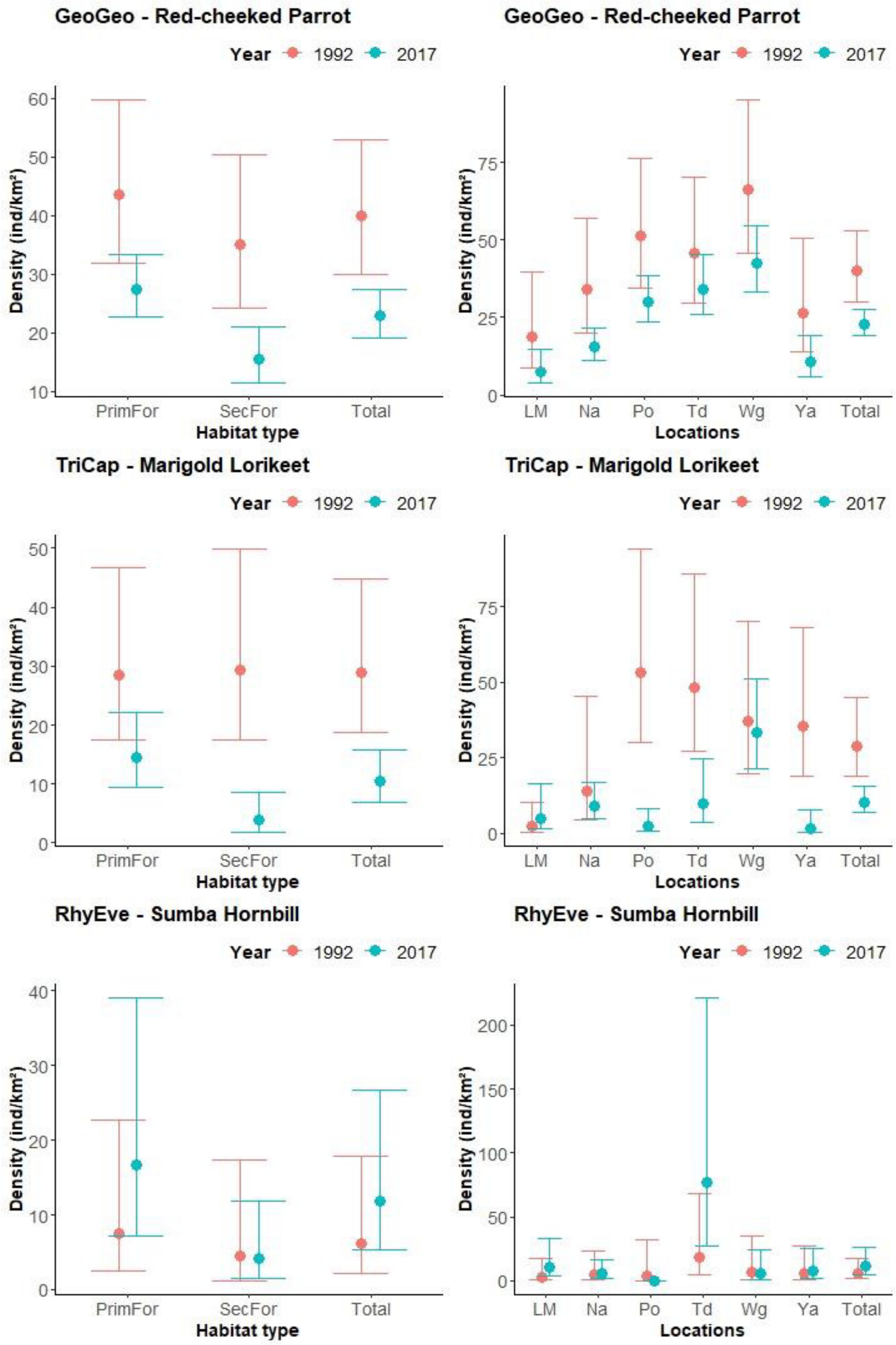


Figure 4.5: Density Estimates of Sumba’s three large parrots, stratified by habitat and location. **PrimFor** includes primary and old growth forest, **SecFor** secondary forest, all other types of forest. **Na** Narip , **Td** Matayangu and **Wg** Wanggameti are located in Matalawa National Park, **LM** Luku Melolo, **Po** Poronumbu and **Ya** Yawila in smaller isolated forest patches outside protected areas.


GeoGeo - Red-cheeked Parrot

GeoGeo - Red-cheeked Parrot

TriCap - Marigold Lorikeet

TriCap - Marigold Lorikeet

RhyEve - Sumba Hornbill

RhyEve - Sumba Hornbill

Figure 4.6: Density estimates for Sumba’s two smaller parrots and the hornbill, stratified by habitat and location. **PrimFor** includes primary and old growth forest, **SecFor** secondary forest, all other types of forest. **Na** Narip , **Td** Matayangu and **Wg** Wanggameti are located in Matalawa National Park, **LM** Luku Melolo, **Po** Poronumbu and **Ya** Yawila in smaller isolated forest patches outside protected areas.

4.3.4 Extrapolation to population numbers

Population estimates from likely occupied forest areas show a similar pattern as the density estimates: decreases in the two common small parrot species and changes in the large parrot species and hornbill are not significant owing to large confidence intervals.

Allocation of density results from survey sites to unsurveyed forest patches (Figure 4.7, Figure 4.8) had a large influence on confidence intervals and absolute abundance estimates (Table 4.6).

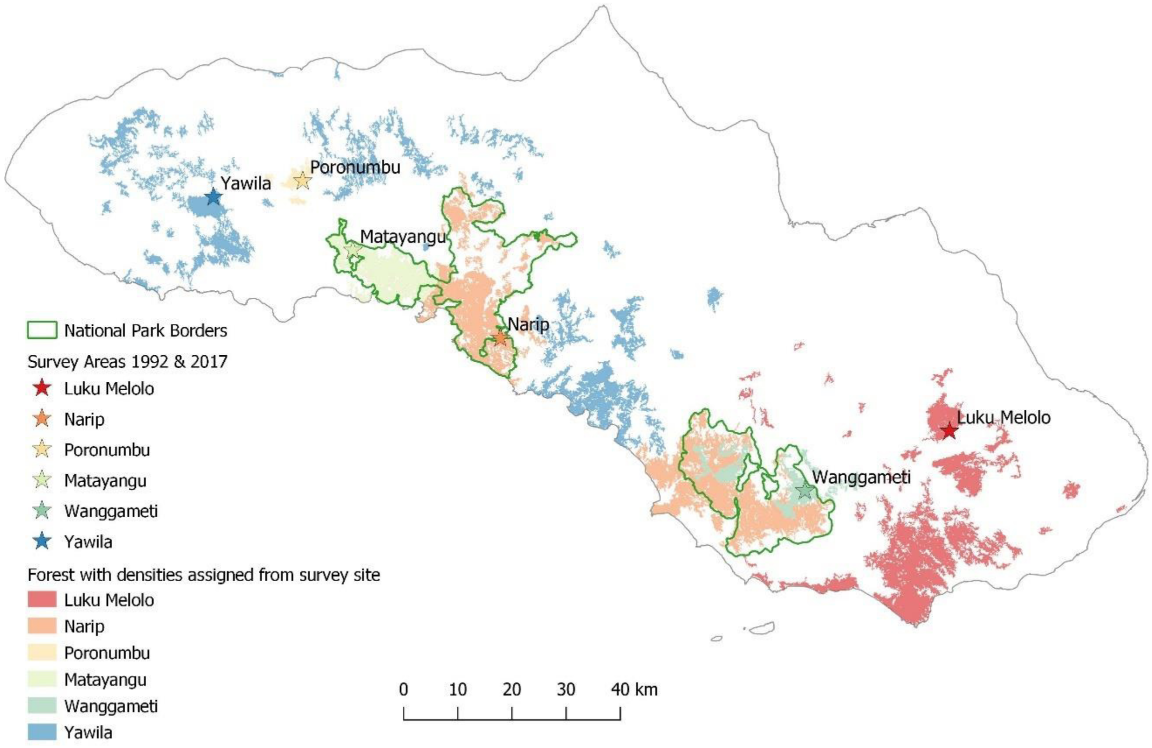


Figure 4.7: Allocation of 1992 density results from survey sites to forest patches

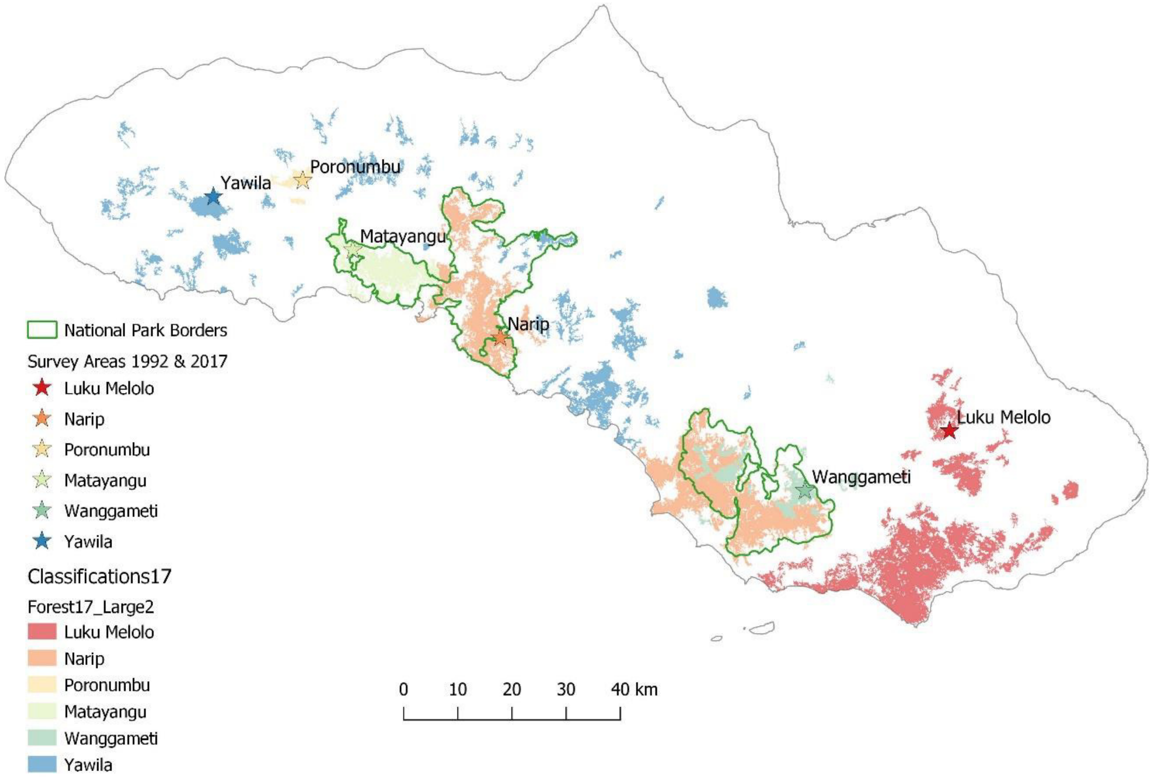


Figure 4.8: Allocation of 2017 density results from survey sites to forest patches

Table 4.6: Estimates of parrot and hornbill population numbers (individuals) for the island of Sumba

Species	Year	Estimate	se	%CV	CI	n
Citron-crested Cockatoo	1992	1914	1174	61.3	648–5844	17
Cacatua citrinocristata	2017	1380	729	52.8	558–3680	30
Sumba Eclectus	1992	11172	6745	60.4	3753–34523	26
Eclectus cornelia	2017	3847	1105.8	28.7	2219–6932	41
Red-cheeked Parrot	1992	51044	13955	27.3	30038–87699	150
Geoffroyus geoffroyi	2017	18378	3442.1	18.7	12792–26953	207
Sumba Hornbill	1992	9042	8130	89.9	1954–42957	10
Rhyticeros everetti	2017	15512	8927.3	57.6	5275–45861	24
Great-billed Parrot	1992	4176	3522	84.3	1283–20192	19
Tanygnathus megalorynchos	2017	8655	2473	28.6	5059–15683	58
Marigold Lorikeet	1992	34068	13759	40.4	15747–79522	60
Trichoglossus capistratus	2017	8995	3519.3	39.1	4465–19768	48

4.4 Discussion

Considering the insecure status of Sumba’s parrots and hornbill it is essential to their conservation to monitor their population sizes and trends. All threats that led to catastrophic declines during the last century still persist, but at lower levels: deforestation and selective logging have slowed in the national parks but are still ongoing in smaller forest fragments and at the perimeter of the larger high-quality forest patches. There is also evidence that selective logging continues at the interface between forests and villages. Trapping has been hampered by legal restrictions and efforts of law enforcement and awareness work, but rising prices per bird provide enough incentive for some trappers and traders to take the risk (Pires et al., 2021; Reuleaux, Siregar, et al., 2022). Repeating the survey from 1992 and replicating methods so closely, both in the field and during analysis, gave us the best possible opportunity to detect change over the last 25 years. Our results highlight that the large parrots and the hornbill have probably not continued on their trajectory to extinction as quickly as was feared in the 1990s (Jones et al., 1995; PHPA et al., 1998), whereas Sumba’s two formerly common small parrot species have declined at alarming rates in the last 25 years.

4.4.1 Main caveats

Although replicating methods of the first survey benefited comparability between the surveys, the inflexibility of methods also limited the usefulness of results. The main limitation is the study design, with unequal numbers of clustered transects in just six deliberately picked areas of the island. The most important areas of the national park (especially the eastern part) were not represented well in the samples. While we have many forest edge stations, we have no samples in truly poor-quality forest that is not adjacent to one of the best forest habitats of the island. This makes extrapolation to a population estimate for Sumba difficult. We utilised technological advances such as GPS and rangefinder in 2017 but could not take full advantage of them as the location of points had already been determined in 1992 without these aids. Any improvement in methods, e.g. measuring distances instead of estimating, avoiding a settling-down period, or standardising distance between points, had to be weighed against the decrease in comparability. Parrots’ and hornbills’ habit of flying far and fast relative to observer speed (Marsden, 1999) combined with 72–96% aural-only encounters could potentially cause considerable bias depending on observer differences in assigning detections as stationary or moving. There are considerable differences in proportion of detections in flight between the years (see Table S1). Assessment of forest change is essential for extrapolating from local densities to island-wide population estimates. While we managed to base the estimate of forest area from satellite images on more evidence for both survey years than previous studies (which used broad estimates of forest area evaluated by the ministries of agriculture and forestry), we were not able improve the assessment of change in forest quality. We could distinguish primary and secondary forest reasonably well for each year on its own, but could not standardise the cut-off between the two forest classes over both surveys. We did not have sufficient training data from our clustered survey sites and were only able to supplement this for 2017 with locations that we visited during other research activities or from detailed satellite imagery with much finer resolution than was available for 1992.

We did not apply a correction factor to account for the exclusion of birds in flight. Therefore our results are likely to be underestimates (Marsden, 1995, 1999). For purely aural contacts it was often difficult to decide in the field whether a group or individual was flying or stationary, especially if only one call was heard. Therefore, the detections excluded as aerial are a potential source of bias.

4.4.2 Citron-crested Cockatoo trends and previous surveys

A key conservation aim of our research was the assessment of the population status of the Citron-crested Cockatoo on Sumba. Many attempts at population estimates have been made over the decades with varying methods and amounts of effort (Table 4.7). Only two have been published, one of them twice with different analyses of the same survey data (Jones et al., 1995; Marsden, 1995; Cahill et al., 2006). The majority of surveys are unpublished reports by NGOs; this includes two distance sampling surveys (Persulessy et al., 2003; Wungo, 2011) with considerable effort (several months to a year), but reported density results do not appear to match with reported encounter rates and analysis methods. All surveys including ours struggled with low numbers of encounters owing to the species' rarity. This creates large confidence intervals and little chance to detect changes. Marsden (1995) calculated that over 1700 point counts would have been necessary to achieve coefficients of variation <20% in good habitat in 1992. For marginal habitat the number would be much larger.

Table 4.7: Previous population surveys and estimates of Citron-crested Cockatoo on Sumba

Study	**Year**	**Methods**	**Scope**	**Density (individuals/km²)**	**Population (individuals)**	**Notes**	**Reference**
Riedel	1880	hunting				First collection on Sumba	Mayr and Stein (1944)
Doherty	1891	incidental			'So numerous that I have seen the trees white with them'		In Inskipp et al. (1988)
Kendall	1978	search	East (Melolo and Waingapu)			Still feared as crop pest	Kendall (1979)
Bruce	1984	incidental			'Reasonably good numbers in selected localities of suitable habitat'		Low 1984 in Inskipp et al. (1988)
Bishop	1986	incidental	Patches of primary and near-primary forest			'not abundant' but 'single birds or groups of up to three were seen regularly'	Bishop (1986)
Anonymous in Riffel & Bekti 1991	1986	unknown		8 ind/km² in appropriate habitat	12,000	'internal anonymous study'	Riffel & Bekti 1991 in PHPA et al. (1998)
Anonymous in Riffel & Bekti 1991	1989	unknown		1.9 ind/km² in appropriate habitat	-	'internal anonymous study'; Apparent decline of 80% in three years	Riffel & Bekti 1991 in PHPA et al. (1998)
Jones et al.	1992	Point count distance sampling	Density surveys at 6 forest sites, population estimate for all forest of Sumba	2.2±1.1 ind/km²	2376±1188 ('likely true figure 3200 individuals')		Jones et al. (1995)
Marsden	1992	Point count distance sampling	Density surveys at 8 forest sites, population estimate for all forest of Sumba		1150–2644	Based on same dataset as Jones et al. (1995)	Marsden (1995)

Study	**Year**	**Methods**	**Scope**	**Density (individuals/km²)**	**Population (individuals)**	**Notes**	**Reference**
Setiawan pers. obs. in O'Brien 1997	1995	incidental				Species present in half of Sumba's forest fragments (17 of 33), absent from forests <10 km²	PHPA et al. (1998); BirdLife International (2022)
1992 data re-analysed by Cahill et al. 2006	1992	Point count distance sampling	4 forest sites with high densities	1.98 ±0.6			Cahill et al. (2006)
Persulessy & Trainor 2001	2001	unknown	Manupeu Tanadaru National Park	230 (ind/km² ?)		Original report not available, only results quoted in later report; study not quoted by same lead author 2 years later; confusion of units likely	Persulessy & Trainor in Wungo (2011)
Cahill et al.	2002	Point count distance sampling	4 forest sites with high densities	4.3±1.0			Cahill et al. (2006)
Persulessy et al.	2003	Distance sampling, mostly point count, mixed with line and strip transects	14 forest sites on Sumba, population estimate for all of Sumba	0.2 (0.1–0.4)	598 (229–1195)	Problems with analysis: without allowing for undetected groups encounter rate already gives density 5.4 ind/km² (87 ind/516 point counts)	Persulessey et al. (2003)
Bashari & Wungo	2007/ 2008	Point count distance sampling	Manupeu Tanadaru National Park (MTNP)	Reported 0.1	Reported: max 563 if all suitable habitat was occupied	53 individuals detected in 720 point counts should lead to higher density estimate; Distances only recorded for visual contacts?	Bashari and Wungo (2011); Wungo (2011)
Nandika et al.	2012	'Belt transect and point count method'	3 forest sites in Central Sumba	2.9 in West of MTNP, 2.0 in East of MTNP, 8.1 Poronumbu			Nandika et al. (2012)

The site-by-site comparison between the three published surveys does not form a consistent picture so far. The apparent differences between the years will have to be examined with great care. Owing to the need to follow 1992 methods, comparability between the first and last survey should be good. Comparability with the 2002 survey is hard to judge as sample sizes do not match. Sample size of 1992 presented in Cahill et al. (2006) differs from the numbers found in field diaries and Marsden (1995), and seems to include multiple repetitions of the same transects. An increase cockatoo numbers from 1992 to 2002 (Cahill et al., 2006) and possible subsequent decline to 2017 might at first sight be attributed first to the setting to zero of the legal export quota in 1992 for East Sumba province and in 1994 for West Sumba province, followed by a postulated but unconfirmed relapse into trapping after 2002. However, unpublished reports by Burung Indonesia working on awareness campaigns on Sumba suggest that trapping activity followed an opposite pattern, with the local ban only having a very limited effect in the 1990s until it started to be enforced with jail sentences in the early 2000s (Persulessy et al., 2003; Nandika et al., 2012; Burung Indonesia, 2013). Observations and reports of trapping incidents dropped after this enforcement and after the introduction of a long-term public awareness programme accompanying the creation of the island’s two national parks in 1998. In the light of this and currently relatively low levels of trapping on Sumba (Reuleaux, Siregar, et al., 2022) we judge that a decade of population increase followed by a decade of population decline is an unlikely scenario. The population has more likely simply failed to recover from 1992 levels owing to poor productivity in a naturally K-selected species limited by nest-site availability (Reuleaux, Siregar, et al., 2022).

4.4.3 Other study species

Among Sumba’s other parrot species we can be confident that the two formerly common small parrots have suffered severe declines in both density and absolute population numbers. In the Red-cheeked Parrot the decline is universal for all sites and forest types, whereas the Marigold Lorikeet declined in only three of six sites, two small forest patches and in a large area of primary forest in the national park. We considered subjective decisions about detections in flight as a potential bias, but if the percentage of flying birds was underestimated in 2017 the declines would have been even more severe.

Nest-site competition between the four larger study species did not involve the two smaller ones (Reuleaux, Siregar, et al., 2022). These latter most likely need smaller cavities, which can form in younger trees and can therefore be found in more disturbed forests. We also found more forest loss in the unprotected forest fragments, so this could affect the small parrots more than the large ones. Being more tolerant of human activities might also increase the risk for trapping (Tella and Hiraldo, 2014; Lunstrum and Givá, 2020). Lorikeets are attractive cage birds and are certainly caught and sold opportunistically on Sumba, but the level of organised trapping and trade is unknown. Other lorikeet species in the region have experienced drastic declines in recent decades which have largely been attributed to trapping for the pet trade (Eaton et al., 2015; Arndt and Bashari, 2016; Braun et al., 2017), so traders may have started to focus on Sumba because the species was still relatively common and easy to find. Red-cheeked Parrots are less likely to be specifically targeted for trade but they are known to use open habitats including agricultural areas on Sumba and neighbouring islands (Collar et al., 2020). Consequently, they could be affected by shifts to more intensive agriculture (e.g. rice instead of corn, commercial plantations instead of diverse subsistence farms), the use of pesticides and herbicides, and possibly counter-measures to discourage frugivores despoiling orchards.

If we look past the large confidence intervals for the three large parrot species and compare encounter rates and central density estimates, we find a possible decline in Sumba Eclectus, a slight rise in cockatoos, and an almost significant increase in Great-billed Parrot densities. Sumba Eclectus and Great-billed Parrot have similar habitat preferences (Marsden and Fielding, 1999) and compete for the same nest-holes (Marsden and Jones, 1997; Reuleaux, Siregar, et al., 2022), so the difference in their population trends is most likely due to the much higher attractiveness of the former as a trade item. The preference for the eclectus might be exacerbated by the species' cooperative breeding system (Heinsohn and Legge, 2003; Heinsohn et al., 2007), allowing the capture of more individuals per site and diminishing the effective breeding population disproportionately by removing the more attractive females.

4.4.4 Recommendations for similar surveys

To replicate methods from 1992 closely we did not take full advantage of modern opportunities in survey design such as better knowledge of the island's geography and forest extent, easier access, more sophisticated technology (GPS, detailed satellite maps) and better transport options. If past surveys are to be repeated and methods matched closely, additional effort has to be planned to allow repetition as well as producing the best possible population estimates with modern methods. Seasonal limits mean that more observer teams are required or the repeat survey has to cover the target season twice in different years. Past surveys that are to be repeated cannot be changed retrospectively but for initial surveys that are to be repeated in the future we would recommend the following: The survey period from July to September dry season is ideal for the region as fieldwork is much easier, more efficient and more predictable and breeding has not fully started in most areas, so breeding adults are still available for counting. Transects should be spaced out over all potential habitat as much as logistically possible, and clustered transects avoided at all costs. Effort should be proportional to the size of the forest patch per site. Some surveys of poor-quality forest (away from known strongholds) are also necessary. Island-wide presence/absence data from the same season for all large forest fragments are essential for species limited by trapping or similar factors unrelated to habitat quality. On Sumba the best approach for all but the largest forest areas is staying in the nearest settlement and approaching the transect by motorbike and on foot before sunrise. To survey the centres of large forest areas (remote areas of the national park) camps that are moved daily may be necessary. Line transects on paths are preferable to point transects if rare parrots and hornbills are the main target species (Buckland et al., 2008). It is now universally agreed that no settling-down period should be used for point-counts (Marsden, 1999; Buckland et al., 2008; Chamberlain and Rolando, 2014). Accuracy of distinguishing between perched and flying birds in aural-only detections could be assessed by placing one observer on a vantage point, who notes all flights of parrots with exact time stamps and approximate locations, while the other observers survey mock-transects below the canopy. This would also serve for calibrating correction factors for cluster size of aural-only detections and percentage of time spent in flight.

4.4.5 Implications for conservation and research on Sumba

To avoid future gaps in population estimates, regular monitoring should be carried out at least every 10 years with combined methodology for comparability to the 1992 and 2017 surveys and additional effort to cover the island’s habitat more representatively. This is particularly important for the declining Red-cheeked Parrot and Marigold

Lorikeet, the latter of which may need a re-assessment of its Red List status. Their breeding and feeding ecology on Sumba are also of future interest to understand the reasons for their declines and hence to implement appropriate mitigation and restorative measures. More emphasis should be given to investigate to what extent the small parrots suffer from trapping and trade and consequently in law enforcement and future public awareness campaigns, as they have largely been overshadowed by the rarer and more iconic larger species in the past. The uncertainty in trends for the threatened cockatoo, eclectus and hornbill is of concern as they show no sign of sustainable recovery from the extensive trapping of past decades. The effects of habitat loss and competition could potentially be mitigated by provision of artificial nest sites until forest has had time to recover.

References

Arndt, T. and Bashari, H. (2016) ‘Zum Status der Papageien auf Jampea.’ *Papageien*, 4 pp. 137–141.

Badan Pusat Statistik (2016) *Statistical yearbook of Indonesia*. [Online] [Accessed on 17th October 2017] www.bps.go.id.

Bashari, H. and Wungo, E. (2011) *Survey burung di Taman Nasional Manupeu Tanah Daru, Sumba, Indonesia*. Borgor, Indonesia.

Beaudrot, L., Ahumada, J. A., O'Brien, T., Alvarez-Loayza, P., Boekee, K., Campos-Arceiz, A., Eichberg, D., Espinosa, S., Fegraus, E., Fletcher, C., Gajapersad, K., Hallam, C., Hurtado, J., Jansen, P. A., Kumar, A., Larney, E., Lima, M. G. M., Mahony, C., Martin, E. H., McWilliam, A., Mugerwa, B., Ndoundou-Hockemba, M., Razafimahaimodison, J. C., Romero-Saltos, H., Rovero, F., Salvador, J., Santos, F., Sheil, D., Spironello, W. R., Willig, M. R., Winarni, N. L., Zvoleff, A. and Andelman, S. J. (2016) ‘Standardized Assessment of Biodiversity Trends in Tropical Forest Protected Areas: The End Is Not in Sight.’ *PLOS Biology*, 14(1) p. e1002357.

BirdLife International (2021) *Datazone*. [Online] [Accessed on 11th March 2021] http://datazone.birdlife.org/.

BirdLife International (2022) *Species Factsheet* Cacatua citrinocristata. [Online] [Accessed on 6th January 2022] http://www.birdlife.org.

Bolker, B. M. (2008) *Ecological models and data in R*. Princeton, US: Princton University Press.

Braun, M. P., Reinschmidt, M., Datzmann, T., Waugh, D., Zamora, R., Häbich, A., Neves, L., Gerlach, H., Arndt, T., Mettke-Hofmann, C., Sauer-Gürth, H. and Wink, M. (2017) ‘Influences of oceanic islands and the Pleistocene on the biogeography and evolution of two groups of Australasian parrots (Aves: Psittaciformes: *Eclectus roratus*, *Trichoglossus haematodus* complex). Rapid evolution and implications for taxono.’ *European Journal of Ecology*, 3(2) pp. 47–66.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. (2001) *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.

Buckland, S. T., Marsden, S. J. and Green, R. E. (2008) ‘Estimating bird abundance: making methods work.’ *Bird Conservation International*, 18 pp. 91–108.

Burung Indonesia (2013) *The behavioural ecology of breeding the Yellow-crested Cockatoo* Cacatua sulphurea citrinocristata *in Manupeu Tanadaru National Park, Sumba Island. 1st Progress report 2011*. Bogor, Indonesia: Burung Indonesia.

Cahill, A. J., Walker, J. S. and Marsden, S. J. (2006) ‘Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea citrinocristata* in Indonesia after 10 years of international trade control.’ *Oryx*, 40(2) pp. 161–167.

Casagrande, D. G. and Beissinger, S. R. (1997) ‘Evaluation of four methods for estimating parrot population size.’ *The Condor*, 99(2) pp. 445–457.

Chamberlain, D. and Rolando, A. (2014) ‘The effects of a settling-down period on estimates of bird species richness and occurrence from point counts in the Alps.’ *Bird Study*, 61(1) pp. 121–124.

Collar, N. J. (1997) ‘Family Psittacidae (Parrots).’ *In* del Hoyo, J., Elliott, A., and Sargatal, J. (eds) *Handbook of the Birds of the World, Vol. 4, Sandgrouse to Cuckoos*. Barcelona, Spain: Lynx Ediciones, pp. 280–477.

Collar, N. J., Andreev, A. V, Chan, S., Crosby, M. J., Subramanya, S. and Tobias, J. A. (2001) *Threatened birds of Asia: The BirdLife International Red Data Book*. Cambridge, UK: BirdLife International.

Collar, N. J. and Juniper, A. T. (1992) ‘Dimension and causes of the parrot conservation crisis.’ *In* Beissinger, S. R. and Snyder, N. F. R. (eds) *New world parrots in crisis: solutions from conservation biology.* New York and London: Smithsonian Institution Press, pp. 1–24.

Collar, N. J., Kirwan, G. M. and Boesman, P. F. D. (2020) ‘Red-cheeked Parrot (*Geoffroyus geoffroyi*).’ *In* del Hojo, J., Elliot, A., Sargatal, J., Christie, D. A., and Juana, E. (eds) *Birds of the World*. Ithaca, NY, USA: Cornell Lab of Ornithology.

Collen, B., Ram, M., Zamin, T. and McRae, L. (2008) ‘The Tropical Biodiversity Data Gap: Addressing Disparity in Global Monitoring.’ *Tropical Conservation Science*, 1(2) pp. 75–88.

Congedo, L. (2016) ‘Semi-automatic classification plugin documentation.’ *QGIS-plugin* p. 29.

Congedo, L. (2021) ‘Semi-Automatic Classification Plugin: A Python tool for the download and processing of remote sensing images in QGIS.’ *Journal of Open Source Software*, 6(64) p. 3172.

Dénes, F. V, Tella, J. L. and Beissinger, S. R. (2018) ‘Revisiting methods for estimating parrot abundance and population size.’ *Emu-Austral Ornithology*, 118(1) pp. 67–79.

Djawarai, Y., Bashari, H., Siregar, B. and Widyanto, A. (2014) *The breeding ecology of Sumba Cockatoo* Cacatua sulphurea citrinocristata *in Manupeu Tanadaru National Park and surrounding, Sumba*. *Burung Indonesia*. Bogor, Indonesia: Burung Indonesia.

Eaton, J. A., Van Balen, S. B., Brickle, N. W. and Rheindt, F. E. (2016) *Birds of the Indonesian Archipelago Greater Sundas and Wallacea*. Barcelona, Spain: Lynx Ediciones.

Eaton, J. A., Shepherd, C. R., Rheindt, F. E., Harris, J. B. C., van Balen, S. B., Wilcove, D. S. and Collar, N. J. (2015) ‘Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia.’ *Forktail*, 31 pp. 1–12.

eBird Basic Dataset (2019) ‘Version: EBD_relMay-2019.’ Ithaca, New York: Cornell Lab of Ornithology.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E. and Sodhi, N. S. (2011) ‘Primary forests are irreplaceable for sustaining tropical biodiversity.’ *Nature*, 478(7369) pp. 378–381.

Gregory, R. D., Van Strien, A., Vorisek, P., Meyling, A. W. G., Noble, D. G., Foppen, R. P. B. and Gibbons, D. W. (2005) ‘Developing indicators for European birds.’ *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1454) pp. 269–288.

Heinsohn, R., Ebert, D., Legge, S. and Peakall, R. (2007) ‘Genetic evidence for cooperative polyandry in reverse dichromatic Eclectus parrots.’ *Animal Behaviour*, 74(4) pp. 1047–1054.

Heinsohn, R. and Legge, S. (2003) ‘Breeding biology of the reverse-dichromatic, co-operative parrot *Eclectus roratus*.’ *Journal of Zoology*, 259(02) pp. 197–208.

Hidayat, O. and Kayak (2014) ‘Karakteristik dan preferensi habitat Kakaktua Sumba (*Cacatua sulphurea citrinocristata*) di Taman Nasional Laiwangi Wanggameti Provinsi Nusa Tenggara Timur.’ *Widyariset*, 17(3) pp. 399–408.

del Hoyo, J. and Collar, N. J. (2014) *HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 1: Non-passerines*. Barcelona, Spain and Cambridge, UK: Lynx Edicions and BirdLife International.

del Hoyo, J. and Collar, N. J. (2016) *HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 2: Passerines*. Barcelona, Spain: Lynx Edicions.

Inskipp, T., Broad, S. and Luxmoore, R. (1988) *Significant Trade in Wildlife -A Review of Selected Species in CITES Appendix II, Volume 3: Birds*. Cambridge, UK: IUCN Conservation Monitoring Centre.

Jones, M. J., Linsley, M. D. and Marsden, S. J. (1995) 'Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia.' *Bird Conservation International*, 5(01) pp. 21–52.

Kendall, S. B. (1979) 'Citron-crested cockatoos in Sumba.' *Avicultural Magazine*, 85(2) pp. 93–94.

Kormos, C., Mackey, B., Dellasala, D., Kumpe, N., Jaeger, T., Mittermeier, R. A. and Filardi, C. (2017) 'Primary Forests: Definition, Status and Future Prospects for Global Conservation.' *In Reference Module in Earth Systems and Environmental Sciences*. Elsevier, pp. 1–11.

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. and Steffan-Dewenter, I. (2009) 'Extinction debt: a challenge for biodiversity conservation.' *Trends in Ecology and Evolution*. Elsevier Current Trends pp. 564–571.

Lee, D. C. and Marsden, S. J. (2008) 'Adjusting count period strategies to improve the accuracy of forest bird abundance estimates from point transect distance sampling surveys.' *Ibis*, 150(2) pp. 315–325.

Lunstrum, E. and Givá, N. (2020) 'What drives commercial poaching? From poverty to economic inequality.' *Biological Conservation*, 245, May, p. 108505.

Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M., Elston, D. A., Scott, E. M., Smith, R. I., Somerfield, P. J. and Watt, A. D. (2010) 'Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time.' *Trends in ecology & evolution*, 25(10) pp. 574–582.

Marsden, S. J. (1995) *The ecology and conservation of the parrots of Sumba, Buru and Seram, Indonesia.* PhD-thesis. Manchester Metropolitan University.

Marsden, S. J. (1999) 'Estimation of parrot and hornbill densities using a point count distance sampling method.' *Ibis*, 141(3) pp. 327–390.

Marsden, S. J. and Fielding, A. (1999) 'Habitat associations of parrots on the Wallacean islands of Buru, Seram and Sumba.' *Journal of Biogeography*, 26(3) pp. 439–446.

Marsden, S. J. and Jones, M. J. (1997) 'The nesting requirements of the parrots and hornbill of Sumba, Indonesia.' *Biological Conservation*, 82(3) pp. 279–287.

Marsden, S. J. and Pilgrim, J. D. (2003) 'Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain, PNG.' *Ibis*, 145(1) pp. 45–53.

Marsden, S. J. and Royle, K. (2015) 'Abundance and abundance change in the world's parrots.' *Ibis*, 157(2) pp. 219–229.

Mayr, E. and Stein, G. H. W. (1944) 'The birds of Timor and Sumba.' *Bulletin of the AMNH*, 83.

Miller, D. L., Rexstad, E., Burt, L., Bravington, M. V and Hedley, S. (2019) 'dsm: Density Surface Modelling of distance sampling data.'

Mollon, A. (2010) *The effect of point count duration on avian density estimates*. Imperial College London.

Nandika, D., Agustina, D. and Halouate, M. (2012) *Study of population and conservation of Lesser Sulphur-crested Cockatoo Cacatua sulphurea*. Bekasi, Indonesia.

Persulessy, Y. E., Djawarai, Y. B. and Marut, R. (2003) *Survei populasi dan distribusi kakatua-kecil jambul-kuning* Cacatua sulphurea citrinocristata *dan empat jenis paruh bengkok lain di Pulau Sumba*. Bogor, Indonesia.

PHPA, LIPI and BirdLife International-IP (1998) *Species recovery plan Yellow-crested Cockatoo*. Bogor, Indonesia: PHPA/LIPI/BirdLife International - Indonesia Programme.

Pires, S. F. (2012) 'The illegal parrot trade: a literature review.' *Global Crime*, 13(3) pp. 176–190.

Pires, S. F., Olah, G., Nandika, D., Agustina, D. and Heinsohn, R. (2021) 'What drives the illegal parrot trade? Applying a criminological model to market and seizure data in Indonesia.' *Biological Conservation*, 257, May.

QGIS Development Team (2021) 'QGIS Geographic Information System.' Hannover, Germany: Open Source Geospatial Foundation Project.

Reuleaux, A., Collar, N. J., Siregar, B. A., Limu, R. N. D., Mardiastuti, A. and Marsden, S. J. (2022) 'Correlates of persistence in remnant populations of two Critically Endangered cockatoos.' *Animal Conservation*.

Reuleaux, A., Siregar, B. A., Collar, N. J., Mardiastuti, A. and Marsden, S. J. (2022) 'Productivity constraints on Citron-crested Cockatoos in a rich community of large hole-nesting birds.' *Avian Research*, 13 p. 100015.

Sauer, J. R., Pardieck, K. L., Ziolkowski, D. J., Smith, A. C., Hudson, M. A. R., Rodriguez, V., Berlanga, H., Niven, D. K. and Link, W. A. (2017) 'The first 50 years of the North American Breeding Bird Survey Los primeros 50 años del Conteo de Aves Reproductivas de América del NorteThe North American Breeding Bird Survey at 50.' *The Condor*, 119(3) pp. 576–593.

Sitompul, A. F., Kinnaird, M. F. and O'Brien, T. G. (2004) 'Size matters: The effects of forest fragmentation and resource availability on the endemic Sumba Hornbill *Aceros everetti*.' *Bird Conservation International*, 14(SPEC. ISS.).

Snyder, N. F. R., McGowan, P., Gilardi, J. and Grajal, A. (2000) *Parrots. Status Survey and Conservation Action Plan 2000-2004*. Oxford, UK: IUCN.

SSC IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. Gland, Switzerland and Cambridge, UK: Species Survival Commission. IUCN. [Online] http://www.iucnredlist.org/apps/redlist/static/categories_criteria_3_1.

Tella, J. L. and Hiraldo, F. (2014) 'Illegal and legal parrot trade shows a long-term, cross-cultural preference for the most attractive species increasing their risk of extinction.' *PLoS ONE*, 9(9) p. e107546.

Thiollay, J. M. (2006) 'Severe decline of large birds in the Northern Sahel of West Africa: a long-term assessment.' *Bird Conservation International*, 16(4) pp. 353–365.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B. B., Marques, T. A. and Burnham, K. P. (2010) 'Distance software: design and analysis of distance sampling surveys for estimating population size.' *Journal of Applied Ecology*, 47(1) pp. 5–14.

Torquebiau, E. F. (1986) ‘Mosaic patterns in dipterocarp rain forest in Indonesia, and their implications for practical forestry.’ *Journal of Tropical Ecology*, 2(4) pp. 301–325.

Valle, S., Collar, N. J., Harris, W. E. and Marsden, S. J. (2018) ‘Trapping method and quota observance are pivotal to population stability in a harvested parrot.’ *Biological Conservation*, 217, January, pp. 428–436.

Winiarski, K. J., Miller, D. L., Paton, P. W. C. and McWilliams, S. R. (2013) ‘Spatially explicit model of wintering common loons: conservation implications.’ *Marine Ecology Progress Series*, 492, October, pp. 273–283.

Wungo, E. (2011) *Laporan survei populasi paruh bengkok terancam punah* Cacatua sulphurea citrinocristata*, Sumba, Nusa Tenggara Timur*. Bogor, Indonesia: Burung Indonesia.

Appendices

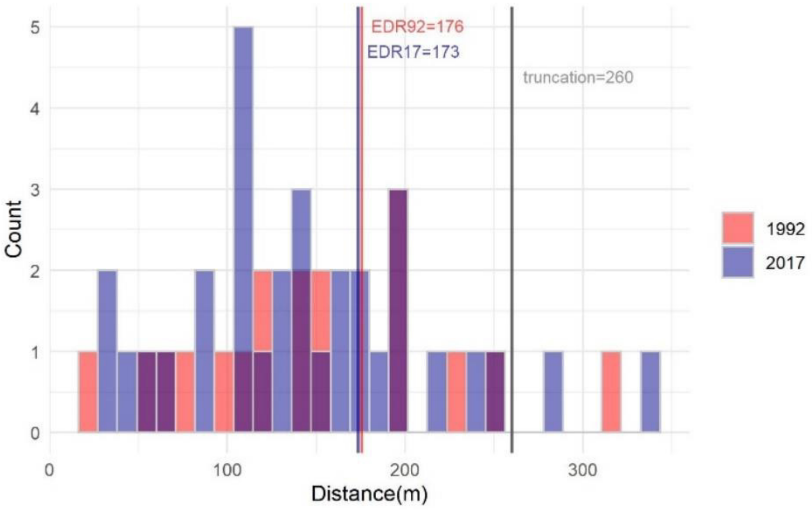
Appendix 4.1 Detections of birds in flight. The proportions of aerial birds among encounters differed between species and years (range 3–73%). In 2017 the proportions of aerial birds were lower than in 1992 for all species except the Marigold Lorikeet. Lorikeets had the highest proportion of aerial detections in both years and hornbills the lowest. Number and percentage of encounters in flight. Publications in 1995 used slightly different subsets: Jones et al. (1995) included up to eight repetitions per point count station whereas we included only the first two repetitions in our analysis. For assessment of the proportion of flying birds, Marsden (1995) excluded point counts in open areas, whereas Jones et al. (1995) and this analysis assessed the proportion in all habitats. χ^2 and p report results of two-sided χ^2-tests comparing aerial proportions from this analysis between years (not the numbers published in 1995).

	Number of detections in flight (% total contacts)				
	Published 1995	This analysis	This analysis		
Species	**1992**	**1992**	**2017**	χ^2	p
Citron-crested Cockatoo	30 (45%)[a]	10 (35%)	6 (11%)	5.40	0.020*
Sumba Eclectus	36 (59%)[a]	32 (36%)	18 (20%)	5.09	0.024*
Great-billed Parrot	23 (59%)[a]	20 (47%)	21 (17%)	13.52	<0.001***
Marigold Lorikeet	196 (73%)[b]	204 (73%)	130 (65%)	2.83	0.092
Red-cheeked Parrot	124 (45%)[b]	126 (40%)	47 (14%)	55.05	<0.001***
Sumba Hornbill	8 (27%)[a]	8 (32%)	1 (3%)	7.30	0.007**

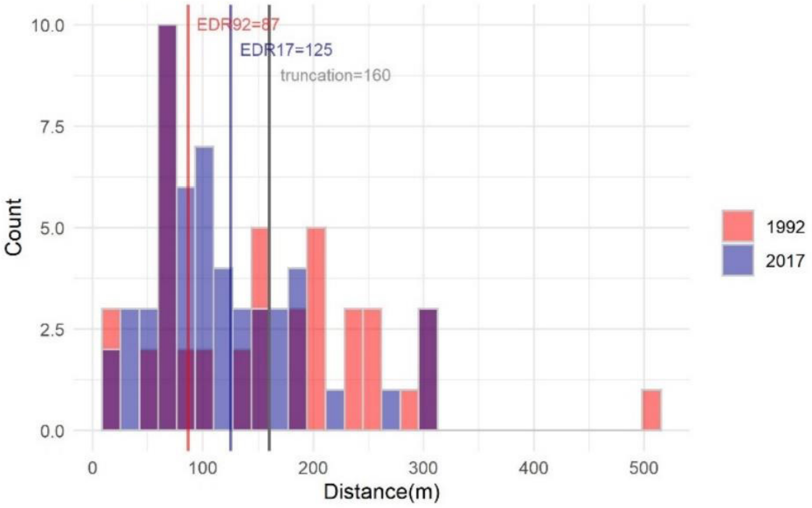
Sources: [a] Jones et al 1995, [b] Marsden 1995

Appendix 4.2: Histograms of detections with truncation distances and effective detection radii (bars are semi-transparent showing overlap between years in purple). Data was truncated at the same distance for both years, except for the Sumba Hornbill where matching the truncation distance worsened the problem of fitting a detection function.

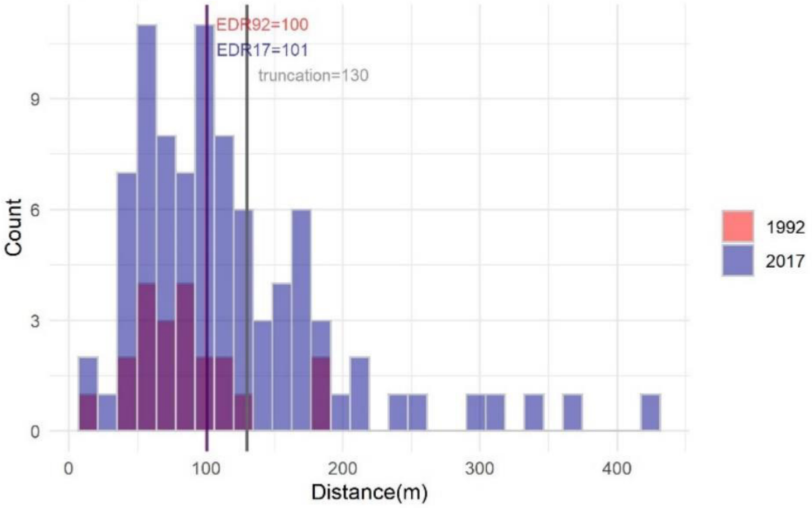
CacSul - Yellow-crested Cockatoo

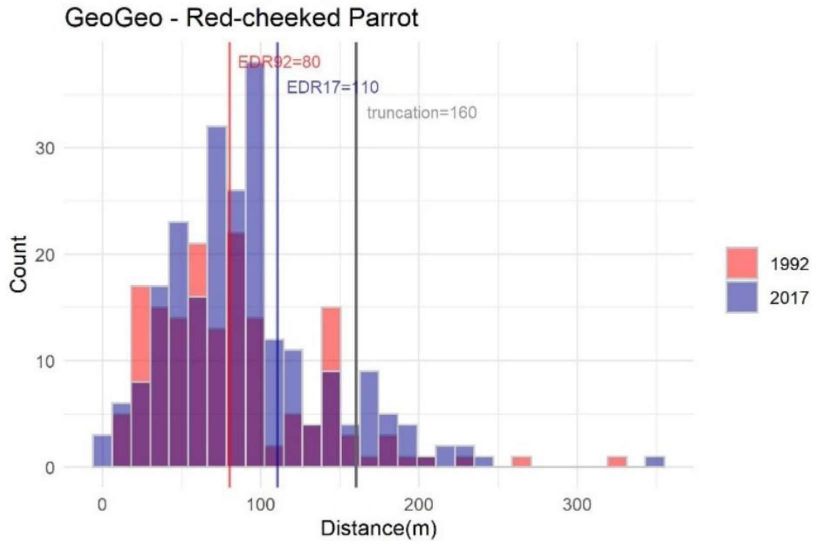


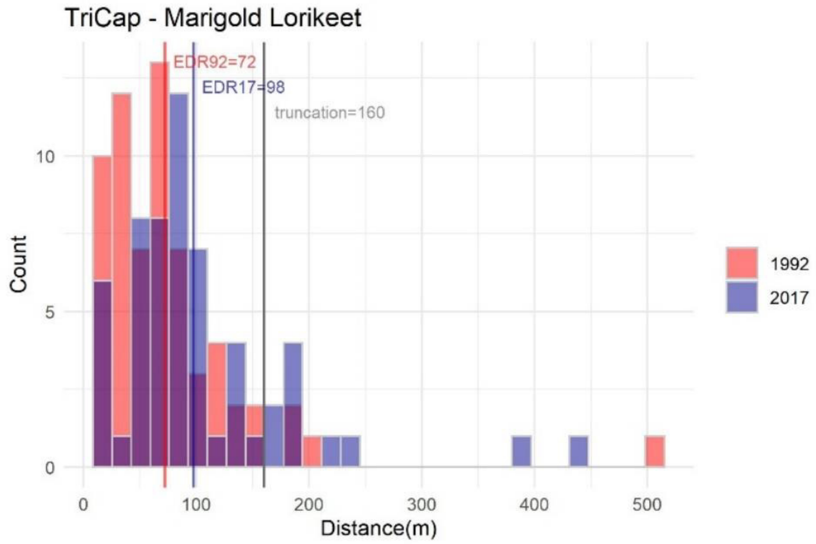
EclRor - Sumba Eclectus

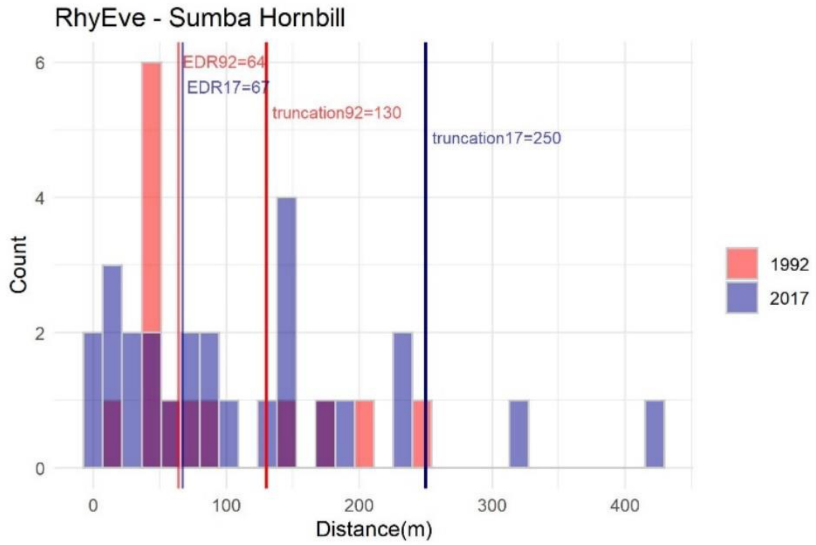


TanMeg - Great-billed Parrot




GeoGeo - Red-cheeked Parrot
EDR92=80
EDR17=110
truncation=160
Count
0
10
20
30
0
100
200
300
Distance(m)
1992
2017


TriCap - Marigold Lorikeet
EDR92=72
EDR17=98
truncation=160
Count
0
5
10
0
100
200
300
400
500
Distance(m)
1992
2017


RhyEve - Sumba Hornbill
EDR92=64
EDR17=67
truncation92=130
truncation17=250
Count
0
2
4
6
0
100
200
300
400
Distance(m)
1992
2017

5 Productivity constraints on Citron-crested Cockatoos in a rich community of large hole-nesting birds

This is an edited version of the publication: Reuleaux, A., Siregar, B. A., Collar, N. J., Mardiastuti, A. and Marsden, S. J. (2022) ‘Productivity constraints on Citron-crested Cockatoos in a rich community of large hole-nesting birds.’ *Avian Research*, 13 p. 100015.

Abstract

Knowledge of breeding success and its limiting factors is crucial in assessing species’ conservation needs. As cavity-nesters, parrots are particularly influenced by the availability of suitable cavities and low breeding output, whether due to natural processes or trapping. On the island of Sumba, Indonesia, the Critically Endangered Citron-crested Cockatoo Cacatua citrinocristata has the added problem of co-existing with an unusually rich hole-nesting bird community in a forested environment much constrained by habitat loss. We monitored 95 nesting cavities of cockatoos and their competitors and potential nest-predators, over one to four breeding seasons, using a combination of camera-traps, direct checks on nest contents, and observations from the ground. Competition for suitable cavities was intense among three large parrot species, two owls and a hornbill. Visitation rates by potential competitors were higher at unoccupied cavities than at those containing active nests, reflecting the guarding behaviour of the occupants. The Endangered Sumba Hornbill Rhyticeros everetti dominated observed direct confrontations and was the most frequent visitor to active parrot nests, suggesting a further role as a potential nest-predator. Cockatoos prospected many cavities but rarely then attempted to nest: instead the sites were usually occupied by other cavity-nesters, or by bees. At the few cavities where cockatoos did breed, predation pressure was likely low, and observed success rate high (10 successful of 15 nests), although the low number of nests found early in the breeding cycle suggests that some may have failed before detection. Intense competition for cavities suggests a shortage of suitable nest-sites, the need for preservation of old hole bearing trees and a role for nestboxes. Accessible, known, safe artificial nest-sites would also provide opportunities to assess the scale of nest-site shortage, allow camera placements to study productivity, exclude some competitors and predators and prevent illegal trapping. Especially given continued trapping

pressure, the species would benefit from targeted local awareness-raising and law enforcement, with the whole endeavour backed up by longer-term forest restoration.

5.1 Background

A great variety of bird species nest in tree cavities (van der Hoek et al., 2017). Cavities provide clear advantages over open nesting in terms of shelter from weather and protection from predators, but have the considerable disadvantage of limited availability, either of the holes themselves or of the substrates in which to make them (Lack, 1968; Nilsson, 1986; Brightsmith, 2005; Olah et al., 2016). In contrast to primary cavity-nesters, such as woodpeckers (Picidae), secondary cavity-nesters, such as most parrots (Psittaciformes), are particularly constrained by availability, commonly resulting in much intra- or interspecific competition for favoured sites (Collias, 1964). Availability can further decline, and competition increase, in circumstances where much the most important cavity-bearing substrate—larger, older trees—is itself reduced by forestry practices such as selective logging (van Balen et al., 1982; Nilsson, 1986; Cockle et al., 2010; Schaaf et al., 2021). For this reason, the plight of secondary cavity-nesters represents a particular conservation concern (Cockle et al., 2010; Altamirano et al., 2017; Gutzat and Dormann, 2018; Schaaf et al., 2020, 2021). In the case of parrots, owing to their unique appeal as pets, this concern is greatly amplified by the fact that trappers learn where the birds' favoured cavities are and take their nestlings year after year, thereby greatly suppressing productivity and recruitment (Marsden and Jones, 1997; González, 2003; Martin et al., 2014; Valle et al., 2018). Parrots are long-lived birds, and population size may be a poor correlate of population health if breeding success and other demographic rates are not taken into account (Shoemaker et al., 2013). Certainly a knowledge of productivity and its limiting factors is essential for assessing population viability and urgently needed for many poorly known and threatened parrots (Monterrubio et al., 2002; Spoon, 2006; Heinsohn et al., 2009; Olah et al., 2016). The difficult task of acquiring such knowledge has recently been made somewhat easier by advances in camera technology for checking nest contents (e.g. Reuleaux et al., 2014; Bonaparte and Cockle, 2017), observing behaviour at the nest (e.g. Sanders and Maloney, 2002; Richardson et al., 2009) and monitoring predation (e.g. Clout and Merton, 1998; Masello et al., 2006; Ribeiro-Silva et al., 2018).

The Citron-crested Cockatoo *Cacatua citrinocristata* is endemic to the island of Sumba, East Nusa Tenggara, Indonesia, having recently been elevated to species rank from the Wallacean region's Yellow-crested Cockatoo *C. sulphurea* (Collar and Marsden, 2014; Eaton et al., 2016). Despite being larger than Sumba (11,000 km^2), the adjacent islands of Sumbawa (15,400 km^2), Flores (13,500 km^2) and Timor (29,700 km^2) have just one or two large parrots (Sumba has three), no hornbills (Sumba has one) and one or two large owls (Sumba has two); thus in total Sumba has six large hole-nesters, Timor four, Flores three and Sumbawa just two. Studies of the Yellow-crested Cockatoo's breeding biology in the wild have been very limited and most were just side notes in studies of population size, usually involving <10 nests whose contents were not investigated (Agista and Rubyanto, 2001; Hidayat, 2012; Nandika and Agustina, 2012; Imansyah et al., 2016; Ihsannudin et al., 2020; Nandika et al., 2020). Studies of the Citron-crested Cockatoo have been slightly more extensive (Marsden, 1995; Marsden and Jones, 1997), even including some nest access (Walker et al., 2005; Djawarai et al., 2014), but owing to the difficulties in locating active nests the sample sizes still remained low (Marsden and Jones, 1997; Walker et al., 2001, 2005; Djawarai et al., 2014).

After decades of intense pressure from the international pet trade and resultant dramatic declines in numbers, the trapping of cockatoos has been illegal on Sumba since 1992/93 (Marsden, 1995; PHPA et al., 1998). In 2002, evidence of increased densities (2.0 individuals/km^2 in 1992 to 4.3 in 2002, Jones et al., 1995; Cahill et al., 2006) gave hope that populations were recovering. However, current estimated numbers are not significantly higher than those immediately before the ban (Jones et al., 1995; Wungo, 2011; AR unpubl. data). The only published total population estimate based on field work remains the 1992 figure of 3,200 individuals (Jones et al., 1995). In the absence of reports of trapping, this apparent failure to recover significantly has been suspected to relate to low productivity (Djawarai et al., 2014). Here, therefore, we aim to assess the recent productivity of Citron-crested Cockatoos and the factors that might affect it. Typically, breeding success in parrots is limited by lack of suitable nest sites, competition for these sites (e.g. Heinsohn et al., 2003), nest predation (Moorhouse et al., 2003; Harper and Bunbury, 2015) and taking chicks and adults for the pet trade (Pires, 2012; Valle et al., 2018). Natural productivity in Citron-crested Cockatoos may always have been low even without human interference, but an understanding of the current limiting factors may nevertheless be crucial for identifying conservation interventions that might improve the status of the species (e.g. predator management, provision of artificial nest-sites, exclusion of competitors from current nest-sites) at least until sufficient habitat can be restored. We investigated the occupancy and fate of potential cockatoo nest sites, seasonal cavity use across the community of large hole-nesters, and visitation rates to nests by potential competitors and predators, and we present new knowledge on the Citron-crested Cockatoo's breeding behaviour in the wild.

5.2 Methods

The island of Sumba (9.3–10.3°S 118.9–120.8°E) is an important centre of endemism which, in the taxonomy of the late 1990s, supported seven bird species known nowhere else (Stattersfield et al., 1998). To this tally the elevation of Citron-crested Cockatoo (Critically Endangered), Sumba Eclectus *Eclectus cornelia* (Endangered) and—depending on taxonomy—up to four other avian taxa to species rank has added further evidence of the island's high biological significance. Sumba is dominated by relatively low limestone hills reaching up to 1,200 m asl, with a dry season from May to November and a rainy season from December to April. With one of Indonesia's lowest per capita incomes and large number of livestock, it has lost most of its forest cover to pasture and agriculture, on which many of its 650,000 inhabitants rely for subsistence (Monk et al., 1997; Badan Pusat Statistik, 2016). By 2020 the number of inhabitants had risen to 779,000 (Badan Pusat Statistik, 2021). We undertook fieldwork in the forested areas of central and western Sumba, mostly in Matalawa National Park (the 501 km² block formerly called Manupeu Tanah Daru National Park), but we also included four smaller forest patches in the centre of the island. Following recommendations on conservation considerations (Collar et al., 2017), we omit all details on locations here and do not present maps to avoid supplying information to potential trappers and traders. The locations and maps are however available for bona-fide researchers or conservation purposes from the authors.

The entire study period was June 2015–May 2019, encompassing four breeding seasons, but with effort varying between years and seasons. Our methods for locating nest-sites were: checking all cavities recorded as parrot nests in the past (Djawarai et al., 2014); long watches from vantage points over areas with cockatoo activity;

checking trees with potentially suitable cavities; searching for twigs snapped off large trees by cockatoos during nest-prospecting; and following tip-offs from forest users and information from former trappers about once-occupied cavities. At the start of the study in 2015, we knew from previous work by the non-governmental organisation Burung Indonesia of twelve cavities with past cockatoo activity. We learnt of a further 53 nests from former trappers at various points in time throughout the study period. In addition, we located 30 prospected cavities by following cockatoo activity. Nests were difficult to find in the dense forest, particularly when no good vantage points were present. Even cavities we repeatedly observed being entered by cockatoos had only a small chance of being nests, as less than a quarter of prospected sites became active (Table 5.1). Ethical and legal issues prohibited cooperation with any of the few trappers who were still active. The former trappers we consulted had, by then, not raided nests for over ten years, and most sites they identified (47 out of 53) were not occupied by cockatoos in the study period.

Table 5.1: Number of potential nests found and monitored per season. Cavities are split by method of finding them: B cavity was part of the Burung Indonesia (BI) dataset before 2014, O cavity found by own fieldwork, T cavity shown by former trappers or other forest users; Breeding season headings contain two years because they span the turn of the year. Data for monitoring by the BI team in 2014/15 are not included here.

	2015–2016	2016–2017	2017–2018	2018–2019	All seasons
No. potential nests monitored (B/O/T)	42(11/21/10)	62(12/21/29)	68(11/19/38)	68(10/17/41)	95(12/30/53)
First monitored that year (O/T)	31(21/10)	23(2/21)	20(6/14)	9(1/8)	83(30/53)
No. cavities occupied by cockatoos (B/O/T)	3(1/2/0)	3(1/0/2)	4(0/3/1)	5(1/1/3)	12 (1/6/5)
Working period	Aug–Apr	Nov–Feb	Dec–Mar	Jun–Oct, Mar, May	—

Once we located a cavity with cockatoo activity, we watched it from a distance of 300–1,000 m with optics or from a hide near the tree to determine breeding stage. If the cavity was accessible (i.e. in a living tree, with no dead branches at or directly above it and not beyond the reach of safe rope placement points), we checked its contents using a single-rope climbing technique. We inspected the contents visually or using a compact camera, a mobile phone camera or an endoscopic camera attached to a mobile phone. We deployed camera-traps sporadically within the period November 2016–May 2019. Where possible, a camera-trap (Acorn 5210A or Bushnell Natureview) was installed 1–2 m above the entrance with a metal brace (Figure 5.1), following a method developed in the New Zealand Department of Conservation (J. Malham *in litt.* 2016). In the absence of branches or suitably positioned trunk, cameras had to be installed nearer or further away from the entrance and/or to the side instead of above. We set the cameras to be triggered by motion at the nest entrance and to take still photographs during the day and infra-red photographs with an invisible IR flash at night (a series of three photos was taken automatically each time the motion sensor was triggered), with medium motion sensitivity, 50–80% of IR-LED blocked with tape to reduce over-exposure depending on distance from the nest. We serviced the cameras every two weeks when a cavity was hosting nesting birds, and otherwise every 2–6 months. Camera malfunctions due to various factors (ants, moisture, falling branches, false triggers by newly grown foliage, rapid battery depletion from unexpected nocturnal activity) were frequent. We compiled camera data by viewing photographs with each day as a datapoint and recording each species that visited or occupied the cavity. For clarity, figures only show the visiting five taxa that also appeared as occupants in our study (three large parrots, two owls, here combined, and a hornbill) and the potential predators are grouped into hornbill, owls, hawks, reptiles and mammals.

Figure 5.1: a) Nest tree in deciduous forest, b) rope access at emergent nest tree in closed-canopy forest, c) camera set-up above nest-cavity in *Tetrameles nudiflora* tree occupied by a Barn Owl *Tyto alba*, d) camera-trap with brace and rain protection, e) camera above a cavity with upwards-facing entrance. (Photos a,c: AR; b: Romy ND Limu with permission; d,e: BAS)

We sought always to avoid disturbance to breeding birds. Nests were watched from as far away as visibility of the cavity entrance permitted. If cockatoos started alarm-calling without another discernible cause, the observers left the area and later tried to approach it undetected from another direction. We watched nests from early in the morning and accessed them when both parents had left the cavity. Disturbance was limited to 30 minutes from the time the climber was noticed by a guarding parent to his or her leaving the area. Eggs of unknown age were examined in place by candling without moving them, to determine if they were old enough to handle. If candling in place was not possible, we waited for 7–10 days to ensure the egg was sufficiently developed to be handled without risk to the embryo. Eggs older than seven days were candled more thoroughly by handling them within the dark of the cavity to determine fertility, age and any problems, following Delany et al. (1999). We did not access nests during the suspected laying period (to prevent potential abandonment), the calculated hatching period (to avoid disrupting a delicate process) or the week before anticipated fledging (to eliminate the chance of accidental force-fledging).

We included a cavity in our dataset if cockatoos ever showed an interest in it, as defined by at least one cockatoo entering it with its whole body at least once (referred to hereafter as 'prospected'). We also included cavities that were reported by former trappers to have been prospected by cockatoos in the past. Cavities reportedly once used by cockatoos but subsequently destroyed, filled by termites (Termitoidae) or blocked by epiphytes were recorded as 'unusable' and excluded from the dataset. We defined cavities as 'occupied/active nests' if we confirmed eggs or broods through direct access or had strong behavioural evidence that the adult cockatoos had eggs or chicks (e.g. swift changeover between partners attending the nest). Older chicks (>30 days) were often fed in the entrance and could therefore be observed directly.

5.2.1 Statistical analysis

To assess differences between occupied and unoccupied cavities in terms of visitation rates (daily and weekly) by nest-competitors and potential nest-predators, we used generalized linear mixed models (GLMM with package lme4 v1.1-26) fit by maximum likelihood with logit link and cavity as random effect (Bates et al., 2015; R Core Team, 2021). We created four competing models for each species combination: one with a random intercept and a random slope, one with only a random intercept, one without a random effect and one with only the random effect. We used AIC to chose between the models, and checked significance of the random effect with an ANOVA. We report the coefficient β ± standard error. For the comparisons between occupied and unoccupied cavities, we excluded the occupying species as visitors for the duration of the nesting attempt including a period of one month before and after use unless this overlapped with the exclusion period of a different species' nesting attempt. In case of overlap, the species to be excluded changed half-way between the occupied periods.

5.3 Results

5.3.1 Nest trees and cameras

In total, we investigated 95 cavities as cockatoo nest-sites over the four-year period (with 266 monitored cavity-seasons). Of these, 36 cavities with repeated cockatoo activity were monitored more intensively, for a total of 128 cavity-seasons, with 103 occupied by cockatoos or their competitors, 13 unusable and 12 apparently available but unused. All investigated cavities were in large mature trees (minimum diameter at breast height = 82 cm, minimum height = 27 m), with 67% in Tetrameles sp. (Tetramelaceae), 13% in Chisocheton sp. (Meliaceae), and 8% in Palaquium sp. (Sapotaceae) (Figure 5.2). Only 11% were in dead trees.

Over 30 months spanning three breeding seasons, a total of 5,675 camera-days of monitoring was undertaken at twelve cavities (range 115–889 days). We excluded three other, unoccupied cavities (381 camera-days) owing to poor cavity quality, unmonitored alternative entrances and safety reasons. A total of 27 animal species—five parrots, a hornbill, three owls, four raptors, a dove, five passerines, three reptiles and five mammals—were photographed near the cavity entrances. Of these, 16 were hole-nesters, so we considered them for the role of cavity-competitors. Eggs or chicks featured in the diets of 15 species, which we therefore investigated as potential nest-predators of parrots.

Figure 5.2: a) Cockatoo nest tree found with traditional climbing set-up prepared for harvest by illegal trappers in 2018; b) guide demonstrating traditional Sumba cockatoo tree-climbing method in 2017; c) twig with nylon nooses left behind by cockatoo trappers after use at a cockatoo roost site in 2018. (Photos a,b: Charles U. Daula used with permission, c: AR)

5.3.2 Seasonal cavity use across the community

Cockatoo breeding activity was observed in almost every month of the year, but the laying stage was limited to late June to early December and fledging only occurred from January to April (Figure 5.3). Most chicks fledged during the rainy season. Owls, although not included in the graph, were found breeding in every month of the year (Figure 5.4).

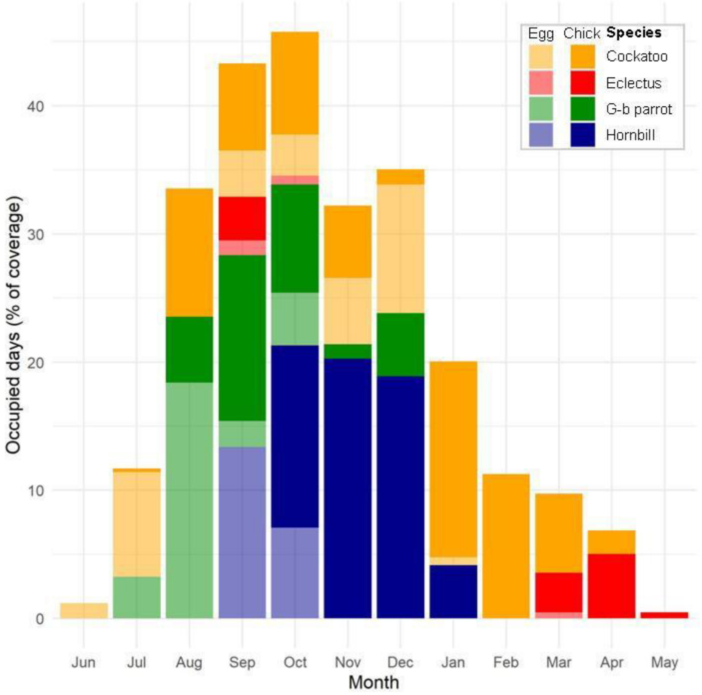


Figure 5.3: Seasonality of cavity-nesting monitored by camera-traps over 2.5 years (2016–2019) in the forested areas of central and western Sumba. Paler colours indicate days at egg stage, darker colours chick stage. Data were pooled across four breeding seasons and twelve cavities that had cockatoos prospecting them at some point.

5.3.3 Visitation rates and competition

Overall visitation rates and species visiting varied considerably across cavities (Figure 5.4, $\chi^2 = 54.3$, df = 3, p<0.001). Six of the twelve cavities were occupied by two different species during the study period, and all of them were visited by at least three of the five large cavity-nesters (Figure 5.4). Competing species visited occupied cavities less often than unoccupied ones (GLMM fit by maximum likelihood, $\beta = -0.29 \pm 0.05$ [SE], $p < 0.001$).

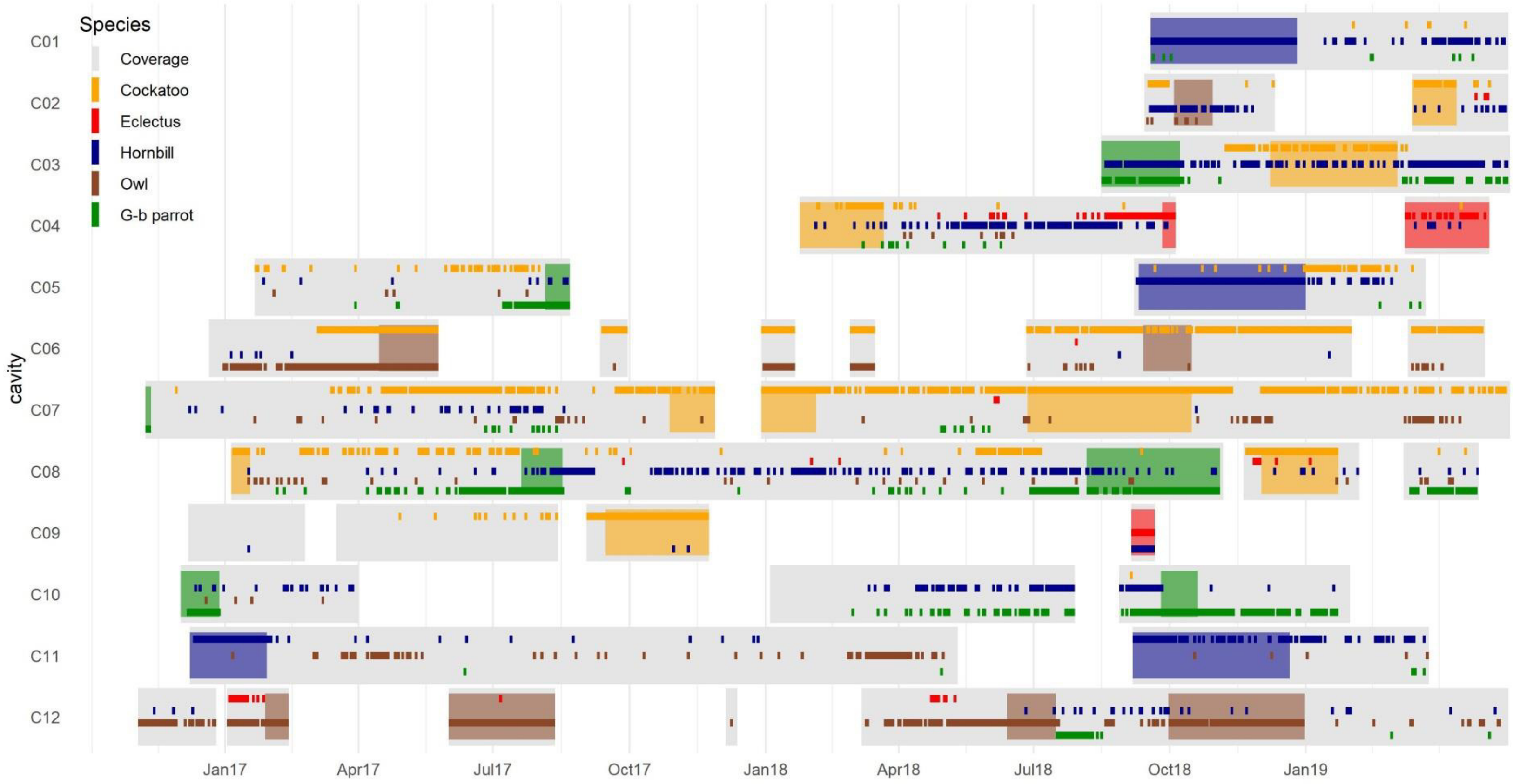


Figure 5.4: Visitors and occupants of nesting cavities monitored by camera-traps over three breeding seasons, November 2016–April 2019, in the forested areas of central and western Sumba. Each row represents one of twelve cavities with cockatoo interest. Small narrow, darker bars indicate visits. Broad paler bars indicate that the respective species occupied the cavity, i.e. had either eggs or chicks within. Grey background indicates the days covered by camera footage.

Figure 5.5: Direct evidence of competitive interaction at Citron-crested Cockatoo cavities: a) Sumba Eclectus attempting to take over a cockatoo cavity; b) Sumba Hornbill and Great-billed Parrot competing for a cavity used by Citron-crested Cockatoos in the previous season; c) Sumba Hornbill displacing a cockatoo from its prospected cavity; d) a cockatoo repeatedly evicting a Great-billed Parrot from its cavity before either laid eggs; e) Sumba Hornbill attempting to take over an active Great-billed Parrot nest; f) cockatoo finding a Barn Owl inside the cavity the cockatoo pair had been prospecting for weeks, while a second cavity occupied by different cockatoo pair can be seen 10 m below in the top left corner of the photo. (Photos: camera traps deployed, programmed, serviced and collected by team AR, BAS, Romy ND Limu, used with permission)

Direct confrontations between competing hole-nesting species caught by the camera-traps were relatively rare (30 occasions in 5,675 cavity-days monitored), as many directly observed conflicts took place in the tops of the nest trees and were often decided vocally without the intruders approaching the cavities. The majority of camera-trapped confrontations were won by Sumba Hornbill *Rhyticeros everetti* (two against cockatoos, one against Sumba Eclectus and four against Great-billed Parrots *Tanygnathus megalorynchos*) and by owls (five against cockatoos and one against Sumba Eclectus). Confrontations between cockatoos and Great-billed Parrots were the commonest of all observed confrontations, with cockatoos dominating in 14 of 16 interactions. Great-billed Parrots were the species to lose most confrontations (Table 5.2). Three cases of direct intra-specific confrontations were recorded (one each among two hornbill males, two Eclectus females and two Great-billed Parrots).

Table 5.2: Direct confrontations between nest-cavity competitors captured by camera-traps at 12 cavities in 5,675 camera-days. Interspecific confrontations in other parts of the tree were not captured by the cameras aimed at the cavity entrances and are therefore not included here.

Dominant taxon→ **Displaced taxon↓**	**Hornbill**	**Cockato o**	**Eclectu s**	**Great-billed Parrot**	**Owl s**	**Total losses**
Sumba Hornbill	1	0	0	0	0	1
Citron-crested Cockatoo	2	0	0	2	9	13
Sumba Eclectus	1	0	1	0	0	2
Great-billed Parrot	3	14	0	1	0	18
Owl spp.	0	1	0	0	0	1
Total wins	7	15	1	3	9	35

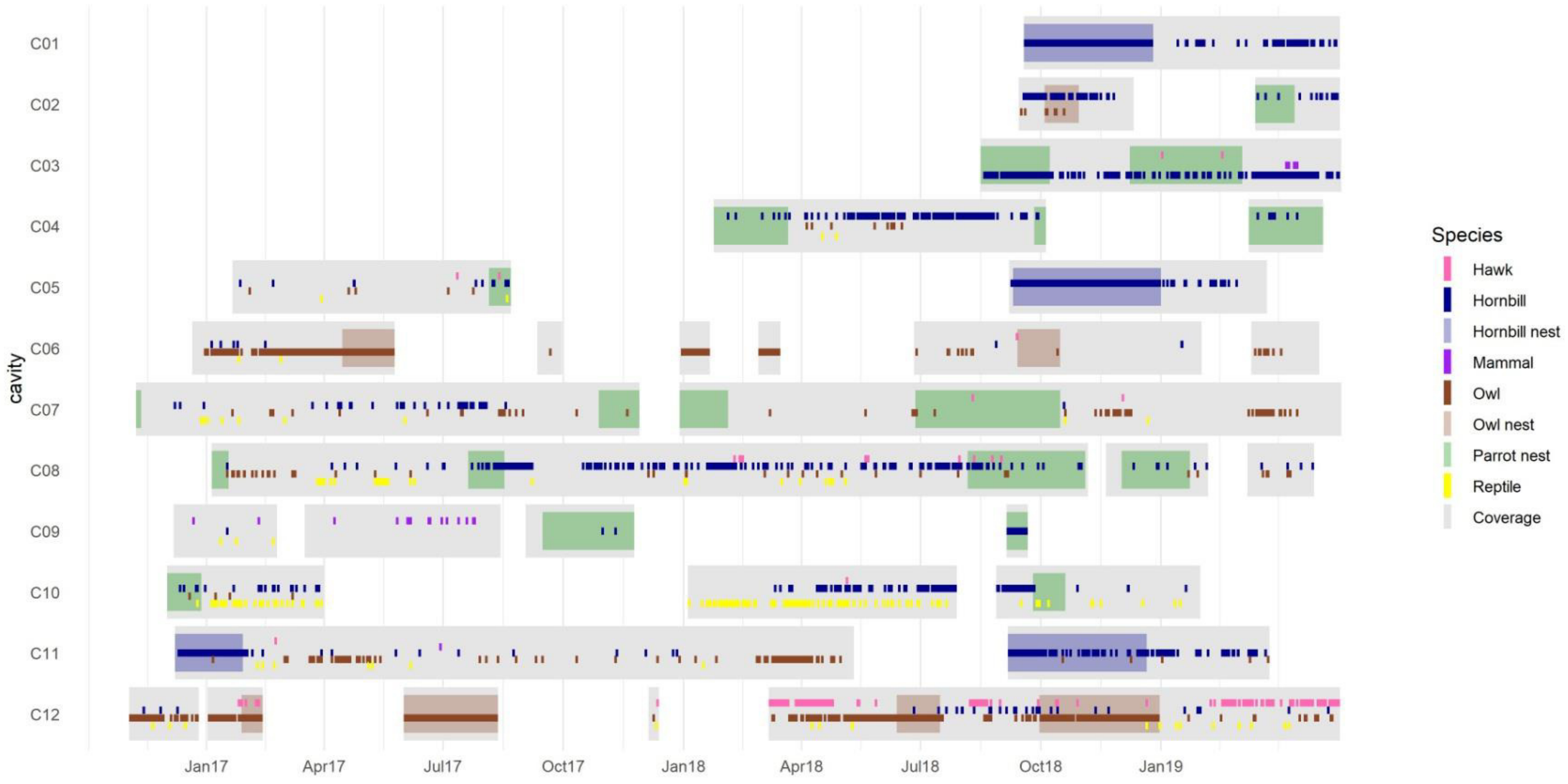


Figure 5.6: Visits to nest-cavities by potential predators recorded by 12 camera-traps at cavity entrances. Grey background indicates days monitored by camera-traps; periods with active nests (with eggs or chicks) are shaded in the colour of the occupying species. Species recorded as occupants or predators include (parrots): Citron-crested Cockatoo *Cacatua citrinocristata*, Sumba Eclectus *Eclectus cornelia* and Great-billed Parrot *Tanygnathus megalorynchos*; (owls): Sumba Boobook *Ninox rudolfi*, Least Boobook *Ninox sumbaensis* and Barn Owl *Tyto alba*; (hornbill) Sumba Hornbill *Rhyticeros everetti*; (hawks): Eastern Buzzard *Buteo japonicus*, Brown Goshawk *Accipiter fasciatus* (and other *Accipiter* spp.), Spotted Kestrel *Falco moluccensis* and Australian Hobby *F. longipennis*; (mammals): Long-tailed Macaque *Macaca fascicularis*, Common Palm Civet *Paradoxurus hermaphroditus* and rats *Rattus* sp.; (reptiles): Tokay Gecko *Gecko gecko* and Emerald Tree Skink *Lamprolepis smaragdina*, Lesser Sundas Bronzeback snake *Dendrelaphis inornatus*.

5.3.4 Predation

Among the animals that could theoretically prey on the monitored nests, 14 taxa were captured by our cameras near the nest entrances (Figure 5.6): the Sumba Hornbill visitation rate was 5.8 (i.e. birds visited on average 5.8 days per monitored 30 days), Brown Goshawk Accipiter fasciatus (and other Accipiter spp.) 0.1; Eastern Buzzard Buteo japonicus 0.01; two falcons (Spotted Kestrel Falco moluccensis, Australian Hobby F. longipennis) 0.65; three owls (Sumba Boobook Ninox rudolfi 1.1, Least Boobook N. sumbaensis 0.01, Barn Owl Tyto alba 2.8); three mammals (Long-tailed Macaque Macaca fascicularis 0.4; Common Palm Civet Paradoxurus hermaphroditus 0.01, and rats Rattus spp. 0.06); and three reptiles (Tokay Gecko *Gecko gecko* 0.6, Emerald Tree Skink Lamprolepis smaragdina 0.4, Lesser Sundas Bronzeback snake *Dendrelaphis inornatus* 0.01)(Marini and Melo, 1998). Among these, the hornbill, owls and falcons likely have a dual potential as both nest competitors and nest predators. Hornbills visited nests occupied by owls and parrots as often as unoccupied nests (GLMM $\beta = -0.05 \pm 0.20$ [SE], $p = 0.77$), whereas hawks visited unoccupied nests more frequently than occupied owl and parrot nests ($\beta = -0.48 \pm 0.18$, $p = 0.007$). Geckos and skinks visited unoccupied cavities more often than those occupied by parrots or owls ($\beta = -1.15 \pm 0.33$, $p < 0.001$). While we found no evidence for predation by reptiles, eggs of both lizard species often occurred in cavities, unused by birds. Similarly, owls visited active parrot nests less than unoccupied cavities ($\beta = -0.69 \pm 0.28$, $p = 0.001$). Weekly predator visit rates varied between cavities, and cavity identity featured as a significant random factor in all GLMMs above. Mammals were not recorded visiting any active nests and only appeared on 20 occasions at the entrances of unoccupied nests. During nest watches we often encountered troupes of macaques in the vicinity, which triggered alarm calls from parrots on three occasions, but no predation attempts were observed. According to incidental direct observations and camera-trap footage of direct confrontations, only hornbills and hawks are a threat to active parrot nests (Table 5.2, Appendix 5.2).

5.3.5 Cockatoo nesting attempts

Among the 95 monitored cavities, 12 nest-sites became active cockatoo nests during the study period (six found from trapper reports, six from own fieldwork and one cavity from Burung Indonesia's records, the latter occupied thrice). Fifteen nest attempts took place in these cavities, 10 successful and five not (Table 5.1, Table 5.3). Eggs were laid between the last week of June and first week of December (median date = 14 November). Chicks fledged between October and April (median date = 24 January), aged 55–70 days (n = 3 cavities with lay dates known to ±2 days). Causes of nest failure were uncertain but evidence suggested nest takeover by a hornbill during incubation, interference by a Sumba Boobook at chick stage, falling of a dead cavity tree soon after laying, unknown predation shortly before fledging, and trapping of parents and chick.

Although most cavities not claimed early in the season by competitors were prospected by cockatoos (49 of 79 monitored cavity-seasons), repeated occupancy of cavities was low for cockatoos: only one cavity hosted active cockatoo nests in two consecutive years (the first year's nest having failed, Table 5.4). Cockatoos tended to nest only once in individual cavities, whereas other species nested multiple times in the same cavity, although the difference was not significant (χ^2=2.0, df=1, p=0.15).

Table 5.3: Summary of Citron-crested Cockatoo *Cacatua citrinocristata* nest success and timing over four breeding seasons on Sumba.

	2015–2016	**2016–2017**	**2017–2018**	**2018–2019**	**all 4 seasons**
No. successful nests	1	3	3	3	10
No. fledglings	2	4	5	4	12
Observed nest failures	4	0	1	0	5
No. nests found at egg stage	2	0	1	2	5
Laying period (calculated)	Sep–Nov	Nov	Oct–Jan	Jun–Dec	Jun–Jan
Last fledging date	Mar	Mar	Apr	Mar	Apr

Table 5.4: Fate of monitored cavities with past or present cockatoo interest. **ID** cavity identification number, **C p** prospected by cockatoos, **C s** successful cockatoo nest attempt, **C f** failed cockatoo nest attempt, **E** occupied by Sumba Eclectus, **H** occupied by Sumba Hornbill, **B** occupied by Sumba Boobook, **T** occupied by Barn Owl., **G** occupied by Great-billed Parrot, **K** occupied by Spotted Kestrel, **u** cavity was unusable due to e.g. structural damage, epiphytes, termites, bees, **X** no occupation detected despite some monitoring, **grey cell** site not checked, or not sufficiently to determine status; **Camera**: camera-trap installed on the tree (yes/no), **Climbed:** nest contents checked directly by climbing (yes/no), **Found**: **BI** cavity was part of Burung Indonesia's dataset before 2014, **OF** cavity found by own fieldwork, **FT** cavity shown by former trappers; Breeding season headings contain two years because they span the turn of the year. The 2014/15 breeding season data collected by the BI team are included here to show prospected and failed sites that were subsequently included in regular monitoring. The totals given in the text only cover the four seasons 2015–2019.

ID	2014/15	2015/16	2016/17	2017/18	2018/19	Camera	Climbed	Found
1[1]	C p	C f	C s	C p/G	C s	y	y	BI
2[2]	C f	B	K	G	T	y	y	BI
3[2]	C p	u	u	u	u	n	n	BI
4[3]	C p	u	u	u	u	n	y	BI
5[2]	C p	u	u	u	u	n	n	OF
6[2]	C p	H/E	H/E	H/E	H/E	n	y	BI
7[1]	▨	C s	C p/G	G	E	y	y	OF
8[2]	▨	C f	H	G/H	H	y	y	OF
9[1]	▨	C p/B	C p/T	C p/T	C p/B	y	y	OF
10[2]	▨	C p	C p	X	C p	y	y	OF
11[2]	▨	C p	C p	G	X	n	n	OF
12[2]	▨	C p	G	G	G	y	y	OF
13[4]	▨	X	C p/G	C p	X	n	n	BI
14[1]	▨	G	G	G	G	n	y	BI
15[1]	▨	T	T	T	T	n	n	OF
16[5]	▨	C p/T	X	T	▨	y	y	BI
17[2]	▨	C p	X	X	▨	n	n	OF
18[2]	▨	C p	▨	▨	▨	n	n	FT
19[2]	▨	C p	▨	▨	▨	n	n	OF
20[2]	▨	C p	▨	▨	▨	n	y	OF
21[2]	▨	▨	C s	G	G/C f	y	y	FT
22[6]	▨	▨	C s	G	G	n	n	FT
23[2]	▨	▨	C p/E	C s	C p	n	n	OF
24[2]	▨	▨	C p	C p	C p	n	y	FT
25[6]	▨	▨	C p	X	X	n	y	FT
26[2]	▨	▨	C p	X	▨	n	y	FT
27[2]	▨	▨	▨	C s	X	n	n	OF
28[7]	▨	▨	▨	C f	u	n	n	OF
29[2]	▨	▨	▨	C s	E	y	y	FT
30[8]	▨	▨	▨	C p	C s	y	y	FT
31[6]	▨	▨	▨	H/C p	C p	y	y	OF
32[2]	▨	▨	▨	C p/K	C p/H	y	y	FT
33[2]	▨	▨	▨	X	C p	y	y	FT
34[2]	▨	▨	▨	C p/T	▨	n	n	FT
35[2]	▨	▨	▨	▨	B/C s	y	y	OF
36[2]	▨	▨	▨	▨	C f	n	n	FT

Tree species: [1]*Chisocheton* sp., [2]*Tetrameles* sp., [3]*Millingtonia hortensis*, [4]*Glochidion* sp., [5]*Syzygium* sp., [6]*Palaquium* sp., [7]unknown, [8]*Artocarpus elasticus*

5.4 Discussion

Productivity in the Citron-crested Cockatoo appears to be remarkably and perhaps alarmingly low. During around 300 person-days spent searching within approximately 60% of the Manupeu Tanah Daru National Park and the other remnant forest patches with known cockatoo presence in Central and West Sumba, just ten successful nests of the species were found, involving just twelve fledged young. No doubt we missed nesting attempts within the study area, but this was not due to a lack of search effort. Similar patterns of strikingly low output despite seemingly high opportunity have been found in previous studies: 47 nests found, 16 'occupied' (Marsden and Jones, 1997); 62 sites monitored, 24 visited by cockatoos, 8 with repeated activity and only 1 successful nest (Walker et al., 2005); and 10 trees monitored, 7 with cockatoo activity and 2 active nests (Djawarai et al., 2014). The clutch and brood size of 1–2 observed during our study are at the lower end of the spectrum even for large parrots (Smith and Saunders, 1986; Forshaw, 1989; Collar, 1997; Murphy et al., 2003). The low observed ratio of prospecting pairs to successful breeding attempts and apparent lack of fledglings joining the population after the breeding season are further indicators of low productivity (Elliott et al., 2006; Matuzak and Brightsmith, 2007; Widmann and Lacerna-Widmann, 2008; Tossas et al., 2013). Even allowing that cockatoos are K-selected species which offset low breeding rates against long life-spans (Murphy et al., 2003), this circumstance appears too extreme to represent a stable balance between these two parameters. The possible factors underlying the situation therefore needed to be examined. These clearly involve the natural pressures from nest competition and the anthropogenic pressures from exploitation for trade and habitat degradation.

Nest competition appears to be intense in terms of both the richness of the cavity-nesting community and our direct observations of nest uptake. A more species-rich community of large cavity-nesting species exists on Sumba than on nearby islands. Our work and earlier studies on Sumba (Marsden and Jones, 1997; Walker et al., 2005; Hidayat, 2012) found many instances of multiple nests in the same tree—both multiple cavities frequented by different cockatoo pairs and mixed 'colonies' involving Sumba Eclectus and Great-billed Parrot. Competition between the three large parrots was intense in the prospecting phase, as in other communities of large parrots (Saunders et al., 1982, 2020; Heinsohn et al., 2003; Igag et al., 2019), but there was no evidence that any parrot nests failed due to interference from other parrots. We also saw no intraspecific competition among cockatoos although two pairs attempted to nest in two cavities in the same tree, which would have led to aggression in some other parrot species (e.g. Renton, 2004). The synergies of joint nest site guarding may be an advantage for all neighbouring parrot pairs once cavity ownership has been established (Danchin and Wagner, 1997; Rolland et al., 1998), and indeed, colonial nesting may have evolved in other parrot species to reduce predation risk (Masello and Quillfeldt, 2002; Heinsohn and Legge, 2003). However, it is still unclear what happens when parrots and owls prospect the same cavity alternately each day and night; in the four cases we observed (one monitored by camera), none of the species managed to establish an active nest. Hornbill interference at cockatoo nests, whether for competition or predation (Pierce and Pobprasert, 2013; as in other hornbill species: Loong et al., 2021), appeared to cause nest failure and stress in cockatoos.

By contrast, the threat of predation at cockatoo nests on Sumba appears surprisingly low. Mammals, reptiles and hawks seem to have minor roles as predators at most, and even hornbills rarely destroyed nest contents despite very frequent visits to parrots nests. Cockatoos are known to protect their nest sites well (e.g. Rowley, 1990; Rowley and Chapman, 1991; Murphy et al., 2003), and our observations confirmed this: during incubation and early brooding, one parent usually stayed in the nest until the other arrived to take over duties, and once the chicks were older (> ca 3 weeks) we frequently found the guarding parent perched near the nest. Moreover, cockatoos remove foliage around the entrance of potential nest holes, and vines and small branches connecting theirs to neighbouring trees (Walker et al., 2005; Djawarai et al., 2014; Hidayat and Kayat, 2020), presumably thereby reducing access for potential predators (Koenig et al., 2007; Britt et al., 2014).

Considering that introduced mammals are one of the commonest causes of extinctions of island species (Howald et al., 2007; Harper and Bunbury, 2015), and that rodents, macaques and civets are all known to predate parrot nests elsewhere (Jones, 1987; Clout and Merton, 1998; e.g. Jones et al., 2013; Pierce and Pobprasert, 2013; Reuleaux et al., 2014), the lack of evidence for predation at our monitored nests is remarkable. All three mammal species were camera-trapped near (and even looking into) previously cockatoo-occupied cavities, but they never entered any cavities or disrupted any active nests monitored by cameras. By their size and body:tail ratio, the rodents were likely Pacific Rats *Rattus exulans* or possibly Ricefield Rats *R.*

argentiventer, both of which arrived on Sumba with early seafarers in the Holocene (Heinsohn, 2003). Long-tailed Macaques, which are common in Sumba's forests (pers. obs.), were introduced prehistorically or historically to the Lesser Sunda Islands by humans (Heinsohn, 2001; Murphy et al., 2003), suggesting that the avifauna has had time to adapt (e.g. by nest guarding) to the threat to nests that they pose. We encountered troupes of monkeys during most nest watches and during 150 (38%) of 393 bird survey point counts in forest (AR unpublished data). Macaques have been shown to predate cavity nests almost as often as open-cup nests in other contexts (Kaisin et al., 2018), so the absence of predation events in our camera-monitored cavities is interesting. A possible explanation is that *Tetrameles*, the preferred species for nesting (Marsden and Jones, 1997), grows very tall, often becoming emergent, and has a smooth bark, rendering access, at least by mammals, difficult.

The combination of direct and indirect evidence suggests that anthropogenic factors have a decisive limiting influence on cockatoo numbers, although this is hard to establish unequivocally. In the dense tall forests of our study area we found nests very hard to find, in large part because the behaviour of breeding cockatoos was so discreet. This may have been due to decades of trapping: Yellow-crested Cockatoo populations under known trapping pressure, e.g. on Sumbawa and Alor (Setiawan, 1996; Trainor et al., 2012), showed similar behaviour, whereas populations without recent trapping pressure, e.g. on Komodo and at one West Timor site, were almost indifferent to human presence (Imansyah et al., 2016; Reuleaux et al., 2020) . On Sumba, nests higher up in the tree were less likely to be exploited by trappers than lower ones (Marsden and Jones, 1997), which could over decades select for the use of higher cavities (Eggers et al., 2005; Chen et al., 2011; Linhart et al., 2012). It is possible, however, that higher cavities are both less suitable and less abundant than lower ones, and these factors may help explain the cockatoo's pronounced fastidiousness over nest-site selection in what may be for them sub-optimal breeding habitat: the ratio of prospected sites to active nests found shows that cockatoos spend much time exploring and preparing cavities before eventually rejecting them (or being displaced).

Apart from these potential indirect effects of exploitation, we also found evidence of recent cockatoo trapping (climbing set-ups, nooses and bunches of flight feathers at roosts and nests; Figure 5.2) in at least twelve cases, and investigations confirmed that trapping of adults and young, although at low levels, appears to have been increasing since 2017. We saw fewer fledglings accompanying their parents to communal roosts than would be expected after a productive breeding season (Matuzak and Brightsmith, 2007; Widmann and Lacerna-Widmann, 2008). If other typical limiting factors of nest productivity—predation, infertile eggs, embryo death, malnutrition, parasites (Clout and Merton, 1998; Arendt, 2000; White et al., 2015; Stojanovic et al., 2017; Vigo-Trauco et al., 2021)—were frequent, we would expect to have found some evidence for them. Their absence leaves nest site availability and human interference as the likeliest causes for concern.

Forest loss and degradation throughout the 20th century on Sumba has certainly played a role in the cockatoo's decline (Jones et al., 1995) and constrains its current population as is common for most parrot species (e.g. Snyder et al., 2000; BirdLife International, 2021). Cavities of sufficient size for cockatoos and their competitors only form in certain tree species at maturity or in senescence. If selective logging targets the same trees for timber, forest quality as nesting habitat may be much lower than forest cover would suggest. The majority of cockatoo nests were in *Tetrameles* trees. Whether this is out of preference or a consequence of cavity availability was not examined. During field work we found no signs of *Tetrameles* logging inside the park but there was evidence for it outside the park in the other surveyed forests. Although *Tetrameles* trees are not ideal for traditional house-building, the wood is used for walls and boats (Karande, 1967; Monk et al., 1997; Djawarai et al., 2014). Sumba's long history of selective logging and forest clearance (Monk et al., 1997) may have so greatly depleted preferred timber trees that local communities now exploit suboptimal species. This may place an undetected but important effect on the cockatoo and some monitoring of *Tetrameles* utilisation may be warranted.

5.5 Conclusion

Based on the evidence for nest site competition and ongoing trapping accruing here, conservation actions for the Citron-crested Cockatoo should target the prevention of both trapping and further habitat deterioration or loss of old hole-bearing trees, and the provision of safe artificial nest-sites. Past conservation interventions on Sumba (Persulessy et al., 2003; Djawarai et al., 2014) and elsewhere (Ihsannudin et al., 2020; Indraswari et al., 2020; Pires et al., 2021; Sánchez-Mercado et al., 2021) show that trapping can be reduced locally by raising awareness among communities who control access to the habitat and increasing law enforcement against middlemen and traders. The most sustainable way to address nest-site shortage in the long term is the protection, restoration and re-creation of forest with large cavity-forming trees (Newton, 1994; van der Hoek et al., 2017). To date no extensive nestbox trial has been done on Sumba, so in the short term, we recommend provision of artificial nest-sites as a bridging solution. Wild parrots sometimes ignore nestboxes (e.g. Jones, 1980; Walker et al., 2001; Brightsmith and Bravo, 2006; Tatayah et al., 2007; Rocamora and Laboudallon, 2013), but there are many cases where appropriately designed and positioned nestboxes are successfully supporting threatened parrot species through a period of nest-site shortage (White Jr et al., 2006; Cockle et al., 2010; Jones et al., 2013; Saunders et al., 2020). Accessible, known, safe nestboxes could also provide opportunities to assess the scale of nest-site shortage, allow camera placements to study productivity, exclude some competitors, and prevent illegal trapping.

References

Agista, D. and Rubyanto, D. (2001) *Telaah awal status, penyebaran, dan populasi kakatua kecil jambul kuning,* Cacatua sulphurea parvula*: di Taman Nasional Komodo, Nusa Tenggara Timur*. Bogor, Indonesia: Birdlife International Indonesia Programme.

Altamirano, T. A., Ibarra, J. T., Martin, K. and Bonacic, C. (2017) 'The conservation value of tree decay processes as a key driver structuring tree cavity nest webs in South American temperate rainforests.' *Biodiversity and Conservation*, 26(10) pp. 2453–2472.

Arendt, W. J. (2000) 'Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery.' *Ornitologia Neotropical*, 11 pp. 13–63.

Badan Pusat Statistik (2016) *Statistical yearbook of Indonesia*. [Online] [Accessed on 17th October 2017] www.bps.go.id.

Badan Pusat Statistik (2021) *Statistical yearbook of Indonesia 2020*. [Online] [Accessed on 20th December 2021] www.bps.go.id.

van Balen, J. H., Booy, C. J. H., van Franeker, J. A. and Osieck, E. R. (1982) 'Studies on hole-nesting birds in natural nest sites.' *Ardea*, 70(1) pp. 1–24.

Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015) 'Fitting linear mixed-effects models using lme4.' *Journal of Statistical Software*, 67(1) pp. 1–48.

BirdLife International (2021) *Datazone*. [Online] [Accessed on 11th March 2021] http://datazone.birdlife.org/.

Bonaparte, E. B. and Cockle, K. L. (2017) 'Nest niche overlap among the endangered Vinaceous-breasted Parrot (*Amazona vinacea*) and sympatric cavity-using birds, mammals, and social insects in the subtropical Atlantic Forest, Argentina.' *The Condor*, 119(1) pp. 58–72.

Brightsmith, D. and Bravo, A. (2006) 'Ecology and management of nesting Blue-and-Yellow Macaws (*Ara ararauna*) in Mauritia palm swamps.' *Biodiversity & Conservation*, 15(13) pp. 4271–4287.

Brightsmith, D. J. (2005) 'Competition, predation and nest niche shifts among tropical cavity nesters: phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes).' *Journal of Avian Biology*, 36(1) pp. 64–73.

Britt, C. R., García Anleu, R. and Desmond, M. J. (2014) 'Nest survival of a long-lived psittacid: Scarlet Macaws (*Ara macao cyanoptera*) in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize.' *The Condor*, 116(2) pp. 265–276.

Cahill, A. J., Walker, J. S. and Marsden, S. J. (2006) 'Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea citrinocristata* in Indonesia after 10 years of international trade control.' *Oryx*, 40(2) pp. 161–167.

Chen, J.-N., Liu, N.-F., Yan, C. and An, B. (2011) 'Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance.' *J Ornithol*, 152 pp. 603–608.

Clout, M. N. and Merton, D. V. (1998) 'Saving the kakapo: the conservation of the world's most peculiar parrot.' *Bird Conservation International*, 8(3) pp. 281–296.

Cockle, K. L., Martin, K. and Drever, M. C. (2010) 'Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest.' *Biological Conservation*, 143(11) pp. 2851–2857.

Collar, N. J. (1997) ‘Order Psittaciformes, Family Psittacidae (Parrots), Genus Cyanoliseus, Burrowing Parakeet.’ In del Hoyo, J., Elliot, A., and Sargatal, J. (eds) *Handbook of the birds of the world*. Vol. 4. Sandgrouse to Cuckoos. Barcelona: Lynx Edicions, pp. 436–437.

Collar, N. J., Eaton, J. A. and Sykes, B. (2017) ‘Conservation and the redaction of locality data.’ *BirdingASIA*, 28 pp. 3–4.

Collar, N. J. and Marsden, S. J. (2014) ‘The subspecies of Yellow-crested Cockatoo *Cacatua sulphurea*.’ *Forktail*, (30) pp. 23–27.

Collias, N. E. (1964) ‘The Evolution of nests and nest-building in birds.’ *American Zoologist*, 4(2) pp. 175–190.

Danchin, E. and Wagner, R. H. (1997) ‘The evolution of coloniality: the emergence of new perspectives.’ *Trends in Ecology & Evolution*, 12(9) pp. 342–347.

Delany, M. E., Tell, L. A., Millam, J. R. and Preisler, D. M. (1999) ‘Photographic candling analysis of the embryonic development of orange-winged amazon parrots (*Amazona amazonica*).’ *Journal of Avian Medicine and Surgery*, 13(2) pp. 116–123.

Djawarai, Y., Bashari, H., Siregar, B. and Widyanto, A. (2014) *The breeding ecology of Sumba Cockatoo* Cacatua sulphurea citrinocristata *in Manupeu Tanadaru National Park and surrounding, Sumba*. *Burung Indonesia*. Bogor, Indonesia: Burung Indonesia.

Eaton, J. A., Van Balen, S. B., Brickle, N. W. and Rheindt, F. E. (2016) *Birds of the Indonesian Archipelago Greater Sundas and Wallacea*. Barcelona, Spain: Lynx Ediciones.

Eggers, S., Griesser, M., Nystrand, M. and Ekman, J. (2005) ‘Predation risk induces changes in nest-site selection and clutch size in the Siberian jay.’ *Proceedings of the Royal Society B: Biological Sciences*, 273(1587) pp. 701–706.

Elliott, G. P., Eason, D. K., Jansen, P. W., Merton, D. V, Harper, G. A. and Moorhouse, R. J. (2006) ‘Productivity of kakapo (*Strigops habroptilus*) on offshore island refuges.’ *Notornis*, 53 pp. 138–142.Forshaw, J. M. (1989) ‘Introduction.’ *In Parrots of the world*. 3rd ed., Willoughby, Australia: Lansdowne, pp. 19–39.

González, J. A. (2003) ‘Harvesting, local trade, and conservation of parrots in the Northeastern Peruvian Amazon.’ *Biological Conservation*, 114(3) pp. 437–446.

Gutzat, F. and Dormann, C. F. (2018) ‘Decaying trees improve nesting opportunities for cavity-nesting birds in temperate and boreal forests: A meta-analysis and implications for retention forestry.’ *Ecology and Evolution*, 8(16) pp. 8616–8626.

Harper, G. A. and Bunbury, N. (2015) ‘Invasive rats on tropical islands: Their population biology and impacts on native species.’ *Global Ecology and Conservation*, 3 pp. 607–627.

Heinsohn, R. and Legge, S. (2003) ‘Breeding biology of the reverse-dichromatic, co-operative parrot *Eclectus roratus*.’ *Journal of Zoology*, 259(02) pp. 197–208.

Heinsohn, R., Murphy, S. and Legge, S. (2003) ‘Overlap and competition for nest holes among eclectus parrots, palm cockatoos and sulphur-crested cockatoos.’ *Australian Journal of Zoology*, 51(1) pp. 81–94.

Heinsohn, R., Zeriga, T., Murphy, S., Igag, P., Legge, S. and MacK, A. L. (2009) ‘Do Palm Cockatoos (*Probosciger aterrimus*) have long enough lifespans to support their low reproductive success?’ *Emu*, 109(3) pp. 183–191.

Heinsohn, T. E. (2001) ‘Human influences on vertebrate zoogeography: animal translocation and biological invasions across and to the east of Wallace’s Line.’ *In* Metcalfe, I., Smith, J. M. B., Morwood, M., and Davidson, I. (eds) *Faunal and floral migrations and evolution in SE Asia--Australasia*. Boca Raton, US: CRC Press, pp. 153–170.

Heinsohn, T. E. (2003) ‘Animal translocation: long-term human influences on the vertebrate zoogeography of Australasia (natural dispersal versus ethnophoresy).’ *Zoologist*, 32(3) pp. 351–376.

Hidayat, O. (2012) ‘Lubang masa depan.’ *Biodiversitas Indonesia*, 2 pp. 110–118.

Hidayat, O. and Kayat (2020) ‘Pendekatan preferensi habitat dalam penyusunan strategi konservasi in situ Kakatua Sumba (*Cacatua sulphurea citrinocristata*, Fraser 1844).’ *Jurnal Penelitian Hutan dan Konservasi Alam*, 17(2) pp. 113–126.

van der Hoek, Y., Gaona, G. V. and Martin, K. (2017) ‘The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world.’ *Diversity and Distributions*, 23(10) pp. 1120–1131.

Howald, G., Donlan, C. J., Galván, J. P., Russell, J. C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A. and Tershy, B. (2007) ‘Invasive rodent eradication on islands.’ *Conservation Biology*, 21(5) pp. 1258–1268.

Igag, P., Mack, A. L., Legge, S. and Heinsohn, R. (2019) ‘Breeding biology of three large, sympatric rainforest parrots in New Guinea: Palm Cockatoo, Pesquet’s Parrot and Eclectus Parrot.’ *Emu*, 119(3) pp. 196–204.

Ihsannudin, I., Hidayat, K., Sukesi, K. and Yuliati, Y. (2020) ‘Perception of the local community toward the yellow-crested cockatoo (*Cacatua sulphurea abbotti*), a critically endangered species in Masakambing Island, Indonesia.’ *Geografia*, 16(4) pp. 1–14.

Imansyah, M. J., Purwandana, D., Ariefiandy, A., Benu, Y. J., Jessop, T. S. and Trainor, C. R. (2016) ‘Valley-floor censuses of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea occidentalis* on Komodo Island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period.’ *Forktail*, 32 pp. 66–72.

Indraswari, K., Friedman, R. S., Noske, R., Shepherd, C. R., Biggs, D., Susilawati, C. and Wilson, C. (2020) ‘It’s in the news: Characterising Indonesia’s wild bird trade network from media-reported seizure incidents.’ *Biological Conservation*, 243 p. 108431.

Jones, C. G. (1980) ‘Parrot on the Way to Extinction.’ *Oryx*, 15(4) pp. 350–354.

Jones, C. G. (1987) ‘The larger native landbirds of Mauritius.’ *In* Diamon, A. W. (ed.) *Studies of Mascarene Island Birds*. Cambridge, UK: Cambridge University Press, pp. 271–300.

Jones, C. G., Malham, J., Reuleaux, A., Richards, H. A., Raisin, C., Tollington, S., Zuel, N., Chowrimootoo, A. and Tatayah, V. (2013) ‘Echo parakeet *Psittacula eques* Perruche de Maurice.’ *In* Safford, R. and Hawkins, F. (eds) *The Birds of Africa: Volume VIII: The Malagasy Region: Madagascar, Seychelles, Comoros, Mascarenes*. A&C Black, pp. 433–438.

Jones, M. J., Linsley, M. D. and Marsden, S. J. (1995) ‘Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia.’ *Bird Conservation International*, 5(01) pp. 21–52.

Kaisin, O., Gazagne, E., Savini, T., Huynen, M.-C. and Brotcorne, F. (2018) ‘Foraging strategies underlying bird egg predation by macaques: A study using artificial nests.’ *American Journal of Primatology*, 80(11) p. e22916.

Karande, A. A. (1967) ‘Timber, Tetrameles nudiflora R., resistant to teredid borers in Bombay Harbour [53].’ *Nature*, 213(5071) p. 105.

Koenig, S. E., Wunderle, J. M. and Enkerlin-Hoeflich, E. C. (2007) ‘Vines and canopy contact: A route for snake predation on parrot nests.’ *Bird Conservation International*, 17(1) pp. 79–91.

Lack, D. (1968) *Ecological adaptations for breeding in birds*. London, UK: Methuen & Co Ltd.

Linhart, P., Fuchs, R., Poláková, S. and Slabbekoorn, H. (2012) ‘Once bitten twice shy: long-term behavioural changes caused by trapping experience in willow warblers Phylloscopus trochilus.’ *Journal of Avian Biology*, 43(2) pp. 186–192.

Loong, S., Sin, Y. C. K., Johns, P., Plowden, T., Yong, D. L., Lee, J. and Jian, A. (2021) ‘Nest predation by Oriental Pied Hornbills Anthracoceros albirostris in urban Singapore.’ *BirdingASIA*, 35 pp. 86–91.

Marini, M. Â. and Melo, C. (1998) ‘Predators of Quail Eggs, and the Evidence of the Remains: Implications for Nest Predation Studies.’ *The Condor*, 100(2) pp. 395–399.

Marsden, S. J. (1995) *The ecology and conservation of the parrots of Sumba, Buru and Seram, Indonesia.* PhD-thesis. Manchester Metropolitan University.

Marsden, S. J. and Jones, M. J. (1997) ‘The nesting requirements of the parrots and hornbill of Sumba, Indonesia.’ *Biological Conservation*, 82(3) pp. 279–287.

Martin, R. O., Perrin, M. R., Boyes, R. S., Abebe, Y. D., Annorbah, N. D., Asamoah, A., Bizimana, D., Bobo, K. S., Bunbury, N. and Brouwer, J. (2014) ‘Research and conservation of the larger parrots of Africa and Madagascar: a review of knowledge gaps and opportunities.’ *Ostrich*, 85(3) pp. 205–233.

Masello, J. F., Pagnossin, M. L., Sommer, C. and Quillfeldt, P. (2006) ‘Population size, provisioning frequency, flock size and foraging range at the largest known colony of Psittaciformes: The Burrowing Parrots of the north-eastern Patagonian coastal cliffs.’ *Emu*, 106(1) pp. 69–79.

Masello, J. F. and Quillfeldt, P. (2002) ‘Chick growth and breeding success of the Burrowing Parrot.’ *The Condor*, 104(3) pp. 574–586.

Matuzak, G. D. and Brightsmith, D. J. (2007) ‘Roosting of Yellow-naped Parrots in Costa Rica: estimating the size and recruitment of threatened populations.’ *Journal of Field Ornithology*, 78(2) pp. 159–169.

Monk, K., De Fretes, Y. and Reksodiharjo-Lilley, G. (1997) *Ecology of Nusa Tenggara and Maluku*. 1st ed., Oxford, UK: Oxford University Press.

Monterrubio, T., Enkerlin-Hoeflich, E. and Hamilton, R. B. (2002) ‘Productivity and nesting success of Thick-billed Parrots.’ *The Condor*, 104(4) pp. 788–794.

Moorhouse, R., Greene, T., Dilks, P., Powlesland, R., Moran, L., Taylor, G., Jones, A., Knegtmans, J., Wills, D., Pryde, M., Fraser, I., August, A. and August, C. (2003) ‘Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: reversing the decline of a threatened New Zealand parrot.’ *Biological Conservation*, 110(1) pp. 33–44.

Murphy, S., Legge, S. and Heinsohn, R. (2003) ‘The breeding biology of palm cockatoos (*Probosciger aterrimus*): A case of a slow life history.’ *Journal of Zoology*, 261(4) pp. 327–339.

Nandika, D. and Agustina, D. (2012) ‘Few and far between. Saving the Yellow-crested Cockatoos.’ *PsittaScene*, 24(3) pp. 130–134.

Nandika, D., Mulyani, Y. A., Prawiradilaga, D. M. and Agustina, D. (2020) ‘Monitoring of *Cacatua sulphurea abbotti* in Masakambing Island, Indonesia.’ *Biotropia-The Southeast Asian Journal of Tropical Biology*, 27(3) pp. 271–281.

Newton, I. (1994) ‘The role of nest sites in limiting the numbers of hole-nesting birds: A review.’ *Biological Conservation*, 70(3) pp. 265–276.

Nilsson, S. G. (1986) ‘Evolution of hole-nesting in birds: on balancing selection pressures.’ *The Auk*, 103(2) pp. 432–435.

Olah, G., Butchart, S. H. M., Symes, A., Guzmán, I. M., Cunningham, R., Brightsmith, D. J. and Heinsohn, R. (2016) ‘Ecological and socio-economic factors affecting extinction risk in parrots.’ *Biodiversity and Conservation*, 25(2) pp. 205–223.

Persulessy, Y. E., Djawarai, Y. B. and Marut, R. (2003) *Survei populasi dan distribusi kakatua-kecil jambul-kuning* Cacatua sulphurea citrinocristata *dan empat jenis paruh bengkok lain di Pulau Sumba*. Bogor, Indonesia.

PHPA, LIPI and BirdLife International-IP (1998) *Species recovery plan Yellow-crested Cockatoo*. Bogor, Indonesia: PHPA/LIPI/BirdLife International - Indonesia Programme.

Pierce, A. J. and Pobprasert, K. (2013) ‘Nest predators of southeast Asian evergreen forest birds identified through continuous video recording.’ *Ibis*, 155(2) pp. 419–423.

Pires, S. F. (2012) ‘The illegal parrot trade: a literature review.’ *Global Crime*, 13(3) pp. 176–190.

Pires, S. F., Olah, G., Nandika, D., Agustina, D. and Heinsohn, R. (2021) ‘What drives the illegal parrot trade? Applying a criminological model to market and seizure data in Indonesia.’ *Biological Conservation*, 257, May.

R Core Team (2021) ‘R: A language and environment for statistical computing.’ Vienna, Austria: R Foundation for Statistical Computing.

Renton, K. (2004) ‘Agonistic interactions of nesting and nonbreeding macaws.’ *The Condor*, 106(2) pp. 354–362.

Reuleaux, A., Richards, H., Payet, T., Villard, P., Waltert, M. and Bunbury, N. (2014) ‘Breeding ecology of the Seychelles Black Parrot *Coracopsis barklyi*.’ *Ostrich*, 85(3) pp. 255–265.

Reuleaux, A., Siregar, B. A., Collar, N. J., Panggur, M. R., Mardiastuti, A., Jones, M. J. and Marsden, S. J. (2020) ‘Protected by dragons: Density surface modeling confirms large population of the critically endangered Yellow-crested Cockatoo on Komodo Island.’ *The Condor*, 122(4) p. duaa042.

Ribeiro-Silva, L., Perrella, D. F., Biagolini-Jr, C. H., Zima, P. V. Q., Piratelli, A. J., Schlindwein, M. N., Galetti, P. M. and Francisco, M. R. (2018) ‘Testing camera traps as a potential tool for detecting nest predation of birds in a tropical rainforest environment.’ *Zoologia (Curitiba)*, 35, June.

Richardson, T. W., Gardali, T. and Jenkins, S. H. (2009) ‘Review and meta-analysis of camera effects on avian nest success.’ *Journal of Wildlife Management*, 73(2) pp. 287–293.

Rocamora, G. and Laboudallon, V. (2013) ‘Seychelles Black Parrot *Coracopsis barklyi*.’ *In* Safford, R. and Hawkins, F. (eds) *The Birds of Africa: Volume VIII: The Malagasy Region: Madagascar, Seychelles, Comoros, Mascarenes*. A&C Black, pp. 445–447.

Rolland, C., Danchin, E. and de Fraipont, M. (1998) ‘The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: A comparative analysis.’ *American Naturalist*, 151(6) pp. 514–529.

Rowley, I. (1990) *Behavioural ecology of the galah,* Eolophus roseicapillus. Chipping Norton, Australia: Surrey Beatty & Sons.

Rowley, I. and Chapman, G. (1991) ‘The breeding biology, food, social organisation, demography and conservation of the Major Mitchell or Pink Cockatoo, *Cacatua leadbeateri*, on the margin of the Western Australian Wheatbelt.’ *Australian Journal of Zoology*, 39(2) pp. 131–142.

Sánchez-Mercado, A., Ferrer-Paris, J. R., Rodríguez, J. P. and Tella, J. L. (2021) ‘A literature synthesis of actions to tackle illegal parrot trade.’ *Diversity*, 13(5) p. 191.

Sanders, M. D. and Maloney, R. F. (2002) ‘Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study.’ *Biological Conservation*, 106(2) pp. 225–236.

Saunders, D. A., Dawson, R., Mawson, P. R. and Cunningham, R. B. (2020) ‘Artificial hollows provide an effective short-term solution to the loss of natural nesting hollows for Carnaby’s Cockatoo *Calyptorhynchus latirostris*.’ *Biological Conservation*, 245, May, p. 108556.

Saunders, D. A., Smith, G. T. and Rowley, I. (1982) ‘The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia.’ *Australian Wildlife Research*, 9(3) pp. 541–556.

Schaaf, A. A., García, C. G., Ruggera, R. A., Tallei, E., Vivanco, C. G., Rivera, L. and Politi, N. (2021) ‘Influence of logging on nest density and nesting microsites of cavity-nesting birds in the subtropical forests of the Andes.’ *Forestry: An International Journal Of Forest Research*, June, pp. 1–10.

Schaaf, A. A., Ruggera, R. A., Vivanco, C. G., Tallei, E., Benavidez, A., Albanesi, S., Rivera, L. O. and Politi, N. (2020) ‘Tree use, niche breadth and overlap for excavation by woodpeckers in subtropical piedmont forests of northwestern Argentina.’ *Acta Ornithologica*, 55(1) pp. 111–119.

Setiawan, I. (1996) *The status of* Cacatua sulphurea parvula *in Nusa Penida, Bali, and Sumbawa*. *PHPA/BirdLife International*. Bogor, Indonesia: PHPA/BirdLife International.

Shoemaker, K. T., Breisch, A. R., Jaycox, J. W. and Gibbs, J. P. (2013) ‘Reexamining the minimum viable population concept for long-lived species.’ *Conservation Biology*, 27(3) pp. 542–551.

Smith, G. T. and Saunders, D. A. (1986) ‘Clutch size and productivity in three sympatric species of cockatoo (Psittaciformes) in the south-west of Western Australia.’ *Australian Wildlife Research*, 13 pp. 275–285.

Snyder, N. F. R., McGowan, P., Gilardi, J. and Grajal, A. (2000) *Parrots. Status Survey and Conservation Action Plan 2000-2004*. Oxford, UK: IUCN.

Spoon, T. R. (2006) ‘Parrot reproductive behavior, or who associates, who mates, and who cares.’ *In* Luescher, A. (ed.) *Manual of parrot behavior*. 1st ed., Ames, Iowa US: Blackwell Publishing Ltd, pp. 63–78.

Stattersfield, A. J., Crosby, M. J., Long, A. J. and Wege, D. C. (1998) *Endemic bird areas of the world: priorities for biodiversity conservation*. *Endemic bird areas of the world: priorities for biodiversity conservation*.

Stojanovic, D., Alves, F., Cook, H., Crates, R., Heinsohn, R., Peters, A., Rayner, L., Troy, S. N. and Webb, M. H. (2017) ‘Further knowledge and urgent action required to save Orange-bellied Parrots from extinction.’ *Emu*, 118(1) pp. 126–134.

Tatayah, R. V. V, Malham, J., Haverson, P., Reuleaux, A. and Van de Wetering, J. (2007) ‘Design and provision of nest boxes for echo parakeets *Psittacula eques* in Black River Gorges National Park, Mauritius.’ *Conservation Evidence*, 4 pp. 16–19.

Tossas, A. G., Colón, Y. M. and Sanders, I. (2013) 'Seasonal changes in roost counts of the non-native White-winged Parakeet (Brotogeris versicolurus) in San Germán, Puerto Rico.' *Journal of Caribbean Ornithology*, 25 pp. 1–6.

Trainor, C. R., Verbelen, P. and Johnstone, R. E. (2012) 'The avifauna of Alor and Pantar, Lesser Sundas, Indonesia.' *Forktail*, 28 pp. 77–92.

Valle, S., Collar, N. J., Harris, W. E. and Marsden, S. J. (2018) 'Trapping method and quota observance are pivotal to population stability in a harvested parrot.' *Biological Conservation*, 217, January, pp. 428–436.

Vigo-Trauco, G., Garcia-Anleu, R. and Brightsmith, D. J. (2021) 'Increasing survival of wild macaw chicks using foster parents and supplemental feeding.' *Diversity*, 13(3) p. 121.

Walker, J. S., Cahill, A. J. and Marsden, S. J. (2001) *The nesting ecology of Yellow-crested Cockatoo* Cacatua sulphurea *on Sumba and the potential for using artificial nest sites to increase recruitment. Preliminary report 2001*. Manchester, UK: Manchester Metropolitan University.

Walker, J. S., Cahill, A. J. and Marsden, S. J. (2005) 'Factors influencing nest-site occupancy and low reproductive output in the Critically Endangered Yellow-crested Cockatoo Cacatua sulphurea on Sumba, Indonesia.' *Bird Conservation International*, 15(4) pp. 347–359.

White Jr, T. H., Brown, G. G. and Collazo, J. A. (2006) 'Artificial cavities and nest site selection by Puerto Rican Parrots: a multiscale assessment.' *Avian Conservation and Ecology*, 1(3) p. e5.1-e5.13.

White, K. L., Eason, D. K., Jamieson, I. G. and Robertson, B. C. (2015) 'Evidence of inbreeding depression in the critically endangered parrot, the kakapo.' *Animal Conservation*, 18(4) pp. 341–347.

Widmann, P. and Lacerna-Widmann, I. D. (2008) 'The cockatoo and the community: ten years of Philippine Cockatoo Conservation Programme.' *BirdingASIA*, 10 pp. 23–29.

Wungo, E. (2011) *Laporan survei populasi paruh bengkok terancam punah* Cacatua sulphurea citrinocristata*, Sumba, Nusa Tenggara Timur*. Bogor, Indonesia: Burung Indonesia.

Appendices

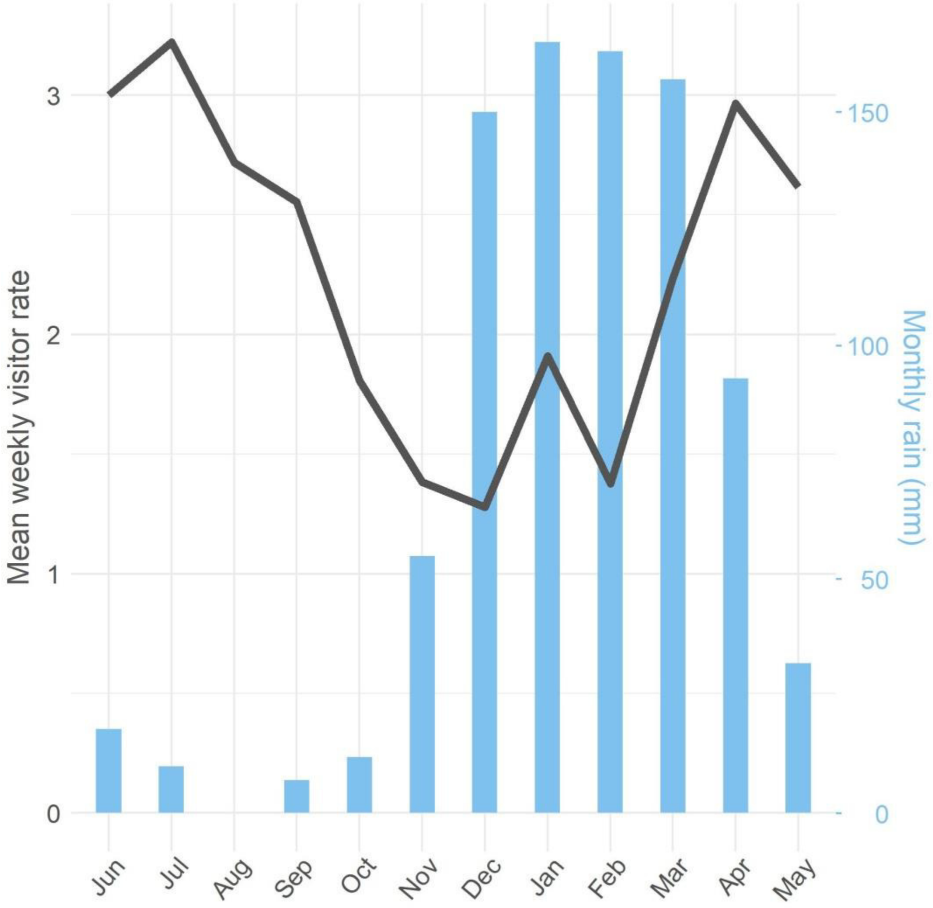
Appendix 5.1: Visits of potential predators to active nesting cavities occupied by the target species. Values represent number of days on which the respective predator species visited the nest. As predators the table includes all species that could theoretically prey on eggs or chicks from the monitored cavities and visited any of the cavities (occupied or empty); only visits to active nests were tallied. * Short-tailed Starling *Aplonis minor*, **Oriental Dollarbird *Eurystomus orientalis*

Occupants→ Predators ↓	**Cockatoo**	**Eclectus**	**G-b parrot**	**Hornbill**	**Owls**	**Unoccup.**	**Total**
Birds of prey							
Goshawks	3	0	0	0	4	11	**18**
Other falcons	0	0	0	8	0	115	**123**
Other hawks	0	0	0	0	0	1	**1**
Owls	5	0	3	243	4	482	**737**
Hornbill							
Hornbill	49	23	319	20	85	608	**1104**
Parrots							
Cockatoo	392	1	7	53	4	942	**1399**
Eclectus	2	49	0	1	0	91	**143**
G-b parrot	2	0	3	0	206	397	**608**
Mammals							
Civet	0	0	0	0	0	1	**1**
Macaque	0	0	0	0	0	8	**8**
Rat	0	0	0	0	0	11	**11**
Smaller sp.							
Starling*	16	0	2	14	22	439	**493**
Skink	0	0	0	1	5	69	**75**
Gecko	0	0	0	0	1	113	**114**
Other							
Snakes	0	0	0	0	0	1	**1**
Dollarbird**	0	0	0	0	0	10	**10**
Total	**469**	**73**	**334**	**340**	**331**	**3299**	**4846**

Appendix 5.2: Coefficients of visitation rate as predictor for cavity occupancy in GLMMs

Predator	**Occupant**	**β**	**Std. Error**	**z**	**P**
Hawks	Parrot/owl	−0.479	0.178	−2.685	0.007
Hornbill	Parrot/owl	−0.079	0.066	−1.197	0.231
Owl	Parrot	−0.689	0.279	−2.474	0.013
Reptiles	Parrot/owl	−1.153	0.337	−3.426	0.001

Appendix 5.3: Seasonality of average monthly rainfall (2000–2014) and weekly number of species visiting 12 tree cavities monitored by camera-traps.



6 General conclusions and recommendations

Summary of chapter conclusions

The goal of this thesis was to understand patterns of persistence, size, trends and productivity in populations of two Critically Endangered and heavily traded Indonesian cockatoos: the Yellow-crested Cockatoo *Cacatua sulphurea* and Citron-crested Cockatoo *Cacatua citrinocristata*. After dramatic declines of these once abundant species, information on the remnant populations is essential to guide future conservation management.

Chapter 2: The once abundant Yellow-crested Cockatoo has declined precipitously across its large original range because of loss of habitat and decades of exploitation for the pet trade; the Citron-crested Cockatoo has also undergone a sharp contraction in numbers and range on the island of Sumba. This first comprehensive assessment of status in 20 years covered almost the entire range of the two species and found a combined minimum 2,110 individuals at 76 sites. These numbers warrant concern, as the great majority of birds are concentrated in just three strongholds that are far from constituting a collective barrier against extinction: *C. citrinocristata* is confined to a single island, Sumba, and neither of the two strongholds of *C. sulphurea* is secure. The main factors associated with survival are island group, high tree cover, low road densities and low human densities, but local circumstances such as sacred groves or a highly motivated NGO, community leader or government official can arguably be at least as beneficial, and conservationists should actively seek to engage communities in cockatoo protection by fostering collective local identities and goodwill. Some of these local influences add complexity to the task of conserving cockatoo strongholds, but also offer exciting possibilities for low-cost conservation prescriptions tailored to individual sites. Similar patterns of persistence can be expected in other parrots in Indonesia (Pires et al., 2021) and have been observed in the region's other exploited threatened species, such as Tenggara Hill Myna *Gracula venerata* (Reuleaux et al., 2018) and megapodes Megapodiidae (Argeloo and Dekker, 1996; Froese and Mustari, 2019). Although the types of informal protection and cultural determinants may differ in other geographic and taxonomic contexts, this site-by-site review of predictors of persistence represents a novel approach to identifying the most effective bespoke measures for conserving fragmented populations of exploited species.

Chapter 3: I used density surface modelling of local abundance estimates from distance sampling to estimate the population of the Critically Endangered Yellow-crested Cockatoo on the 340 km² island of Komodo. The estimated population size of 1,113 individuals and the spatial density predictions strongly suggest that the population on Komodo Island is substantial, and I found no evidence that the steep decline reported for the early 2000s (Imansyah et al., 2016) has continued. Direct counts collected annually by experienced national park rangers show an increase from 2011 to 2017 (Taman Nasional Komodo, 2016; unpublished data KNP). This is evidence that the population has certainly been stable and probably increasing over the last six years. As such, in addition to providing protection to the iconic Komodo Dragon (Purwandana et al., 2014), Komodo National Park appears to be working as a long-term stronghold for the cockatoo. This park's population is by far the largest of the subspecies *occidentalis* and became the largest for the entire species when the distinctive *C. s. citrinocristata* was accorded species rank (BirdLife International, 2022b). To my knowledge this is the first time DSM has been applied to a Critically Endangered species. The findings highlight the potential of DSM for locating abundance hotspots, identifying habitat associations, and estimating global population size in a range of threatened taxa, especially if independent datasets can be used to validate model predictions.

Chapter 4: Considering the insecure status of Sumba's parrots — including the Citron-crested Cockatoo — it is essential to their conservation to monitor their population sizes and trends. All threats that led to catastrophic declines during the last century still persist, albeit at lower levels. There is evidence for ongoing local forest loss. Trapping has been hampered by legal restrictions and awareness work, but rising prices per bird provide enough incentive for some trappers and traders to take the risk (Pires et al., 2021; Chapter 5). Repeating the survey from 1992 and replicating methods so closely, both in the field and during analysis, offered the best possible opportunity to detect change over the last 25 years. Results highlight that the large parrots and the hornbill have probably not continued on their trajectory to extinction as quickly as was feared in the 1990s (Jones et al., 1995; PHPA et al., 1998), whereas Sumba's two formerly common small parrot species have declined at alarming rates in the last 25 years. To avoid future gaps in population estimates, regular monitoring should be carried out at least every 10 years with combined methodology for comparability to the 1992 and 2017 surveys and additional effort to cover the island's habitat more representatively. This is particularly important for the declining Red-cheeked Parrot and Marigold Lorikeet, the latter of which may need a re-assessment of its Red List status. The uncertainty in trends for the threatened cockatoo, eclectus and hornbill is of concern as they show no sign of sustainable recovery from the extensive trapping of past decades. The effects of habitat loss and competition could potentially be mitigated by providing nestboxes until the forest has had time to recover.

Chapter 5: Competition for suitable cavities was intense among three large parrot species, two owls and a hornbill. Cockatoos prospected many cavities but rarely then attempted to nest; however, at the few cavities where cockatoos did breed, predation pressure was likely low, and observed success rate high. Based on the evidence for nest site competition and ongoing trapping accruing from the chapter, conservation actions for the Citron-crested Cockatoo should target the prevention of both trapping and further habitat deterioration or loss of old hole-bearing trees, and the provision of safe artificial nest-sites. Past conservation interventions on Sumba (Persulessy et al., 2003; Djawarai et al., 2014) and elsewhere (Ihsannudin et al., 2020; Indraswari et al., 2020; Pires et al., 2021; Sánchez-Mercado et al., 2021) show that trapping can be reduced locally by raising awareness among communities who control access to the habitat and increasing law enforcement against middlemen and traders. The most sustainable way to address nest-site shortage in the long term is the protection, restoration and re-creation of forest with large cavity-forming trees (Newton, 1994; van der Hoek et al., 2017). Accessible, known, safe nestboxes could provide opportunities to assess the scale of nest-site shortage, allow camera placements to study productivity, exclude some competitors, and prevent illegal trapping. There are many cases where appropriately designed and positioned nestboxes are successfully supporting threatened parrot species through a period of nest-site shortage (White Jr et al., 2006; Cockle et al., 2010; Jones et al., 2013; Saunders et al., 2020).

6.1 Current status of both cockatoos

The recent split of Citron-crested Cockatoo leaves the resultant two species at higher risk of extinction than when they were assessed combined. The population on Sumba remains under pressure from illegal trapping and habitat loss and appears to have low productivity (Chapter 4 and 5). As densities in forest today are similar to the levels in 1992, the hoped-for recovery to pre-trapping levels is apparently not underway. Owing to the slow accumulation of nesting data more investigations of productivity limits are needed, both on Sumba and for the Yellow-crested Cockatoo on other islands. The subspecies *occidentalis* and *parvula* of the Yellow-crested Cockatoo may seem relatively safe with one stronghold each (Komodo for *occidentalis*, Timor-Leste for *parvula*). However, the Komodo population depends on intense patrolling and local goodwill, both of which may be under threat if the recently proposed drastic reduction in visitor numbers to Komodo National Park (CNN Travel, 2019) is implemented, or if international travel is curtailed due to unforeseen issues such the current Covid-19 pandemic (Caraka et al., 2020; Jeon and Yang, 2021). Meanwhile in Timor-Leste (subspecies *parvula*) conservation infrastructure is still being established, and the probable softening of the currently highly controlled border with Indonesia (Thu, 2012) could increase illegal wildlife trade, as seen elsewhere (Shepherd and Nijman, 2008; Zhang et al., 2008). The other subspecies all survive in very low numbers and their status remains highly precarious. Currently *C. s. sulphurea* is of greatest concern: the national park formerly considered its last stronghold (Cahyadin et al., 1994; Agista et al., 2001) harbours a much smaller population than previously believed, in only a small area. The populations of *djampeana* and *paulandrewi* have a realistic chance of survival only if there is legal protection for their habitat and enforced protection for the birds themselves.

The study species are not the only Indonesian cockatoos under threat: among Indonesia's six other cockatoo species the three country-endemics are all either threatened or near threatened (BirdLife International, 2021a) and suffer from lack of abundance data (Marsden, 1992; Poulsen and Jepson, 1996; Coates and Bishop, 1997; Kinnaird et al., 2003; Marsden and Royle, 2015; Winkler et al., 2020). Therefore, the methods used in this study to assess persistence, estimate population sizes, research productivity and limiting factors are highly applicable in the taxonomic and geographic neighbourhood. Such research has already been started for the Salmon-crested Cockatoo *Cacatua moluccensis* and White Cockatoo *Cacatua alba* in the Maluku Archipelago by the Indonesian collaborators of this study and co-authors of the resulting publications (B. A. Siregar *in litt.*, 2022).

6.2 Implications for Red List classification

In addition to gauging population changes over long periods, Red List reassessment of the cockatoos is complicated by several other considerations. The population estimates for Yellow-crested Cockatoos in this study are similar to those quoted by BirdLife before this study's results were considered for the assessment, once the numbers for Sumba are subtracted (BirdLife International, 2021b). For the Citron-crested Cockatoo on Sumba, BirdLife previously used 563 individuals (BirdLife International, 2021b) and the new estimate is considerably higher (Chapter 4). However, in previous assessments, IUCN's population size reduction criterion (A2) has always been the cause for the classification of the species pair as Critically Endangered (SSC IUCN, 2001; BirdLife International, 2021b). There have undoubtedly been severe declines across the species' range over the last 40 years (three generations of 14.3 years each, BirdLife International, 2022b). Local extinctions were particularly prominent in the 1990s and 2000s when both trade records and field surveys (Inskipp et al., 1988; PHPA et al., 1998; Cahill et al., 2006) showed that market prices of birds had already risen and remnant populations had fallen victim to further trapping. Very little is known about the numbers in the 1970s but the reported export and import numbers in the 1980s suggest that populations must still have been substantial enough to support the international trafficking of 5,200–12,000 *C. sulphurea* every year for more than a decade (non-captive exports to CITES countries via Singapore with origin Indonesia from CITES annual report statistics) (PHPA et al., 1998) with a total of at least 96,785 individuals documented as exports in the years 1981–1992 (Inskipp et al., 1988; Cahill et al., 2006). Due to losses in transit (Collar and Juniper, 1992; Pires, 2012; Jain et al., 2022), numbers trapped must have been much higher than those recorded in trade in Singapore. To allow removal of several thousand individuals annually the population in 1978 must have been well above 15,000, which means that declines in the last three generations must have been > 80%. After the taxonomic split both species have been classified as Critically Endangered (BirdLife International, 2022a, 2022b).

6.3 Conservation recommendations

6.3.1 General recommendations

The only species recovery plan for the Yellow-crested Cockatoo was compiled in 1998 and the key activities listed were designed to be implemented in the subsequent five years (PHPA et al., 1998). Initiatives to compile an updated recovery plan started years ago but have not yet succeeded. Despite the delay, such a recovery plan may be a practical method for apportioning, publicising and rationalising the efforts of the various governmental and non-governmental organisations and individuals working on the species (Snyder et al., 2000). With its large distribution, spanning many provinces and islands and multiple conservation interests targeting the species in different organisations, the Yellow-crested Cockatoo and its citron-crested sister species would undoubtedly benefit from a more cooperative and coherent effort catalysed by a new species recovery plan.

Illegal trapping remains one of the two main threats for both cockatoo species and the problem was detected in almost every population. Although trapping and trade were not the focus in any of the chapters of this thesis, it features heavily in the conservation recommendations. This study, in particular the extensive survey presented in Chapter 2, provides pertinent local details of trappers' origins, methods, motivations, impacts, allies, adversaries, and trading partners. However, key information on the status of the species in particular areas, which would allow tailored conservation approaches for each island, region and especially village, could not be presented in this thesis explicitly for fear of becoming available to trappers (Collar et al., 2017). Nevertheless, results including detailed locations have been compiled and are available to other researchers and conservation practitioners (deposited with Burung Indonesia and BirdLife International).

Trade is not a purely ecological problem and inter-disciplinary work is required to initiate public awareness programmes, alternative livelihood strategies and improvement of law enforcement. The information gathered in this study on trapping covers the opposite end of the trade chain than most existing research, which predominantly documents demand, market surveys, exports and imports (Chng and Eaton, 2016; Nandika et al., 2021; Pires et al., 2021; Jain et al., 2022). Some useful strategies and actions can be adopted from crime prevention measures at trapper and middlemen stage (Pires, 2012), e.g. making it more difficult to trap and sell parrots by increasing guardianship, removing climbing gear from trees, and implementing law enforcement stops on key roads and in harbours.

6.3.2 Recommendations for each species and subspecies

Subspecies *occidentalis* (Nusa Penida to Alor)

This appears to be the most secure of the *C. sulphurea* subspecies, owing to its stronghold on Komodo, which has the highest numbers, most protection effort, regular monitoring, monetary value for the local population and the support of a large governmental organisation (Komodo National Park) including local ecologists. Much of this depends on tourism with its associated personnel presence, patrols and income for the local communities and the region. However, the situation on Komodo is currently highly political and advocating for conservation needs is an important way to improve the long-term safety of this stronghold population after the planned changes in the tourism regime. Highly motivated national parks staff and Burung Indonesia are important allies in this. Komodo National Park's monitoring scheme works well and deserves additional support to be continued and disseminated in the scientific community. It should also function as a model for effective monitoring in other Indonesian national parks with threatened parrots. Almost all sites where *C. occidentalis* survives outside of Komodo National Park are relatively remote and have in common that there is little awareness for the cockatoo's plight, worth and needs. Local communities have control over most sites where cockatoos are trapped in this region and a mobile small-scale public awareness programme would be highly beneficial. Currently, in some cases cockatoos are not confiscated illegally kept by local traders are not confiscated when reported because they cannot be housed on the island and transport to other islands causes legal and potential ecological problems. A system for keeping, rehabilitating, and possibly releasing confiscated cockatoos back to the wild where they were caught, is needed as a prerequisite for improving enforcement of the legal trade ban in the region.

Subspecies *parvula* (Timor area)

More research both on the density of the large population in Timor-Leste's largest national park and into the country's small mountain populations is urgently needed in order to understand trends and limiting factors. Government conservation agencies are setting the course for successful conservation management. For these relatively new organisations in a small, isolated country, capacity building for field staff and logistical improvements are still needed to facilitate their future work. All the smaller populations in Timor-Leste would benefit from tailored public awareness approaches as they currently receive very little attention. People are not dependent on hunting cockatoos for nutrition nowadays and can probably be easily persuaded to avoid cockatoos and other threatened species when hunting. This would also prime local communities to protect their cockatoos in the event that Timor-Leste loses its immunity to Indonesian bird market forces in future. Agricultural systems that allow peaceful coexistence of cockatoos and farmers (e.g. below-canopy coffee plantations like those that are already established in some parts of the country) should be evaluated for their ecological benefits and encouraged (Hernandez-Aguilera et al., 2019; Williams et al., 2021).

Only a small part of this subspecies' population lives outside Timor-Leste, but two of the small remnant populations in Indonesia are located in actively protected areas and monitored regularly by the government. These would be ideal locations for exchange of expertise between the two counties. While stronger links between conservation and science are desirable, information about the location of Timor-Leste's cockatoo populations should be carefully controlled (Meijaard and Nijman, 2014; Collar et al., 2017; Marshall et al., 2020).

Subspecies *sulphurea* (Sulawesi)

This is probably the subspecies closest to extinction, maybe aside from *abbotti*. It is urgent to work together with the national park that supports the majority of surviving individuals and with local communities to improve forest protection within the park, otherwise the most viable but still very small population of the subspecies will soon disappear. In central Sulawesi unconfirmed reports of recent wild cockatoo sightings should be checked and any remnant population's conservation potential evaluated. A satellite island that harboured 17 individuals until a few years ago and has now lost most of its population (Ihsan et al., 2021) might have potential as a release site for confiscated individuals of this nominate subspecies. The remaining population on the small island is likely to wink out in the absence of additional genetic material (Ihsan et al., 2021), so the risks associated with releases (White Jr. et al., 2012; Collar et al., 2015) may be smaller than those that stem from doing nothing. The remnant population has been studied intensively and conditions on such a small island are more easily controlled, nevertheless thorough vetting of the releasees is essential in any case (Collar et al., 2015).

Subspecies *paulandrewi* (Tukangbesi Islands)

The main concerns for the small remnant populations of this subspecies are ongoing capture of adults, competition by introduced parrot species and potential intensification of agriculture if the terrestrial areas of the national park are not better protected in future. The threats could be mitigated and better monitored if cockatoo habitat was included in the existing national park, which is currently limited to marine conservation. A first step would be inclusion of the three Yellow-crested Cockatoo subpopulations into the regular bird monitoring carried out by the existing and highly motivated national park field staff. The necessary administrative changes might not meet too much resistance once higher-level government officials become aware that a Critically Endangered national conservation priority species with ecotourism potential is struggling to survive virtually unprotected, surrounded by an existing national park (WWF Indonesia, 2007; KLHK and DJ KSDAE, 2018).

Subspecies *djampeana* (Selayar Islands)

Two of the three populations of this subspecies have good survival chances if habitat destruction and trapping can be tackled. The small size of the islands with their closely-knit communities controlling access to the habitat offer ideal conditions for community awareness programmes to be effective, as long as livelihoods can be guaranteed from alternative sources. The largest of the populations, for example, is threatened by a sole elderly trapper, who could probably be convinced to retire from illegal trapping, if he is hired to trap the introduced Tanimbar Corella *Cacatua goffiniana* that is starting to outcompete the native species.

Subspecies *abbotti* (Masalembu Islands)

The tiny population of this subspecies seems to be stable and supported by the local human population thanks to past conservation and awareness programmes (Ihsannudin et al., 2020). Inbreeding is a major concern for this subspecies. Genetic research would be able to indicate the severity of inbreeding and possibly clarify the origin of the taxon in this exceptional location far from its nearest relatives (Collar and Marsden, 2014).

Cacatua citrinocristata (Sumba)

Considering the insecure status of Sumba's cockatoo, it is essential to monitor its population sizes and trends. All threats that led to catastrophic declines during the last century still persist, albeit at lower levels. Reducing forest loss and trade require cooperation with local communities and the enforcement of the regulations already in place. Public awareness programmes have shown local successes in curbing trapping in the past (Djawarai et al., 2014) but more locations on Sumba need to be covered and longer-term efforts are probably needed (PHPA et al., 1998). In addition, trapping should be made less attractive by increasing the risk of being caught and sentenced through law enforcement (Pires et al., 2021). Raising conservation awareness among law enforcement personnel would likely improve motivation and success rate in intercepting bird transports and identifying middlemen.

To date, no extensive trial of the efficacy of nestboxes has been done on Sumba, so in the short term I recommend their provision as an experiment in boosting productivity. Wild parrots sometimes ignore nestboxes (e.g. Jones, 1980; Walker et al., 2001; Brightsmith and Bravo, 2006; Tatayah et al., 2007; Rocamora and Laboudallon, 2013), but there are many cases where appropriately designed and positioned nestboxes are successfully supporting threatened parrot species through a period of nest-site shortage (White Jr et al., 2006; Cockle et al., 2010; Jones et al., 2013; Saunders et al., 2020). Accessible, known, safe nestboxes could also provide opportunities to assess the scale of nest-site shortage, allow camera placements to study productivity, exclude some competitors, and prevent illegal trapping.

Potential for releases and re-introductions

The existence of relatively large captive and naturalised populations of both species has sparked the idea of using these populations as source for re-introduction to sites where the cockatoos have become extinct or for the supplementation of struggling remnant populations (Leven and Corlett, 2004; Neo, 2012; Andersson et al., 2021). These conservation techniques are intensive, expensive, and have many problems associated with them (e.g. subspecies identification, hybridisation, behavioural issues and fitness disadvantages of tame, urban or captive birds, potential introduction of pathogens, etc), so they should be contemplated with great caution (White Jr. et al., 2012; Collar et al., 2015). Wild-living Citron-crested and Yellow-crested Cockatoos can recover well without supplementation if properly managed, and this is where efforts should be directed in my opinion. The situation is slightly different for confiscated individuals, especially if they are intercepted locally, near where they were caught. The logistical problems posed by confiscated birds to law enforcement agencies have been cited as reasons to avoid confiscations altogether. Release into the range of their subspecies should be considered for confiscated birds if they have lived in the wild before, are not tame, have not been exposed to other birds potentially carrying diseases and are confidently identified to subspecies (Collar et al., 2015).

References

Agista, D., Sumardin, Hamid, A., Mallo, F. N., Alam, S., Harjun and Mamengko, C. (2001) *Status Kakatua-kecil Jambul-kuning di Sulawesi Tenggara dan Sulawesi Tengah*. Bogor, Indonesia: Birdlife International - Indonesia Programme.

Andersson, A. A., Gibson, L., Baker, D. M., Cybulski, J. D., Wang, S., Leung, B., Chu, L. M. and Dingle, C. (2021) 'Stable isotope analysis as a tool to detect illegal trade in critically endangered cockatoos.' *Animal Conservation*, 24(6) pp. 1021–1031.

Argeloo, M. and Dekker, R. W. R. J. (1996) 'Exploitation of megapode eggs in Indonesia: The role of traditional methods in the conservation of megapodes.' *ORYX*, 30(1) pp. 59–64.

BirdLife International (2021a) *Datazone*. [Online] [Accessed on 11th March 2021] http://datazone.birdlife.org/.

BirdLife International (2021b) *Species factsheet* Cacatua sulphurea. [Online] [Accessed on 16th July 2021] http://www.birdlife.org.

BirdLife International (2022a) *Species Factsheet* Cacatua citrinocristata. [Online] [Accessed on 6th January 2022] http://www.birdlife.org.

BirdLife International (2022b) *Species Factsheet* Cacatua sulphurea. [Online] [Accessed on 6th January 2022] http://www.birdlife.org.

Brightsmith, D. and Bravo, A. (2006) 'Ecology and management of nesting Blue-and-Yellow Macaws (*Ara ararauna*) in Mauritia palm swamps.' *Biodiversity & Conservation*, 15(13) pp. 4271–4287.

Cahill, A. J., Walker, J. S. and Marsden, S. J. (2006) 'Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea citrinocristata* in Indonesia after 10 years of international trade control.' *Oryx*, 40(2) pp. 161–167.

Cahyadin, Y., Jepson, P. and Syarief, M. (1994) *A rapid status assessment of* Cacatua sulphurea sulphurea *in South Sulawesi Province*. Bogor, Indonesia: PHPA/BirdLife International - Indonesia Programme.

Caraka, R. E., Lee, Y., Kurniawan, R., Herliansyah, R., Kaban, P. A., Nasution, B. I., Gio, P. U., Chen, R. C., Toharudin, T. and Pardamean, B. (2020) 'Impact of COVID-19 large scale restriction on environment and economy in Indonesia.' *Global Journal of Environmental Science and Management*, 6(Special Issue) pp. 65–84.

Chng, S. C. L. and Eaton, J. A. (2016) 'Snapshot of an on-going trade: an inventory of birds for sale in Chatuchak weekend market, Bangkok, Thailand.' *BirdingASIA*, 25 pp. 24–29.

CNN Travel (2019) *Indonesia cancels plan to ban tourists from Komodo Island*. CNN Travel. [Online] [Accessed on 27th November 2019] https://edition.cnn.com/travel/article/indonesia-komodo-islands-reverse-tourist-ban-intl-hnk/index.html.

Coates, B. J. and Bishop, D. (1997) *A guide to the birds of Wallacea*. Queensland, Australia: Dove Publications.

Cockle, K. L., Martin, K. and Drever, M. C. (2010) 'Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest.' *Biological Conservation*, 143(11) pp. 2851–2857.

Collar, N. J., Eaton, J. A. and Sykes, B. (2017) ‘Conservation and the redaction of locality data.’ *BirdingASIA*, 28 pp. 3–4.

Collar, N. J. and Juniper, A. T. (1992) ‘Dimension and causes of the parrot conservation crisis.’ *In* Beissinger, S. R. and Snyder, N. F. R. (eds) *New world parrots in crisis: solutions from conservation biology.* New York and London: Smithsonian Institution Press, pp. 1–24.

Collar, N. J., Lierz, M., Price, M. R. S. and Wirth, R. Z. (2015) ‘Release of confiscated and captive-bred parrots: is it ever acceptable?’ *Oryx*, 49 pp. 202–203.

Collar, N. J. and Marsden, S. J. (2014) ‘The subspecies of Yellow-crested Cockatoo *Cacatua sulphurea*.’ *Forktail*, (30) pp. 23–27.

Djawarai, Y., Bashari, H., Siregar, B. and Widyanto, A. (2014) *The breeding ecology of Sumba Cockatoo* Cacatua sulphurea citrinocristata *in Manupeu Tanadaru National Park and surrounding, Sumba*. *Burung Indonesia*. Bogor, Indonesia: Burung Indonesia.

Froese, G. Z. L. and Mustari, A. H. (2019) ‘Assessments of Maleo Macrocephalon maleo nesting grounds in South-east Sulawesi reveal severely threatened populations.’ *Bird Conservation International*, 29 pp. 497–502.

Hernandez-Aguilera, J. N., Conrad, J. M., Gómez, M. I. and Rodewald, A. D. (2019) ‘The Economics and Ecology of Shade-grown Coffee: A Model to Incentivize Shade and Bird Conservation.’ *Ecological Economics*, 159, May, pp. 110–121.

van der Hoek, Y., Gaona, G. V. and Martin, K. (2017) ‘The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world.’ *Diversity and Distributions*, 23(10) pp. 1120–1131.

Ihsan, M., Mardiastuti, A., Masy’ud, B. and Mulyani, Y. A. (2021) ‘Population status and sustainability of Yellow-crested cockatoo (*Cacatua sulphurea sulphurea*) on Pasoso Island, Central Sulawesi, Indonesia.’ *Biodiversitas Journal of Biological Diversity*, 22(6).

Ihsannudin, I., Hidayat, K., Sukesi, K. and Yuliati, Y. (2020) ‘Perception of the local community toward the yellow-crested cockatoo (*Cacatua sulphurea abbotti*), a critically endangered species in Masakambing Island, Indonesia.’ *Geografia*, 16(4) pp. 1–14.

Imansyah, M. J., Purwandana, D., Ariefiandy, A., Benu, Y. J., Jessop, T. S. and Trainor, C. R. (2016) ‘Valley-floor censuses of the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea occidentalis* on Komodo Island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period.’ *Forktail*, 32 pp. 66–72.

Indraswari, K., Friedman, R. S., Noske, R., Shepherd, C. R., Biggs, D., Susilawati, C. and Wilson, C. (2020) ‘It’s in the news: Characterising Indonesia’s wild bird trade network from media-reported seizure incidents.’ *Biological Conservation*, 243 p. 108431.

Inskipp, T., Broad, S. and Luxmoore, R. (1988) *Significant Trade in Wildlife -A Review of Selected Species in CITES Appendix II, Volume 3: Birds*. Cambridge, UK: IUCN Conservation Monitoring Centre.

Jain, A., Aloysius, S. L. M., Lim, H., Plowden, T., Yong, D. L., Lee, J. G. and Phelps, J. (2022) ‘Understanding Singapore’s dynamic parrot trade ecosystem.’ *Oryx*, 56(2) pp. 184–194.

Jeon, C.-Y. and Yang, H.-W. (2021) ‘The structural changes of a local tourism network: comparison of before and after COVID-19.’ *Current Issues in Tourism*, January, pp. 1–15.

Jones, C. G. (1980) ‘Parrot on the Way to Extinction.’ *Oryx*, 15(4) pp. 350–354.

Jones, C. G., Malham, J., Reuleaux, A., Richards, H. A., Raisin, C., Tollington, S., Zuel, N., Chowrimootoo, A. and Tatayah, V. (2013) 'Echo parakeet *Psittacula eques* Perruche de Maurice.' *In* Safford, R. and Hawkins, F. (eds) *The Birds of Africa: Volume VIII: The Malagasy Region: Madagascar, Seychelles, Comoros, Mascarenes*. A&C Black, pp. 433–438.

Jones, M. J., Linsley, M. D. and Marsden, S. J. (1995) 'Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia.' *Bird Conservation International*, 5(01) pp. 21–52.

Kinnaird, M. F., O'Brien, T. G., Lambert, F. R. and Purmiasa, D. (2003) 'Density and distribution of the endemic Seram cockatoo Cacatua moluccensis in relation to land use patterns.' *Biological Conservation*, 109 pp. 227–235.

KLHK and DJ KSDAE (2018) *Statistik Direktorat Jenderal Konservasi Sumbar Daya Alam dan Ekosistem Tahun 2017*. Jakarta, Indonesia: Kementerian Lingkungan Hidup dan Kehutanan.

Leven, M. R. and Corlett, R. T. (2004) 'Invasive birds in Hong Kong, China.' *Ornithological Science*, 3(1) pp. 43–55.

Marsden, S. J. (1992) 'The distribution, abundance and habitat preferences of the Salmon-crested Cockatoo Cacatua moluccensis on Seram, Indonesia.' *Bird Conservation International*, 2(1) pp. 7–13.

Marsden, S. J. and Royle, K. (2015) 'Abundance and abundance change in the world's parrots.' *Ibis*, 157(2) pp. 219–229.

Marshall, B. M., Strine, C. and Hughes, A. C. (2020) 'Thousands of reptile species threatened by under-regulated global trade.' *Nature Communications*, 11(1) pp. 1–12.

Meijaard, E. and Nijman, V. (2014) 'Secrecy considerations for conserving Lazarus species.' *Biological Conservation*. Elsevier BV pp. 21–24.

Nandika, D., Agustina, D., Heinsohn, R. and Olah, G. (2021) 'Wildlife Trade Influencing Natural Parrot Populations on a Biodiverse Indonesian Island.' *Diversity 2021, Vol. 13, Page 483*, 13(10) p. 483.

Neo, M. L. (2012) 'A review of three alien parrots in Singapore.' *Nature in Singapore*, 5 pp. 241–248.

Newton, I. (1994) 'The role of nest sites in limiting the numbers of hole-nesting birds: A review.' *Biological Conservation*, 70(3) pp. 265–276.

Persulessy, Y. E., Djawarai, Y. B. and Marut, R. (2003) *Survei populasi dan distribusi kakatua-kecil jambul-kuning* Cacatua sulphurea citrinocristata *dan empat jenis paruh bengkok lain di Pulau Sumba*. Bogor, Indonesia.

PHPA, LIPI and BirdLife International-IP (1998) *Species recovery plan Yellow-crested Cockatoo*. Bogor, Indonesia: PHPA/LIPI/BirdLife International - Indonesia Programme.

Pires, S. F. (2012) 'The illegal parrot trade: a literature review.' *Global Crime*, 13(3) pp. 176–190.

Pires, S. F., Olah, G., Nandika, D., Agustina, D. and Heinsohn, R. (2021) 'What drives the illegal parrot trade? Applying a criminological model to market and seizure data in Indonesia.' *Biological Conservation*, 257, May.

Poulsen, M. and Jepson, P. (1996) 'Status of the Salmon-crested Cockatoo and Red Lory on Ambon Island, Maluku.' *Kukila*, 8 pp. 159–160.

Purwandana, D., Ariefiandy, A., Imansyah, M. J., Rudiharto, H., Seno, A., Ciofi, C., Fordham, D. A. and Jessop, T. S. (2014) ‘Demographic status of Komodo dragons populations in Komodo National Park.’ *Biological Conservation*, 171, March, pp. 29–35.

Reuleaux, A., Collar, N. J., Siregar, B. A., Mardiastuti, A. and Marsden, S. J. (2018) ‘Preliminary range-wide surveys of the heavily traded Tenggara Hill Myna *Gracula venerata*.’ *Forktail*, 34 pp. 29–34.

Rocamora, G. and Laboudallon, V. (2013) ‘Seychelles Black Parrot *Coracopsis barklyi*.’ *In* Safford, R. and Hawkins, F. (eds) *The Birds of Africa: Volume VIII: The Malagasy Region: Madagascar, Seychelles, Comoros, Mascarenes*. A&C Black, pp. 445–447.

Sánchez-Mercado, A., Ferrer-Paris, J. R., Rodríguez, J. P. and Tella, J. L. (2021) ‘A literature synthesis of actions to tackle illegal parrot trade.’ *Diversity*, 13(5) p. 191.

Saunders, D. A., Dawson, R., Mawson, P. R. and Cunningham, R. B. (2020) ‘Artificial hollows provide an effective short-term solution to the loss of natural nesting hollows for Carnaby’s Cockatoo *Calyptorhynchus latirostris*.’ *Biological Conservation*, 245, May, p. 108556.

Shepherd, C. R. and Nijman, V. (2008) ‘The trade in bear parts from Myanmar: An illustration of the ineffectiveness of enforcement of international wildlife trade regulations.’ *Biodiversity and Conservation*, 17(1) pp. 35–42.

Snyder, N. F. R., McGowan, P., Gilardi, J. and Grajal, A. (2000) *Parrots. Status Survey and Conservation Action Plan 2000-2004*. Oxford, UK: IUCN.

SSC IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. Gland, Switzerland and Cambridge, UK: Species Survival Commission. IUCN. [Online] http://www.iucnredlist.org/apps/redlist/static/categories_criteria_3_1.

Taman Nasional Komodo (2016) *Statistik Balai Taman Nasional Komodo tahun 2009-2015*. Labuan-Bajo, Indonesia: Kementerian Lingkungan Hidup dan Kehutanan.

Tatayah, R. V. V, Malham, J., Haverson, P., Reuleaux, A. and Van de Wetering, J. (2007) ‘Design and provision of nest boxes for echo parakeets *Psittacula eques* in Black River Gorges National Park, Mauritius.’ *Conservation Evidence*, 4 pp. 16–19.

Thu, P. M. (2012) ‘Access to Land and Livelihoods in Post-conflict Timor-Leste.’ *Australian Geographer*, 43(2) pp. 197–214.

Walker, J. S., Cahill, A. J. and Marsden, S. J. (2001) *The nesting ecology of Yellow-crested Cockatoo* Cacatua sulphurea *on Sumba and the potential for using artificial nest sites to increase recruitment. Preliminary report 2001*. Manchester, UK: Manchester Metropolitan University.

White Jr., T. H., Collar, N. J., Moorhouse, R. J., Sanz, V., Stolen, E. D. and Brightsmith, D. J. (2012) ‘Psittacine reintroductions: Common denominators of success.’ *Biological Conservation*, 148 pp. 106–115.

White Jr, T. H., Brown, G. G. and Collazo, J. A. (2006) ‘Artificial cavities and nest site selection by Puerto Rican Parrots: a multiscale assessment.’ *Avian Conservation and Ecology*, 1(3) p. e5.1-e5.13.

Williams, A., Dayer, A. A., Hernandez-Aguilera, J. N., Phillips, T. B., Faulkner-Grant, H., Gómez, M. I. and Rodewald, A. D. (2021) ‘Tapping birdwatchers to promote bird-friendly coffee consumption and conserve birds.’ *People and Nature*, 3(2) pp. 312–324.

Winkler, D. W., Billerman, S. M. and Lovette, I. J. (2020) ‘Cockatoos (Cacatuidae).’ *In* Billermann, S. M., Keeney, O. G., Rodewald, P. G., and Schulenberg, T. S. (eds) *Birds of the World*. version 1., Ithaca, NY, USA: Cornell Lab of Ornithology.

WWF Indonesia (2007) *Zonasi baru di TN Wakatobi*. Press release. [Online] [Accessed on 1st July 2019] https://www.wwf.or.id/?2723.

Zhang, L., Hua, N. and Sun, S. (2008) ‘Wildlife trade, consumption and conservation awareness in southwest China.’ *Biodiversity and Conservation*, 17(6) pp. 1493–1516.

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Correlates of persistence in remnant populations of two Critically Endangered cockatoos

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Abstract

A challenge with species that have disappeared from most of their range is to identify the correlates of local persistence. With species decimated by trade, site-specific trapping risk is hard to capture by remotely accessed predictors. The recently split yellow-crested cockatoo *Cacatua sulphurea* and citron-crested cockatoo *C. citrinocristata* have undergone catastrophic declines due to habitat loss and especially trapping, and are now extinct in much of their former range across Indonesia. Of 144 sites on 30 islands known to contain the species in 1950, only 76 on 27 islands did so in 2017–2019, with many of the other 68 experiencing extinctions between 1985 and 2000. We compared socio-ecological conditions such as forest cover and loss, human population density and infrastructure, and protected area status between the occupied and unoccupied sites, using ‘random forests’ within decreasing time intervals 1950–2015. Populations on Sulawesi and West Nusa Tenggara were more likely to become extinct than those on Sumba, Timor-Leste and small remote islands. Sites retaining cockatoos had high proportions of tree cover, low road density and low human densities. The relative importance of these factors changed little over time, but road density and human density became respectively more and less important in recent years. The examination of local conditions at ‘false negative’ sites (where cockatoos survived contrary to model predictions) showed that, particularly in recent years, cockatoo survival has been promoted by site-specific protection due to traditional beliefs, NGO activities, dedicated individual residents and local topographic barriers. Some of these local influences add complexity to the task of conserving cockatoo strongholds, but also offer exciting possibilities for low-cost conservation prescriptions tailored to individual sites. Studies combining field and remotely sensed data, and examining false negative sites for beneficial location-specific conditions, have broad application for the conservation of taxa with once-large ranges.

Introduction

Habitat loss and deterioration have rendered almost one in 10 tropical bird species at risk of extinction (Sodhi *et al*., 2010; BirdLife International, 2018, 2021*a*). Attractive, relatively easy-to-keep species such as parrots face the additional impact of unsustainable direct exploitation for the pet trade (Bush, Baker & Macdonald, 2014; Tella & Hiraldo, 2014). As a result of this double pressure, parrots are among the most endangered bird orders in the world (Olah *et al*., 2016; BirdLife International, 2018), with 175 (43%) of the 403 species either threatened or ‘Near Threatened’ (BirdLife International, 2021*a*). Since the establishment of CITES in 1975, the international trade in parrots, of which only four species are not included in its appendices (CITES, 2020), has become increasingly regulated, but evidence of a direct benefit to threatened species is inconclusive (Martin, 2000), not least because of a severe lack of reliable abundance data (Marsden & Royle, 2015). Moreover, CITES does not extend to domestic trade. For species with fragmented remnant populations, understanding why they survive at some sites and die out at others is important for their conservation. While some aspects of trade can be predicted well by factors such as species' characteristics and the effect of distance on supply and demand (Romero-Vidal *et al*., 2020; Pires *et al*., 2021), there are many factors affecting local exploitation levels that are site specific and cannot easily be captured by universally available data, especially for distributions that cross cultural and political boundaries. Local demand varies between cultures, as for maleo *Macrocephalon maleo* eggs (Froese & Mustari, 2019) and turtle (Chelonioidea) products (Garland & Carthy, 2010), and can variously be influenced by traditional beliefs, political circumstances, enforcement activities and conservation interventions (Veríssimo *et al*., 2020). Capture methods vary with local cultures and traditions and can determine the stability of the targeted population (Valle *et al*., 2018). Identifying the factors correlating with survival at some sites and extinction at others offers important leverage points for conservation policy and management.

The yellow-crested cockatoo *Cacatua sulphurea* is endemic to the islands of western Wallacea (BirdLife International, 2021*b*), with the citron-crested cockatoo *C. citrinocristata*, only recently recognized as a separate species from yellow-crested, restricted to Sumba in the south-west of the same region (BirdLife International, 2022*a*). Like many other parrots the species are negatively affected by habitat loss and trade, as a consequence of which they have disappeared from almost all of their range and been listed as Critically Endangered all this century (Collar *et al*., 2001; BirdLife International, 2021*b*). Once the species were so numerous in parts of their ranges that their flocks made trees appear white, and crops had to be guarded against them (Kendall, 1979; Setiawan, 1996; Collar *et al*., 2001). As obligate hole-nesters, the cockatoos are highly vulnerable to trapping when breeding or communally roosting (Marsden & Jones, 1997; Walker, Cahill & Marsden, 2005; Imansyah *et al*., 2016). Consequently, they were trapped and exported in the thousands for the international pet market (Inskipp, Broad & Luxmoore, 1988; Cahill, Walker & Marsden, 2006). Estimated annual exports from Sumba, for example, were as high as 1600 birds in 1992 (Cahill *et al*., 2006) when a population of only 3200 individuals was estimated to remain (Jones, Linsley & Marsden, 1995). A number of regional studies were produced (Mallo & Setiawan, 1996; Catterall, 1997; Agista *et al*., 2001) along with a species recovery plan (PHPA, LIPI & BirdLife International-IP, 1998) and a comprehensive status review (Collar *et al*., 2001). Although export effectively became illegal in 1994 (Cahill *et al*., 2006), difficulties in enforcement allowed trapping and trade to continue (Collar *et al*., 2001; CITES, 2002; Persulessy, Djawarai & Marut, 2003).

Currently, six subspecies of *C. sulphurea* are recognized, all still extant (Collar & Marsden, 2014): the nominate form on Sulawesi and its associated islands, *C. s. occidentalis* on the island chain from Nusa Penida to Alor, *C. s. parvula* on Timor, *C. s. paulandrewi* on the Tukangbesi Islands, *C. s. djampeana* on the Selayar island group and *C. s. abbotti* on the Masalembu Islands in the Java Sea (this last being the only population presumed native outside of Wallacea). Today, the strongholds of the species are the adjacent islands of Komodo and Rinca (Reuleaux *et al*., 2020), although Sumba was regarded as holding the most important population when *citrinocristata* was considered conspecific (Jones *et al*., 1995; Cahill *et al*., 2006). Conservation efforts should of course encompass all seven taxa involved (Collar & Marsden, 2014), but the split of *C. citrinocristata* inevitably makes the updated status of the newly defined *C. sulphurea* even more serious than previously recognized.

To date, such efforts have mostly been limited to legal protection, including the creation of protected areas and the control of trade, except for *C. s. abbotti* on Masalembu and *C. citrinocristata* on Sumba, where NGOs have carried out public awareness campaigns (Burung Indonesia, 2011; Nandika *et al*., 2020). Without urgent intervention, however, the long-term viability of the two species, and particularly the tiny relict populations of some subspecies, appears doubtful, and efforts are long overdue to understand the reasons behind the sharp declines in some populations and the relative stability of others. Many plant and animal species find their strongholds in protected areas (Geldmann *et al*., 2013), the remotest regions (McCauley *et al*., 2013) or, by contrast, urban refuges (Geary *et al*., 2021), where they enjoy popular support (Boal, 2018) or the protection of cultural or religious beliefs (Bhagwat & Rutte, 2006; Plieninger *et al*., 2020).

Although Komodo National Park is known to sustain a currently healthy yellow-crested cockatoo population owing to its high level of protection (Reuleaux *et al*., 2020), little is known about the conditions at other locations that have either maintained or lost their cockatoo populations over the last two to three decades. To address this deficiency, we investigate all known sites for the two species across 41 islands in order to determine the main extrinsic factors, such as habitat intactness, human population characteristics, geography and area protection, that promote or prevent the survival of local populations. With this information, we review the species' overall conservation status and recommend future management priorities for them.

Materials and methods

To obtain information on locations of yellow-crested and citron-crested cockatoo populations, we collated all location-specific sightings of the two species. A review of extinct and surviving cockatoo populations up to the year 2000 (Collar *et al*., 2001) formed the base of the dataset. We then checked online platforms such as eBird, Internet Bird Collection and Xeno-Canto, birding trip reports, technical reports and the scientific literature for subsequent geographically referenced records of the species which we used to allocate search effort (Table S1). Correspondence with other ornithologists, conservation officials, bird guides and local people added further recent information (Table S1), which we used to plan our fieldwork and exclude certain locations with well-documented population sizes and widely agreed absences. Although all locations with documented cockatoo presence were considered in the planning stage and assessed either by field visits or from reports, the locations for older records were less precise, so only those with records after 1950 were used for data analysis. Sites with records in or after 2015 were regarded as holding currently surviving populations. All remaining sites were treated as extinctions for modelling because either the last record was more than a decade old or we had gathered evidence during fieldwork of the population's disappearance.

Local informant interviews

We surveyed known locations in West Nusa Tenggara (March–April 2017), East Nusa Tenggara except Sumba (April–May 2017, November–December 2017, June–August 2018), Timor-Leste (July–August 2018), Sulawesi and Buton (March–April 2019), Selayar Islands (November 2018), Tukangbesi Islands (April–May 2019) and, as a component of other work, Sumba in the period October 2016–May 2019. Fieldwork in each area started with enquiries at the local government office in charge of conservation, followed by short interviews with local farmers, trappers, former trappers and other forest users. The total number of interviewees was 1126 – the number on each island varying with its size and location (up to 10 per location, mean 7.8). In areas where we could not locate cockatoos, we made particular efforts to interview a range of informed local people. We targeted those who were likely to know and recognize cockatoos from their hunting, farming and forest activities. Although these interviewees were usually not experts, the target species are gregarious, easy to see and identify, and regarded as either crop pests, potential pets or exciting wildlife encounters, so people generally notice cockatoos and recall their observations. There was no formal structure to interviews but multiple standard questions were asked during the conversations. Trappers or former trappers often volunteered valuable information about remaining cockatoo populations, catching techniques and limitations (such as dwindling numbers, lack of demand, deteriorating access to habitat and traders, competition from other trappers, climbing hazards, restricted areas and law enforcement). Promising areas were visited, and leads followed from village to village and into the forest until cockatoo presence or likely absence could be established. When remotely gathered information was inconclusive, we visited the site and presumed absence if no birds could be found and if local interviewees either had not encountered cockatoos in the last decade or clearly remembered when the last individuals disappeared.

Field surveys

The field methods used to detect cockatoo presence and to count birds depended on the nature of the sites themselves. We assessed populations in strongholds on Komodo and Sumba in separate studies using point-count distance sampling. On Komodo in November and December 2017, we carried out 8-min point counts at 178 points along 25 randomly located transects in suitable habitat (Reuleaux *et al.*, 2020). On Sumba, to replicate earlier surveys (Jones *et al.*, 1995), from June to October 2017, we carried out five hundred and nineteen 10-min point counts at 328 points along 43 transects in six forested regions distributed in the centre and east of the island (Reuleaux, Siregar, Collar, Jones, Mardiastuti & Marsden, in prep).

In areas with lower densities, we used transects and informal walks with local guides to determine cockatoo presence and long watches from vantage points to determine the minimum number of cockatoos present. Wherever possible, we sought communal roosts to attempt to observe and count all individuals in the area simultaneously, taking the resulting number as an absolute minimum population size and using informed judgement to make a best estimate of a realistic local population size. At some sites (n = 28), there was a suitable vantage point from which most or all cockatoo individuals within the site could be counted at some stage, usually as birds flew to a roost site (n = 15) or travelled between feeding locations. Occasionally, roosts were known to local informants (n = 2), otherwise vantage points (clearings, openings, outcrops, climbable trees, beaches, jetties, stilt houses and boats) were used to follow cockatoo movements at dusk to the roost or to choose another vantage point closer to the suspected roost on the following evening. Cockatoos were counted as they arrived at the roost and recounted with binoculars or a spotting scope as they perched high in trees when it was almost dark. For small islands and areas that could be viewed well from a distance (from above or offshore), this method worked well, whereas continuous flat areas without vantage points were difficult to assess and constrained us to very conservative estimates. At some sites, point-count transects were used (n = 22 excluding Sumba and Komodo, see below) but, owing to very low encounter rates, targeted walks with informants were more appropriate (total walked distance across all sites 830 km). The numbers of transects varied by site depending on area and terrain, and transect length averaged 1.8 km (range 1–2.2 km). Transects and walks were not placed randomly at sites, to maximize the likelihood of encountering birds that were present, and thus no encounter rates are presented. In total, we spent 1199 h surveying suitable habitat (forests, savanna woodland, gardens, diverse fields and tree plantations) at times when cockatoos could be expected to be active and best detectable (dusk – 10.30 and dark – 15.00, Marsden, 1999).

Environmental factors

To examine the factors that correlate with, and potentially drive, the survival or extinction of individual cockatoo populations, we used random forests – a machine learning technique for classification and regression (Breiman, 2001; Liaw & Wiener, 2002) – based on remotely available information on environmental, sociological, economic and ecological factors. All layers were obtained or converted to grids of *c.* 30 × 30 m resolution, and the data associated with each location were assessed over a 2-km-radius circle around it using QGIS (QGIS Development Team, 2021). We examined the following seven factors: (1) island group, (2) gross domestic product (GDP), (3) road density, (4) altitude, (5) tree cover, (6) human population density and (7) protected area. (1) Islands were grouped into Sulawesi; West Nusa Tenggara (Bali, Lombok and Sumbawa); Sumba; East Nusa Tenggara (including West Timor) excluding Sumba; Timor-Leste; and small remote islands. (2) GDP per capita in the respective regency is given in constant 2011 international dollars, the unit used by the World Bank for national GDP (Kummu, Taka & Guillaume, 2018). (3) Road density was calculated from the total length of roads and tracks (all types recorded by OSM, Geofabrik, 2021; OpenStreetMap Contributors, 2021) within each 2-km-radius circle, as a surrogate for accessibility. (4) Altitude was taken at the circle's centre (SRTM Digital elevation model, Van Zyl, 2001). (5) Tree cover is given as percentage of land covered by trees in 2019 (Hansen *et al*., 2013, 2020). (6) Density of the local human population corresponds to United Nations estimates for 2018 (Worldpop, 2018). (7) Protected area was measured as proportion of land in the 2-km-radius circle located inside a legally protected area equivalent to IUCN categories I–VI (Brun *et al*., 2015; KLHK & DJ KSDAE, 2018; IUCN, 2021). For protected areas, we explored alternative formats of the predictor, distinguishing between strictly (equivalent to IUCN categories I–II) and weakly (categories III–IV) protected areas (Table S3). We chose the most recent data available for each variable.

To establish an objective criterion for the separation of locations that tended to match historic site delimitation (Collar *et al*., 2001) and had some geographical and biological justification, we assigned records of cockatoos to a single site if localities were ≤10 km apart, but to different sites if >10 km apart. This was based on distances of <5 km recorded in cockatoos travelling to roost or forage in several years of fieldwork by AR, RNDL and BAS, mostly on Sumba and Komodo. West Timor was grouped with the rest of East Nusa Tenggara because it shares more social and political characteristics with those Indonesian islands than with Timor-Leste. Bali and its satellite Nusa Penida were grouped with West Nusa Tenggara. Small remote islands comprise three separate archipelagos whose basic common characteristic was their high degree of isolation. For security reasons, to avoid divulging precise site information potentially useful to trappers (Collar, Eaton & Sykes, 2017), we include small islands under the name of their large neighbours; moreover, we avoid reference to specific sites as far as possible.

Statistical analysis

We used QGIS (QGIS Development Team, 2021) for spatial analysis and R (R Core Team, 2021) for all other analyses and plots: randomForest (Liaw & Wiener, 2002), vegan (Oksanen *et al*., 2020), viridis (Garnier, 2018) and ggplot2 (Wickham *et al*., 2021). Our random forest classifiers contained 500 tree structures, and the number of factors to try at each step was optimized based on lowest 'out-of-bag' error. To be conservative, we interpreted >60% of tree votes for survival as predicting survival at the respective site and <40% as predicting extinction. The proportions of 40–60% were regarded as marginal predictions. We examined false positive and false negative classifications post hoc to investigate possible causes of survival or extinction not predicted by the models. To examine temporal shifts in factors contributing to extinctions, we created random forests based on 11 subsets of sites with a shift in the starting year (sites regarded as occupied initially) from 1950 to 2000 in 5-year intervals. Ideally, we would have split the extinction periods into equal windows; however, the majority of last records were aggregated in a single decade (Fig. 1), meaning that sample sizes in adjacent decades were too small to build robust models on their own.

Results

Locations where yellow-crested and citron-crested cockatoos were recorded between 1856 and 2019 totalled 375 (data filed with BirdLife International; availability restricted) but, under the definition provided above, grouped into 188 separate sites. Of these, 144 were confirmed as supporting cockatoos in 1950 or later and were therefore included in the analysis. In just over half these sites (76), cockatoos persisted in 2015 (Fig. 1). Populations at individual sites ranged from a single pair to 300 birds, but the large majority of populations are concentrated in just three strongholds, and only 28% elsewhere. Taking the two species together, the majority of the still occupied sites are located in Nusa Tenggara, Timor-Leste and Sumba. Sulawesi has lost 77%, West Nusa Tenggara 67%, East Nusa Tenggara 66%, Timor-Leste 26% and Sumba 25% of cockatoo sites since 1950 (Fig. 1). No extinctions are known from the small remote islands after 1950 (although three individual remote island sites have had no cockatoos recorded since 1901, 1907 and 1927). Extinctions appear to have peaked in the 1990s, as representatives of the majority of extinct subpopulations (62%) were last seen in that decade (Fig. 1).

Modelled predictors of survival

The best predictor of survival was the island or group of islands in which each site was located (Table 1; Fig. 2). Populations on Sulawesi and West Nusa Tenggara were most likely to become extinct, whereas those on Sumba, Timor-Leste and small remote islands were most likely to survive. Among the environmental and socio-economic predictors, more extensive tree cover (above a threshold of 20% of the area), lower human densities and lower road densities were all associated with elevated probability of cockatoo population persistence. Altitude, percentage of land allocated to protected areas and GDP per capita played only minor roles. The relationship between GDP and cockatoo survival showed a negative effect for initial economic development, but turned into a positive effect for very high GDP values (Fig. 3). In models based on shorter time intervals for assessing survival (temporal subsets of the data), there was initially little change in the relative importance of the predictors while moving the baseline for inclusion in the dataset from presence in 1950 towards 1990 (Fig. 2); however,

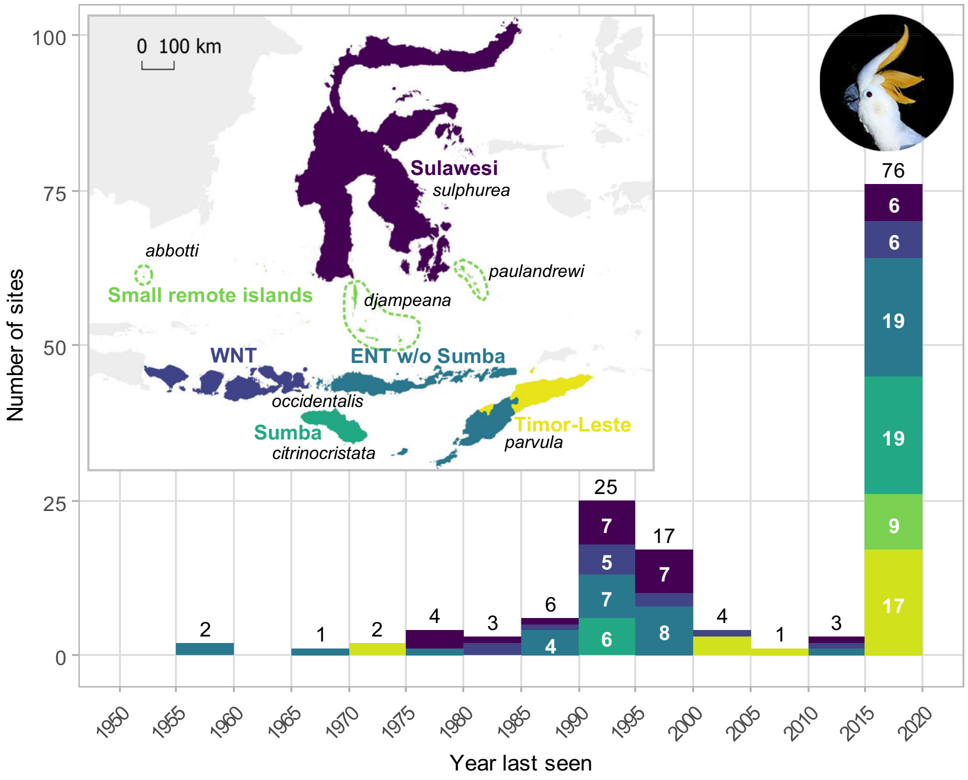

Figure 1 Study area, island grouping and timing of last record at sites with historic and extant yellow-crested cockatoo *Cacatua sulphurea* and citron-crested cockatoo *C. citrinocristata* populations. As a precaution against aiding illegal trapping, we do not show precise location information of extant populations. Sites with records in or after 2015 are regarded as currently surviving. 'Small isolated islands' comprise three separate archipelagos that are geographically separate but share remoteness. WNT = West Nusa Tenggara with Bali (as Bali had too few data to be considered separately), ENT w/o Sumba = East Nusa Tenggara excluding Sumba. Black numbers above the columns specify the column total, that is the number of sites with records in the respective 5-year period. White numbers give the size of the column sections they are within, that is the number of sites with last records in the respective island group and 5-year period.

when examining only extinctions between 1995 and 2015 or 2000 and 2015, the relative and absolute importance of the predictors changed considerably. Tree cover and island group appear to become more important, while human density and area protection lose influence, but for these smaller subsets error rates for extinctions rose and model accuracy decreased (Table 1, Fig. 2).

Unmodelled conditions and examination of prediction errors

At the 76 sites with cockatoos still present in 2015, we found a variety of (often overlapping) site-specific circumstances contributing to their protection which were not considered in the model. At 42 of the sites, highly motivated individuals championed conservation principles, and 10 of these and four others had activities by NGOs focused on conservation (12 sites by four NGOs) or humanitarian aims (two sites and two NGOs). In addition to the 28 sites containing formally protected land under the conditions of our model, 18 were visited regularly by governmental conservation staff, despite being located outside protected areas. Traditional beliefs in 'sacred groves' kept cockatoos safe at six sites. Poor access to markets with demand for cockatoos hampered trapping at 19 sites (17 in Timor-Leste), while 48 were so remote that they were inaccessible or unknown to outsiders. For cockatoo extinctions and persistence between 1950 and 2015, our random forest model misclassified eight sites as having lost populations when they had actually survived (false negatives), and 10 sites as occupied when they had no recent records (false positives; Table S2). All sites with unexpected survival showed one (two sites) or more (six sites) of the unmodelled site-specific beneficial conditions listed above. A notable false negative was a site on Sulawesi where cockatoos have recently become re-established after decades of almost certain absence. Among the false positives, two types of sites dominated: those with good habitat in relatively remote areas but with known (past or present) intense trapping pressure, and those where the current status of cockatoos is not entirely certain, and more search effort is needed.

Population estimates

We recorded a total of 1824 yellow-crested cockatoos over the six subpopulations, and our best estimates of the

Table 1 Accuracy of a series of random forest models examining the survival and extinction of yellow-crested cockatoos *Cacatua sulphurea* and citron-crested cockatoos *C. citrinocristata* with varying start dates of baseline presence data and importance of predictors in each model (measured by the decrease in model accuracy when the predictor is removed). n_{extinct} is the number of sites where cockatoos have become extinct (last record between the respective year and 2014). n_{survived} is the number of sites where cockatoos have survived (at least until 2015). + indicates a positive relationship between the predictor and survival. − indicates a negative relationship. +− indicates a positive influence for small values of the predictor and a negative one for larger values as displayed in Fig. 3, and −+ indicates a negative influence for small values of the predictor and a positive one for larger values as displayed in Fig. 3. AUC is the area under the Receiver Operating Characteristics curve, an indicator of the model's ability to distinguish between classes. 'Road density' is the length of road within each 2-km-radius circle

	1950	1955	1960	1965	1970	1975	1980	1985	1990	1995	2000
n_{extinct}	68	68	67	66	65	63	59	57	51	37	11
n_{survived}	76	76	76	76	76	76	76	76	76	76	76
Error rate total	0.229	0.229	0.224	0.225	0.227	0.223	0.215	0.211	0.228	0.239	0.161
Error rate$_{\text{extinct}}$	0.221	0.221	0.254	0.242	0.262	0.270	0.288	0.316	0.373	0.486	0.727
Error rate$_{\text{survived}}$	0.237	0.237	0.197	0.211	0.197	0.184	0.158	0.132	0.132	0.118	0.079
AUC	0.872	0.872	0.870	0.864	0.862	0.855	0.857	0.864	0.840	0.780	0.758
Island group	22.28	22.28	17.78	18.87	18.46	18.23	17.57	16.83	15.09	14.47	8.37
Tree cover	21.29^{+-}	21.29^{+-}	17.69^{+-}	20.99^{+-}	17.18^{+-}	15.74^{+-}	15.80^{+-}	17.78^{+-}	16.11^{+-}	12.55^{+-}	4.32^{+-}
Pop. density	16.23^{-}	16.23^{-}	15.90^{-}	14.60^{-}	13.91^{-}	12.52^{-}	11.09^{-}	13.23^{-}	9.42^{-}	6.25^{-}	-0.54^{-}
Road density	14.11^{-}	14.11^{-}	14.26^{-}	13.95^{-}	13.77^{-}	14.69^{-}	12.88^{-}	13.38^{-}	13.60^{-}	10.61^{-}	8.02^{-}
Altitude	12.86^{+-}	12.86^{+-}	10.81^{+-}	12.39^{+-}	9.90^{+-}	12.34^{+-}	11.10^{+-}	11.88^{+-}	9.12^{+-}	9.82^{+-}	2.34^{+-}
Protected area	11.44^{+}	11.44^{+}	12.16^{+}	11.86^{+}	11.07^{+}	9.67^{+}	9.91^{+}	11.04^{+}	7.56^{+}	2.81^{+}	-0.72^{+}
Gross domestic product per capita	8.35^{-+}	8.37^{-+}	8.84^{-+}	7.76^{-+}	8.68^{-+}	7.83^{-+}	8.67^{-+}	10.58^{-+}	12.85^{-+}	8.50^{-+}	2.83^{-+}

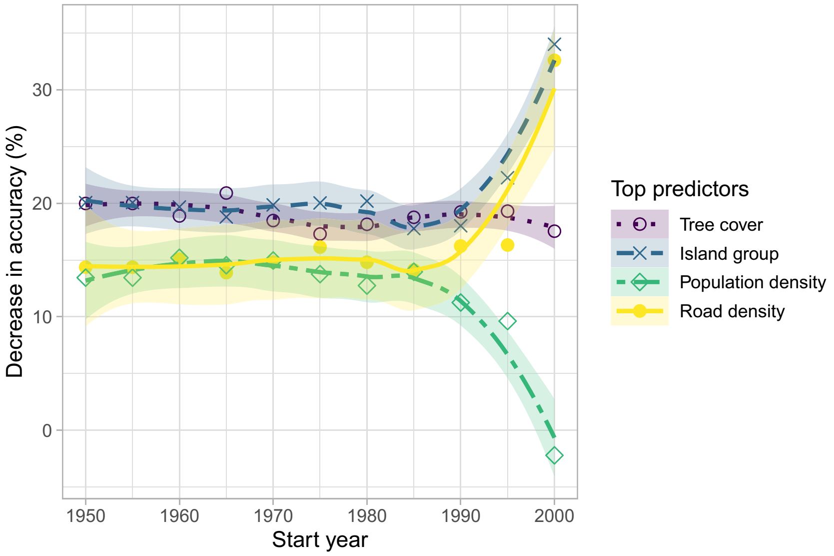

Figure 2 Change of predictor importance in random forest models for different time intervals. Importance is measured in decrease of model accuracy when the respective predictor is removed from the model (i.e. more important predictors would cause a larger decrease in model accuracy when removed). Only the four top predictors are shown for clarity. The *x*-axis represents the baseline year (of sites regarded as occupied initially) for 11 decreasing time intervals (all lasting to 2015).

populations on each island add up to 3000–3500 individuals (Table 2). We identified two strongholds for this species, namely Komodo National Park and Timor-Leste, which together may harbour around 61% of the global population. Despite the size of Sulawesi and the formerly huge range of its endemic subspecies *C. s. sulphurea*, the densities (<1 individual 1000 km^{-2}), current range and total numbers are extremely low (Table 2). Our best estimate of the global population derives from a range of field methods, some of which are informal or unstandardized in nature. However, 34% of our estimated maximum number come from formal surveys on Komodo using tailored distance sampling, an

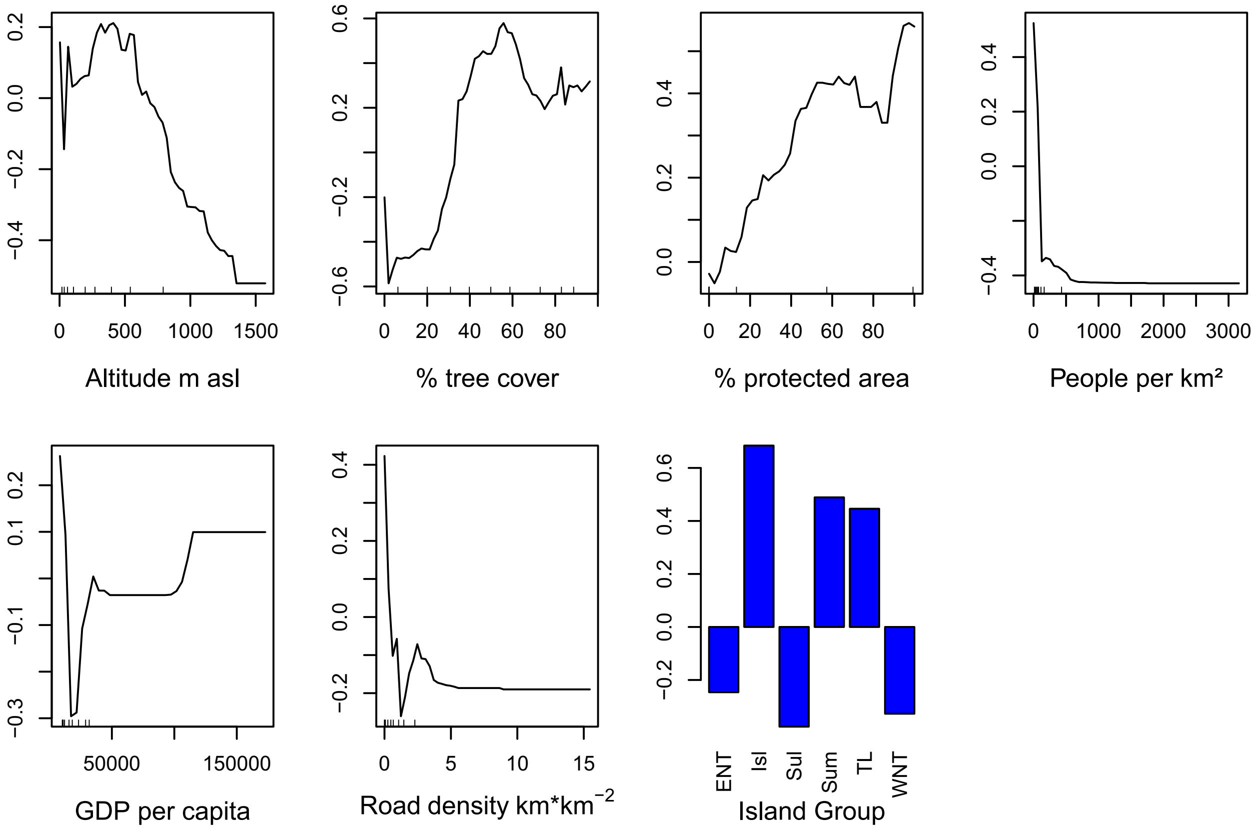

Figure 3 Partial importance of seven predictors for survival of yellow-crested cockatoo and citron-crested cockatoos at 144 sites from 1950 to 2015. ENT, East Nusa Tenggara without Sumba; Isl, small remote islands (see text); Sul, Sulawesi and satellites; Sum, Sumba; TL, Timor-Leste; WNT, West Nusa Tenggara (incl. Bali to Sumbawa).

Table 2 Estimated yellow-crested cockatoo *Cacatua sulphurea* and citron-crested cockatoo *C. citrinocristata* population sizes per subspecies and per island group. ENT, East Nusa Tenggara; w/o, without; WNT, West Nusa Tenggara (Bali to Sumbawa). *Minimum estimate* is derived from the sum of maximum flock sizes seen/reported in separate locations. *Estimated* number is the best estimate including suitable habitat that was only partly surveyed. *Sites survived* is the number of sites with extant cockatoo populations in 2015 versus *total* of all sites with cockatoo reports since 1950. *Density on island* is the number of individuals divided by the whole land area of the island(s) in the subspecies' range or in the island group. *% of island area occupied* is the area of occupied forest patches divided by the area of the island(s)

	Minimum estimate	Estimated	Sites survived/total	Density on island (ind × km^{-2})	% of island area occupied
Subspecies/species					
C. s. occidentalis	1207	1711	22/47	0.09	3.5
C. s. parvula	431	985	20/37	0.03	5.9
C. s. paulandrewi	81	172	4/4	1.27	10.7
C. s. djampeana	61	156	4/4	0.45	14.7
C. s. sulphurea	27	105	6/26	0.001	0.3
C. s. abbotti	17	22	1/1	7.33	11.2
C. citrinocristata	286	1400	19/25	0.11	11.0
Island groups					
ENT w/o Sumba	1210	1716	19/43	0.29	4.8
Timor-Leste	309	830	17/23	0.03	5.6
Remote islands	159	350	9/9	0.72	13.4
WNT	119	150	6/18	0.01	2.9
Sulawesi	27	105	6/26	0.001	0.3
Sumba	286	1400	19/25	0.11	11.0
Total	2110	4551	76/144	0.02	2.2

accepted population estimation method (Buckland *et al.*, 2001). An additional 1091 or 35% of the estimated population were actually directly counted, so we can at least be confident of the size of our minimum population estimate. There is, of course, uncertainty in population sizes at several sites, so it may be best to adopt a precautionary population estimate of 2191 (1100 from our formal survey on Komodo plus 1091 from our minimum estimates from elsewhere). For citron-crested cockatoos on Sumba, we could confidently separate 256 individuals from direct sightings, but numbers are more likely around 1400. A formal population estimate for the island with associated confidence intervals will be given in Reuleaux, Siregar, Collar, Jones, Mardiastuti & Marsden (in prep).

Discussion

The once abundant yellow-crested cockatoo has declined precipitously across its large original range because of loss of habitat and decades of exploitation for the pet trade; the citron-crested cockatoo has also undergone a sharp contraction in numbers and range on Sumba. This first comprehensive assessment of status in 20 years covered almost the entire range of the two species and found a combined minimum 2110 individuals at 76 sites. These numbers warrant concern, as the great majority of birds are concentrated in just three strongholds that are far from constituting a collective barrier against extinction: *C. citrinocristata* is confined to a single island, Sumba, and neither of the two strongholds of *C. sulphurea* is secure (see penultimate paragraph below). The main factors associated with survival are island group, high tree cover and low human densities, but local circumstances such as sacred groves or a highly motivated NGO, community leader or government official can arguably be at least as beneficial, and conservationists should actively seek to engage communities in cockatoo protection by fostering collective local identities and goodwill. Similar patterns of persistence can be expected in other parrots in Indonesia (Pires *et al.*, 2021) and have been observed in the region's other exploited threatened species, such as Tenggara hill myna *Gracula venerata* (Reuleaux *et al.*, 2018) and megapodes Megapodiidae (Argeloo & Dekker, 1996; Froese & Mustari, 2019). Although the types of informal protection and cultural determinants may differ in other geographic and taxonomic contexts, this site-by-site review of predictors of persistence represents a novel approach to identifying the most effective bespoke measures for conserving fragmented populations of exploited species.

Our random forest model predicted extinction and survival well. Island group as the most important factor reflects geographical nestedness, but these groups also have other significant common factors including colonization history, traditions, current dominant religion (Monk, De Fretes & Reksodiharjo-Lilley, 1997; Badan Pusat Statistik, 2016), political affiliation and economic development (Samudro, Bloch & Salim, 2015), some of which clearly influence the intensity of habitat loss and trade, the two major threats to cockatoos. Protected areas, whose benefits for biodiversity are well documented (Douglas-Hamilton, Krink & Vollrath, 2005; Pain *et al.*, 2006; Cazalis *et al.*, 2020; Liévano-Latorre, Brum & Loyola, 2021), also increase the survival chances of cockatoo populations, but some were created expressly to conserve yellow-crested cockatoo populations (such as national parks on Sumba and in south-east Sulawesi), potentially inverting cause and effect. As is common in parrot (Pires, 2012) and other wildlife trade (Robinson & Bodmer, 1999; Peres & Lake, 2003), trapping occurred first at easily accessible locations and only later at remote sites with poorer infrastructure (Cahill *et al.*, 2006; Eaton *et al.*, 2015), after the initial targets had become scarce (as on South Sulawesi or Lombok) or been protected by better law enforcement (as on Komodo). The cockatoos' requirement of large trees (Walker *et al.*, 2005) or palms (Imansyah *et al.*, 2016) for nesting and tracts of woodland or forest for foraging (Rowley, Sharpe & Boesman, 2017) fits with our finding that their survival is associated with high proportions of tree cover. Human population density, road density and GDP per capita are a measure of geographical remoteness and level of economic development and reflect the accessibility of both sites and markets (Wilkie *et al.*, 2005; Pires & Clarke, 2011; Fa *et al.*, 2015; Indraswari *et al.*, 2020). However, these relationships are not linear, and cockatoo survival may be influenced by processes that are sometimes recognized as environmental Kuznet's curves (McPherson & Nieswiadomy, 2005; Mills & Waite, 2009): rising GDP brings motorized transport links and mobile phone connections which initially increase trapping, trading effort and efficiency (Stearman, 2000; Pires, 2012), but with their further wealth local people rely less on illegal activities or forest use to survive or boost their incomes (Lunstrum & Givá, 2020), and cockatoo survival then increases. Direct and indirect negative effects of roads on mammal and bird population densities are well documented for many species globally (Benítez-López, Alkemade & Verweij, 2010; Kociolek et al., 2011); in the case of the cockatoos, the effect is most likely a consequence of the access that roads give for trapping and trade (Harris *et al.*, 2017).

The model's misclassifications are arguably as valuable as the correctly classified locations, since false positives highlight sites for potential re-introductions or where the species might persist undetected while false negatives can reveal unmodelled favourable conditions that might be replicated elsewhere. In the present case, sites predicted to retain cockatoos but which actually lacked recent cockatoo sightings (false positives) were all recent extinctions or lacked search effort. Confirming absences is a classic problem in ecology (Diamond, 1987; Butchart, Stattersfield & Brooks, 2006; Mortelliti & Boitani, 2007), as detectability has an inverse relationship with rarity. We used a last-seen-date cut-off to separate extinctions from presences, which allowed older extinctions (64 of 68 sites, extinction >10 years previously) to be presumed with reasonable certainty, but sites with recent records were more likely to involve false absences. We therefore particularly targeted such sites with fieldwork to increase the certainty of population status, and soon discovered that, because cockatoos are gregarious large white birds, commonly coveted for trapping or reviled as crop pests, residents in rural areas gave dependable information on their local status. This allowed us to presume extinctions, again with reasonable certainty, when (1) locals reported the disappearance of recently and regularly seen cockatoos and (2) we ourselves could not find the birds despite thorough searches. Consequently, we judge that errors in model inputs were likely only in five sites (3–6% of all sites depending on time period). Even so, we examined classification errors from the random forest model and found that these five cases were among those misclassified or classified as marginals. They are therefore in need of further fieldwork to check their status, although any birds remaining will certainly be few in number. Priority sites for future survey include these five doubtful sites and others where persistence was reported but information about population size and reasons for survival is missing due to lack of fieldwork effort, such as areas in Central Sulawesi, where research was not permitted due to a recent tsunami, and Timor-Leste, where the unexpectedly wide distribution and locally high densities of cockatoos relegated some of the smaller remnant populations to low priorities in search effort.

The examination of the eight false negatives from our model shows in every case some tangible local reason for cockatoo persistence. Topographic barriers abetting cockatoo population persistence include steep slopes, volcanoes and rocky coasts. Sacred groves (Bhagwat & Rutte, 2006; Rutte, 2011) appear to offer informal protection for the cockatoos, notably in remoter areas where animistic religions still influence daily life (Webb, 1986; Snodgrass & Tiedje, 2008; Sopian, 2015). Committed individuals acting as champions for particular populations commonly explain the false negatives and marginal classifications in our model. In one case, a former trapper used traditional beliefs to persuade his community to stop bird persecution, so that the cockatoo population in his village rose from four in 1986 to 34 in 2018, one of only two remaining subpopulations within hundreds of kilometres. NGOs working with local communities to raise awareness for cockatoos and biodiversity have managed to preserve the species at sites on Sumba, Flores and Masalembu (Burung Indonesia, 2011; Nandika *et al*., 2020). Although mining is well known for its negative effects on wildlife throughout the world (Gould, 2011; Sonter, Ali & Watson, 2018) and in East Nusa Tenggara itself (Erb, 2016), the security measures associated with such operations can reduce bushmeat consumption (Randriamamonjy *et al*., 2015) or bird trapping (Devenish *et al*., 2021). A mining operation with its associated security, local economic benefits and an enthusiastic ecologist has contributed to the survival of the only known population on Sumbawa (Yusuf, 2014). In one unfortunate case, a trapper's fatal fall deterred a whole community from climbing cockatoo nest trees.

On our evidence, the numbers of yellow-crested cockatoo quoted by BirdLife prior to this fieldwork are similar to our estimates when considered without Sumba (for the species pair 2373–2683 individuals of which 2000 considered mature; without the citron-crested cockatoo 1810–2120 individuals of which 1380–1675 considered mature; BirdLife International, 2021*b*). However, there have undoubtedly been severe declines across the species' range over the last 40 years (three generations, BirdLife International, 2022*b*). Although we can only guess the extent of losses before 1950, local extinctions were particularly prominent in the 1990s and 2000s when both trade records and field surveys (Inskipp *et al*., 1988; PHPA *et al*., 1998; Cahill *et al*., 2006) showed that market prices of birds had already risen and remnant populations had fallen victim to further trapping. Considerable time lags between the onset of population decline and extinction are known in long-lived species (Diamond, 1972; Kuussaari *et al*., 2009), particularly when trappers only target nestlings (Valle *et al*., 2018). In addition to gauging population changes over long periods, Red List reassessment of the cockatoos is complicated by several other considerations. The recent split of citron-crested cockatoo leaves the resultant two species at higher risk of extinction than when combined, as the population on Sumba remains under pressure from illegal trapping and appears to have low productivity (Reuleaux *et al*., 2022). The subspecies *occidentalis* and *parvula* may seem relatively safe with one stronghold each (Komodo for *occidentalis*, Timor-Leste for *parvula*), but the Komodo population depends on intense patrolling and local goodwill, both of which will be under threat if the recently proposed drastic reduction in visitor numbers to Komodo National Park (CNN Travel, 2019) is implemented, or if international travel is curtailed due to unforeseen issues such the current Covid-19 pandemic (Caraka *et al*., 2020; Jeon & Yang, 2021). Conservation infrastructure in Timor-Leste (subspecies *parvula*) is still being established, and the probable softening of the currently highly controlled border with Indonesia (Thu, 2012) could increase illegal wildlife trade, as seen elsewhere (Shepherd & Nijman, 2008; Zhang, Hua & Sun, 2008). The other subspecies all survive in very low numbers and their status remains precarious. Currently, *C. s. sulphurea* is of greatest concern: a national park formerly considered its last stronghold (Cahyadin, Jepson & Syarief, 1994; Agista *et al*., 2001) harbours a much smaller population than previously believed (12–50 individuals), in only a small area, and its staff urgently need support to liaise better with local communities and tackle the ongoing illegal establishment of new plantations in its core. A possible additional remnant population in Central Sulawesi needs urgent investigation. The populations of *djampeana* and *paulandrewi* have a realistic chance of survival only if there is legal protection for their habitat and enforced protection for the birds themselves.

There is an instructive parallel and contrast in the circumstances and management of the yellow-crested cockatoo and the Philippine cockatoo *Cacatua haematuropygia*. Both species were once widespread and common in their respective archipelagos – Wallacea and the Philippines – but have been reduced by forest clearance and trapping to scattered remnant populations (Collar *et al*., 2001). However, while the monotypic Philippine cockatoo has benefited from one major programme (Katala Foundation) focusing almost entirely on one island group (Palawan) (Widmann & Lacerna-Widmann, 2008), the yellow-crested cockatoo requires action in multiple parts of its range if it is to retain its complex taxonomic identity, which doubtless reflects important local adaptations (Collar & Marsden, 2014) as seen in tiger *Panthera tigris* subspecies (Ryder, 1986; Luo *et al*., 2004) and the morphotypes of Aldabra giant tortoises *Aldabrachelys gigantea* (Turnbull *et al*., 2015). In this respect, the particularity of the factors behind the species' local population persistence underlines the value of tailoring conservation efforts to each site and case. Some of these factors can be turned to advantage in differing local contexts and represent exciting opportunities to recover crucial populations through relatively low-cost management interventions. This insight is important not only for the conservation of the yellow-crested and citron-crested cockatoos and other Asian hole-nesters (such as Tenggara hill myna, parrots and hornbills) but also for species in other parts of the world threatened by persecution (brown bears *Ursus arctos*, Naves *et al*., 2003; jaguars *Panthera onca*, De Angelo *et al*., 2013 and other large carnivores under hunting pressure). The models themselves may yield relevant information, such as the importance of human occupation and infrastructure patterns or the role of protected areas in influencing species persistence. However, the approach of looking beyond the model and examining location-specific factors could be applied to many other species with wide but now fragmented ranges for a better understanding of – and stronger measures against – extinction risk. A network of 'cockatoo advocates' (at least one committed individual from each site, such as local residents, protected areas staff, NGO members) would greatly help build local support for the birds' conservation, reducing trapping and upgrading legal protection. The most urgent conservation actions include improving the conditions for law enforcement in south-east Sulawesi, a mobile awareness campaign aimed at communities near remnant populations in Nusa Tenggara and a detailed study of the status and cultural treatment of the species in Timor-Leste. Without these interventions, the future of the two species, regardless of their Red List status, will remain in the balance.

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References

Agista, D.S., Hamid, A., Mallo, F.N., Alam, S. & Mamengko, H.C. (2001). *Status Kakatua-kecil Jambul-kuning di Sulawesi Tenggara dan Sulawesi Tengah*. Bogor: BirdLife International – Indonesia Programme.

Argeloo, M. & Dekker, R.W.R.J. (1996). Exploitation of megapode eggs in Indonesia: the role of traditional methods in the conservation of megapodes. *Oryx* **30**, 59–64.

Badan Pusat Statistik. (2016). *Statistical yearbook of Indonesia*. Available at www.bps.go.id

Benítez-López, A., Alkemade, R. & Verweij, P.A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biol. Conserv.* **143**, 1307–1316.

Bhagwat, S.A. & Rutte, C. (2006). Sacred groves: potential for biodiversity management. *Front. Ecol. Environ.* **4**, 519–524.

BirdLife International. (2018). *State of the world's birds: taking the pulse of the planet*. Cambridge: BirdLife International.

BirdLife International. (2021*a*). *Datazone*. Available at http://datazone.birdlife.org/

BirdLife International. (2021*b*). *Species factsheet* Cacatua sulphurea. Available at http://www.birdlife.org

BirdLife International. (2022*a*). *Species factsheet* Cacatua citrinocristata. Available at http://www.birdlife.org

BirdLife International. (2022*b*). *Species factsheet* Cacatua sulphurea. Available at http://www.birdlife.org

Boal, C.W. (2018). *Urban raptors: ecology and conservation of birds of prey in cities*. Washington: Island Press.

Breiman, L. (2001). Random forests. *Mach. Learn.* **45**, 5–32.

Brun, C., Cook, A.R., Lee, J.S.H., Wich, S.A., Koh, L.P. & Carrasco, L.R. (2015). Analysis of deforestation and protected area effectiveness in Indonesia: a comparison of Bayesian spatial models. *Glob. Environ. Chang.* **31**, 285–295.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001). *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.

Burung Indonesia. (2011). *The behavioural ecology of breeding the yellow-crested Cockatoo in Manupeu Tanahdaru National Park, Sumba Island*. Bogor: Burung Indonesia.

Bush, E.R., Baker, S.E. & Macdonald, D.W. (2014). Global trade in exotic pets 2006–2012. *Conserv. Biol.* **28**, 663–676.

Butchart, S.H.M., Stattersfield, A.J. & Brooks, T.M. (2006). Going or gone: defining “possibly extinct” species to give a truer picture of recent extinctions. *Bull. Br. Ornithol. Club* **126**, 7–24.

Cahill, A.J., Walker, J.S. & Marsden, S.J. (2006). Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea citrinocristata* in Indonesia after 10 years of international trade control. *Oryx* **40**, 161–167.

Cahyadin, Y., Jepson, P. & Syarief, M. (1994). *A rapid status assessment of Cacatua sulphurea sulphurea in South Sulawesi Province*. Bogor: PHPA/BirdLife International – Indonesia Programme.

Caraka, R.E., Lee, Y., Kurniawan, R., Herliansyah, R., Kaban, P.A., Nasution, B.I., Gio, P.U., Chen, R.C., Toharudin, T. & Pardamean, B. (2020). Impact of COVID-19 large scale restriction on environment and economy in Indonesia. *Glob. J. Environ. Sci. Manag.* **6**, 65–84.

Catterall, M. (1997). *Results of the 1996 bird survey of Buton Island, Sulawesi, Indonesia*. Spilsby: Operation Wallacea.

Cazalis, V., Princé, K., Mihoub, J.B., Kelly, J., Butchart, S.H.M. & Rodrigues, A.S.L. (2020). Effectiveness of protected areas in conserving tropical forest birds. *Nat. Commun.* **11**, 1–8.

CITES. (2002). Cacatua sulphurea – *Consideration of proposals for amendment of appendices I and II – CoP13 Prop. 11*. Available at https://cites.org/sites/default/files/eng/cop/13/prop/E13-P11.pdf

CITES. (2020). *Convention on international trade in endangered species of wild fauna and flora – appendices*. Available at https://cites.org/eng/app/appendices.php

CNN Travel. (2019). *Indonesia cancels plan to ban tourists from Komodo Island*. CNN Travel. Available at https://edition.cnn.com/travel/article/indonesia-komodo-islands-reverse-tourist-ban-intl-hnk/index.html

Collar, N.J., Andreev, A.V., Chan, S., Crosby, M.J., Subramanya, S. & Tobias, J.A. (2001). *Threatened birds of Asia: the BirdLife International red data book* (Collar, N.J., Andreev, A.V., Chan, S., Crosby, M.J., Subramanya, S. & Tobias, J.A., Eds). Cambridge: BirdLife International.

Collar, N.J., Eaton, J.A. & Sykes, B. (2017). Conservation and the redaction of locality data. *BirdingASIA* **28**, 3–4.

Collar, N.J. & Marsden, S.J. (2014). The subspecies of yellow-crested cockatoo *Cacatua sulphurea*. *Forktail* **30**, 23–27.

De Angelo, C., Paviolo, A., Wiegand, T., Kanagaraj, R. & Di Bitetti, M.S. (2013). Understanding species persistence for defining conservation actions: a management landscape for jaguars in the Atlantic Forest. *Biol. Conserv.* **159**, 422–433.

Devenish, C., Junaid, A.R., Saryanthi, R., van Balen, S.B., Kaprawi, F., Aprianto, G.C., Stanley, R., Poole, O., Owen, A., Collar, N.J. & Marsden, S.J. (2021). Biological richness of Gunung Slamet, Central Java, and the need for its protection. *Oryx*. https://doi.org/10.1017/S0030605320001222

Diamond, J.M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific islands. *Proc. Natl. Acad. Sci. USA* **69**, 3199–3203.

Diamond, J.M. (1987). Extant unless proven extinct? Or, extinct unless proven extant? *Conserv. Biol.* **1**, 77–79.

Douglas-Hamilton, I., Krink, T. & Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften* **92**, 158–163.

Eaton, J.A., Shepherd, C.R., Rheindt, F.E., Harris, J.B.C., van Balen, S.B., Wilcove, D.S. & Collar, N.J. (2015). Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia. *Forktail* **31**, 1–12.

Erb, M. (2016). Mining and the conflict over values in Nusa Tenggara Timur province, eastern Indonesia. *Extr. Ind. Soc.* **3**, 370–382.

Fa, J.E., Olivero, J., Farfán, M.Á., Márquez, A.L., Duarte, J., Nackoney, J., Hall, A., Dupain, J., Seymour, S., Johnson, P.J., Macdonald, D.W., Real, R. & Vargas, J.M. (2015). Correlates of bushmeat in markets and depletion of wildlife. *Conserv. Biol.* **29**, 805–815.

Froese, G.Z.L. & Mustari, A.H. (2019). Assessments of Maleo *Macrocephalon maleo* nesting grounds in south-East Sulawesi reveal severely threatened populations. *Bird Conserv. Int.* **29**, 497–502.

Garland, K.A. & Carthy, R.R. (2010). Changing taste preferences, market demands and traditions in pearl lagoon, Nicaragua: a community reliant on green turtles for income and nutrition. *Conserv. Soc.* **8**, 55–72.

Garnier, S. (2018). *viridis: default color maps from “matplotlib”. R package version 0.5.1*. Available at https://cran.r-project.org/package=viridis

Geary, M., Brailsford, C.J., Hough, L.I., Baker, F., Guerrero, S., Leon, Y.M., Collar, N.J. & Marsden, S.J. (2021). Street-level green spaces support a key urban population of the threatened Hispaniolan parakeet *Psittacara chloropterus*. *Urban Ecosyst.* **24**, 1–8.

Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M. & Burgess, N.D. (2013). Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biol. Conserv.* **161**, 230–238.

Geofabrik. (2021). *OpenStreetMap data for Indonesia (with East Timor)*. Geofabrik Download Serv. Available at https://download.geofabrik.de/asia/indonesia.html

Gould, S.F. (2011). Does post-mining rehabilitation restore habitat equivalent to that removed by mining? A case study from the monsoonal tropics of northern Australia. *Wildl. Res.* **38**, 482–490.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J. & Loveland, T.R. (2013). High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853.

Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, Sa., Tyukavina, A., Thau, D., Stehman, S. V, Goetz, S. J. & Loveland, T. R. (2020). *Global forest change 2000–2019 dataset Hansen/UMD/Google/USGS/NASA*. Available at http://earthenginepartners.appspot.com/science-2013-global-forest

Harris, J.B.C., Tingley, M.W., Hua, F., Yong, D.L., Adeney, J.M., Lee, T.M., Marthy, W., Prawiradilaga, D.M., Sekercioglu, C.H., Suyadi, Winarni, N. & Wilcove, D.S. (2017). Measuring the impact of the pet trade on Indonesian birds. *Conserv. Biol.* **31**, 394–405.

Imansyah, M.J., Purwandana, D., Ariefiandy, A., Benu, Y.J., Jessop, T.S. & Trainor, C.R. (2016). Valley-floor censuses of the Critically Endangered yellow-crested cockatoo *Cacatua sulphurea occidentalis* on Komodo Island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period. *Forktail* **32**, 66–72.

Indraswari, K., Friedman, R.S., Noske, R., Shepherd, C.R., Biggs, D., Susilawati, C. & Wilson, C. (2020). It's in the news: characterising Indonesia's wild bird trade network from media-reported seizure incidents. *Biol. Conserv.* **243**, 108431.

Inskipp, T., Broad, S. & Luxmoore, R. (1988). *Significant trade in wildlife – a review of selected species in CITES appendix II, vol. 3: birds*. Cambridge: IUCN Conservation Monitoring Centre.

IUCN. (2021). *Protected area categories*. Available at https://www.iucn.org/theme/protected-areas/about/protected-area-categories

Jeon, C.-.Y. & Yang, H.-W. (2021). The structural changes of a local tourism network: comparison of before and after COVID-19. *Curr. Issues Tour.* **24**, 3324–3338.

Jones, M.J., Linsley, M.D. & Marsden, S.J. (1995). Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia. *Bird Conserv. Int.* **5**, 21–52.

Kendall, S.B. (1979). Citron-crested cockatoos in Sumba. *Avic. Mag.* **85**, 93–94.

KLHK & DJ KSDAE. (2018). *Statistik Direktorat Jenderal Konservasi Sumbar Daya Alam dan Ekosistem Tahun 2017*. Jakarta: Kementerian Lingkungan Hidup dan Kehutanan. Available at http://ksdae.menlhk.go.id/assets/publikasi.

Kociolek, A.V., Clevenger, A.P., St. Clair, C.C. & Proppe, D.S. (2011). Effects of road networks on bird populations. *Conserv. Biol.* **25**, 241–249.

Kummu, M., Taka, M. & Guillaume, J.H.A. (2018). Gridded global datasets for gross domestic product and human development index over 1990–2015. *Sci. Data* **5**, 1–15.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009). Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571.

Liaw, A. & Wiener, M. (2002). Classification and regression by randomForest. *R news* **2**, 18–22.

Liévano-Latorre, L.F., Brum, F.T. & Loyola, R. (2021). How effective have been guerrilla occupation and protected areas in avoiding deforestation in Colombia? *Biol. Conserv.* **253**, 108916.

Lunstrum, E. & Givá, N. (2020). What drives commercial poaching? From poverty to economic inequality. *Biol. Conserv.* **245**, 108505.

Luo, S.J., Kim, J.H., Johnson, W.E., Van Der Walt, J., Martenson, J., Yuhki, N., Miquelle, D.G., Uphyrkina, O., Goodrich, J.M., Quigley, H.B., Tilson, R., Brady, G., Martelli, P., Subramaniam, V., McDougal, C., Hean, S., Huang, S.Q., Pan, W., Karanth, U.K., Sunquist, M., Smith, J.L.D. & O'Brien, S.J. (2004). Phylogeography and genetic ancestry of tigers (*Panthera tigris*). *PLoS Biol.* **2**, e442.

Mallo, F.N. & Setiawan, I. (1996). *Telaah status Cacatua sulphurea sulphurea di Sulawesi Tengah*. Bogor: PHPA/BirdLife International.

Marsden, S.J. (1999). Estimation of parrot and hornbill densities using a point count distance sampling method. *Ibis* **141**, 327–390.

Marsden, S.J. & Jones, M.J. (1997). The nesting requirements of the parrots and hornbill of Sumba, Indonesia. *Biol. Conserv.* **82**, 279–287.

Marsden, S.J. & Royle, K. (2015). Abundance and abundance change in the world's parrots. *Ibis* **157**, 219–229.

Martin, R.B. (2000). When CITES works and when it does not. In *Endangered species, threatened convention: the past, present and future of CITES, the Convention on international trade in endangered species of wild fauna and flora*: 29–37. Hutton, J. & Dickson, B. (Eds). London: Earthscan.

McCauley, D.J., Power, E.A., Bird, D.W., McInturff, A., Dunbar, R.B., Durham, W.H., Micheli, F. & Young, H.S. (2013). Conservation at the edges of the world. *Biol. Conserv.* **165**, 139–145.

McPherson, M.A. & Nieswiadomy, M.L. (2005). Environmental Kuznets curve: threatened species and spatial effects. *Ecol. Econ.* **55**, 395–407.

Mills, J.H. & Waite, T.A. (2009). Economic prosperity, biodiversity conservation, and the environmental Kuznets curve. *Ecol. Econ.* **68**, 2087–2095.

Monk, K., De Fretes, Y. & Reksodiharjo-Lilley, G. (1997). *Ecology of Nusa Tenggara and Maluku*. 1st edn. Oxford: Oxford University Press.

Mortelliti, A. & Boitani, L. (2007). Estimating species' absence, colonization and local extinction in patchy landscapes: an application of occupancy models with rodents. *J. Zool.* **273**, 244–248.

Nandika, D., Mulyani, Y.A., Prawiradilaga, D.M. & Agustina, D. (2020). Monitoring of *Cacatua sulphurea abbotti* in Masakambing Island, Indonesia. *Biotropia-Southeast Asian J. Trop. Biol.* **27**, 271–281.

Naves, J., Wiegand, T., Revilla, E. & Delibes, M. (2003). Endangered species constrained by natural and human factors: the case of Brown bears in northern Spain. *Conserv. Biol.* **17**, 1276–1289.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Mininchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. (2020). Vegan: community ecology package. R package version 2.5-7. Available at https://cran.r-project.org/web/packages/vegan/index.html

Olah, G., Butchart, S.H.M., Symes, A., Guzmán, I.M., Cunningham, R., Brightsmith, D.J. & Heinsohn, R. (2016). Ecological and socio-economic factors affecting extinction risk in parrots. *Biodivers. Conserv.* **25**, 205–223.

OpenStreetMap Contributors. (2021). *OpenStreetMap data*. Available at https://www.openstreetmap.org/copyright

Pain, D.J., Martins, T.L.F., Boussekey, M., Diaz, S.H., Downs, C.T., Ekstrom, J.M.M., Garnett, S., Gilardi, J.D., McNiven, D. & Primot, P. (2006). Impact of protection on nest take and nesting success of parrots in Africa, Asia and Australasia. *Anim. Conserv.* **9**, 322–330.

Peres, C.A. & Lake, I.R. (2003). Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon Basin. *Conserv. Biol.* **17**, 521–535.

Persulessy, Y.E., Djawarai, Y.B. & Marut, R. (2003). *Survei populasi dan distribusi kakatua-kecil jambul-kuning Cacatua sulphurea citrinocristata dan empat jenis paruh bengkok lain di Pulau Sumba*. Bogor: BirdLife Indonesia/ZGAP.

PHPA, LIPI & BirdLife International-IP. (1998). *Species recovery plan Yellow-crested Cockatoo*. Bogor: PHPA/LIPI/BirdLife International – Indonesia Programme.

Pires, S.F. (2012). The illegal parrot trade: a literature review. *Glob. Crime* **13**, 176–190.

Pires, S.F. & Clarke, R.V. (2011). Sequential foraging, itinerant fences and parrot poaching in Bolivia. *Br. J. Criminol.* **51**, 314–335.

Pires, S.F., Olah, G., Nandika, D., Agustina, D. & Heinsohn, R. (2021). What drives the illegal parrot trade? Applying a criminological model to market and seizure data in Indonesia. *Biol. Conserv.* **257**, 109098. https://doi.org/10.1016/j.biocon.2021.109098.

Plieninger, T., Quintas-Soriano, C., Torralba, M., Mohammadi Samani, K. & Shakeri, Z. (2020). Social dynamics of values, taboos and perceived threats around sacred groves in Kurdistan, Iran. *People Nat.* **2**, 1237–1250.

QGIS Development Team. (2021). *QGIS geographic information system*. Hannover: Open Source Geospatial Foundation Project.

R Core Team. (2021). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Randriamamonjy, V.C., Keane, A., Razafimanahaka, H.J., Jenkins, R.K.B. & Jones, J.P.G. (2015). Consumption of bushmeat around a major mine, and matched communities, in Madagascar. *Biol. Conserv.* **186**, 35–43.

Reuleaux, A., Collar, N.J., Siregar, B.A., Mardiastuti, A. & Marsden, S.J. (2018). Preliminary range-wide surveys of the heavily traded Tenggara Hill myna *Gracula venerata*. *Forktail* **34**, 29–34.

Reuleaux, A., Siregar, B.A., Collar, N.J., Mardiastuti, A. & Marsden, S.J. (2022). Productivity constraints on citron-crested cockatoos in a rich community of large hole-nesting birds. *Avian Res.* **13**, 100015. https://doi.org/10.1016/J.AVRS.2022.100015.

Reuleaux, A., Siregar, B.A., Collar, N.J., Panggur, M.R., Mardiastuti, A., Jones, M.J. & Marsden, S.J. (2020). Protected by dragons: density surface modeling confirms large population of the critically endangered yellow-crested cockatoo on Komodo Island. *Condor* **122**, duaa042.

Robinson, J.G. & Bodmer, R.E. (1999). Towards wildlife management in tropical forests. *J. Wildl. Manage.* **63**, 1–13.

Romero-Vidal, P., Hiraldo, F., Rosseto, F., Blanco, G., Carrete, M. & Tella, J.L. (2020). Opportunistic or non-random wildlife crime? Attractiveness rather than abundance in the wild leads to selective parrot poaching. *Diversity* **12**, 314.

Rowley, I., Sharpe, C. & Boesman, P. (2017). Yellow-crested Cockatoo (*Cacatua sulphurea*) – HBW Alive. In *Handbook of the birds of the world alive*. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (Eds). Barcelona: Lynx Edicions. Available at https://www.hbw.com

Rutte, C. (2011). The sacred commons: conflicts and solutions of resource management in sacred natural sites. *Biol. Conserv.* **144**, 2387–2394.

Ryder, O.A. (1986). Species conservation and systematics: the dilemma of subspecies. *Trends Ecol. Evol.* **1**, 9–10.

Samudro, B.R., Bloch, H. & Salim, R. (2015). The uneven regional pattern of ecological capital in Indonesia: a political economy perspective. *Int. J. Green Econ.* **9**, 258–272.

Setiawan, I. (1996). *The status of Cacatua sulphurea parvula in Nusa Penida, Bali, and Sumbawa*, Vol. **6**. Bogor: PHPA/BirdLife International. Available at http://www.nusapenida.nl/index.php/biology/birding/sulphur-crested-cockatoo-setiawan-1996.

Shepherd, C.R. & Nijman, V. (2008). The trade in bear parts from Myanmar: an illustration of the ineffectiveness of enforcement of international wildlife trade regulations. *Biodivers. Conserv.* **17**, 35–42.

Snodgrass, J.G. & Tiedje, K. (2008). Indigenous nature reverence and conservation. *J. Study Relig. Nat. Cult.* **2**, 6–29.

Sodhi, N.S., Posa, M.R.C., Lee, T.M., Bickford, D., Koh, L.P. & Brook, B.W. (2010). The state and conservation of southeast Asian biodiversity. *Biodivers. Conserv.* **19**, 317–328.

Sonter, L.J., Ali, S.H. & Watson, J.E.M. (2018). Mining and biodiversity: key issues and research needs in conservation science. *Proc. R. Soc. B Biol. Sci.* **285**, 20181926. https://doi.org/10.1098/rspb.2018.1926.

Sopian, N.L. (2015). Informal dispute resolution based on Adat law: a case study of land dispute in Flores, East Nusa Tenggara, Indonesia. *Indon. L. Rev.* **5**, 106.

Stearman, A.M. (2000). A pound of flesh: social change and modernization as factors in hunting sustainability among neotropical indigenous societies. In *Hunting for sustainability in tropical forests*. 1st edn: 233–250.

Robinson, J. & Bennett, E.L. (Eds). New York: Columbia University Press.

Tella, J.L. & Hiraldo, F. (2014). Illegal and legal parrot trade shows a long-term, cross-cultural preference for the most attractive species increasing their risk of extinction. *PLoS One* **9**, e107546.

Thu, P.M. (2012). Access to land and livelihoods in post-conflict Timor-Leste. *Aust. Geogr.* **43**, 197–214.

Turnbull, L.A., Ozgul, A., Accouche, W., Baxter, R., Chongseng, L., Currie, J.C., Doak, N., Hansen, D.M., Pistorius, P., Richards, H., van de Crommenacker, J., von Brandis, R., Fleischer-Dogley, F. & Bunbury, N. (2015). Persistence of distinctive morphotypes in the native range of the CITES-listed Aldabra giant tortoise. *Ecol. Evol.* **5**, 5499–5508.

Valle, S., Collar, N.J., Harris, W.E. & Marsden, S.J. (2018). Trapping method and quota observance are pivotal to population stability in a harvested parrot. *Biol. Conserv.* **217**, 428–436.

Van Zyl, J.J. (2001). The shuttle radar topography Mission (SRTM): a breakthrough in remote sensing of topography. *Acta Astronaut.* **48**, 559–565.

Verı́ssimo, D., Vieira, S., Monteiro, D., Hancock, J. & Nuno, A. (2020). Audience research as a cornerstone of demand management interventions for illegal wildlife products: demarketing sea turtle meat and eggs. *Conserv. Sci. Pract.* **2**, e164.

Walker, J.S., Cahill, A.J. & Marsden, S.J. (2005). Factors influencing nest-site occupancy and low reproductive output in the Critically Endangered yellow-crested cockatoo *Cacatua sulphurea* on Sumba, Indonesia. *Bird Conserv. Int.* **15**, 347–359.

Webb, R.A.F.P. (1986). Adat and Christianity in Nusa Tenggara Timur: reaction and counteraction: traditional custom and modern development in eastern Indonesia. *Philipp. Q. Cult. Soc.* **14**, 339–365.

Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., Woo, K., Yutani, H. & Dunnington, D. (2021). Package 'ggplot2'. Create elegant data visualisations using the grammar of graphics. Version 3.3.5. Available at https://cran.r-project.org/web/packages/ggplot2/index.html

Widmann, P. & Lacerna-Widmann, I.D. (2008). The cockatoo and the community: ten years of Philippine Cockatoo Conservation Programme. *BirdingASIA* **10**, 23–29.

Wilkie, D.S., Starkey, M., Abernethy, K., Effa, E.N., Telfer, P. & Godoy, R. (2005). Role of prices and wealth in consumer demand for bushmeat in Gabon, Central Africa. *Conserv. Biol.* **19**, 268–274.

Worldpop. (2018). *Global high resolution population denominators project*. Southampton: School of Geography and Environmental Science, University of Southampton.

Yusuf, M.S. (2014). *Status of Yellow-crested Cockatoo at Tatar Spang, West Sumbawa, Indonesia*. Maluk: PT Newmont Nusa Tenggara.

Zhang, L., Hua, N. & Sun, S. (2008). Wildlife trade, consumption and conservation awareness in southwest China. *Biodivers. Conserv.* **17**, 1493–1516.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Sources for presence and absence of yellow-crested cockatoos and citron-crested cockatoos used in this study.

Table S2. Broad locations with surviving cockatoo populations despite random forest model predictions of extinction between 1950 and 2015.

Table S3. Accuracy and variable importance (measured in decrease in model accuracy when the predictor is removed) compared between three different measures of area protection as predictors of yellow-crested and citron-crested cockatoo site-specific survival from 1950 to 2015 in a random forest model.

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RESEARCH ARTICLE

Protected by dragons: Density surface modeling confirms large population of the critically endangered Yellow-crested Cockatoo on Komodo Island

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ABSTRACT

Intense trapping of the critically endangered Yellow-crested Cockatoo (*Cacatua sulphurea*) for the international pet trade has devastated its populations across Indonesia such that populations of >100 individuals remain at only a handful of sites. We combined distance sampling with density surface modeling (DSM) to predict local densities and estimate total population size for one of these areas, Komodo Island, part of Komodo National Park (KNP) in Indonesia. We modeled local density based on topography (topographic wetness index) and habitat types (percentage of palm savanna and deciduous monsoon forest). Our population estimate of 1,113 (95% CI: 587–2,109) individuals on Komodo Island was considerably larger than previous conservative estimates. Our density surface maps showed cockatoos to be absent over much of the island, but present at high densities in wooded valleys. Coincidence between our DSM and a set of independent cockatoo observations was high (93%). Standardized annual counts by KNP staff in selected areas of the island showed increases in cockatoo records from <400 in 2011 to ~650 in 2017. Taken together, our results indicate that KNP, alongside and indeed because of preserving its iconic Komodo dragons (*Varanus komodoensis*), is succeeding in protecting a significant population of Indonesia's rarest cockatoo species. To our knowledge this is the first time DSM has been applied to a critically endangered species. Our findings highlight the potential of DSM for locating abundance hotspots, identifying habitat associations, and estimating global population size in a range of threatened taxa, especially if independent datasets can be used to validate model predictions.

Keywords: Cacatua sulphurea, conservation, density surface model, distance sampling, habitat model, parrots, Psittaciformes, threatened species

LAY SUMMARY

- Yellow-crested Cockatoos are threatened by extinction due to illegal trapping for the pet trade. Komodo Island in Indonesia supports one of the largest remaining populations. The island is part of Komodo National Park, famous for its Komodo dragons. A 2006 survey indicated cockatoo numbers might have been declining.
- In contrast to previous surveys we sampled the whole island instead of focusing on coastal valleys, which are known to harbor the highest cockatoo densities. We used distance sampling and density surface modeling, which allowed us to estimate how many cockatoos remained undetected and to produce a map of predicted cockatoo densities.
- We estimate there are between 600 and 2,100 cockatoos on Komodo, most likely ~1,100. Komodo National Park authorities also reported an increase in their annual counts of cockatoos from below 400 in 2011 to around 650 in 2017. Thus, the cockatoo population on Komodo Island is large and stable; Komodo National Park is successfully protecting its cockatoos.

Terlindungi oleh komodo: density surface modeling pada *Cacatua sulphurea* (Kakatua-kecil Jambul-kuning) di Pulau Komodo

ABSTRAK (BAHASA INDONESIA)

Perburuan ilegal untuk perdagangan internasional terhadap burung *Cacatua sulphurea* (Kakatua-kecil Jambul-kuning)—yang telah dikategorikan sebagai Kritis—telah menyebabkan penurunan populasi pada hampir semua lokasi di Indonesia, sehingga populasi dengan jumlah >100 individu hanya tersisa di beberapa tempat saja. Untuk menduga kepadatan dan jumlah populasi burung ini di Pulau Komodo (salah satu pulau di Taman Nasional Komodo; TNK), dilakukan penelitian dengan menggunakan perpaduan antara *distance sampling* dan *density surface modeling* (DSM). Permodelan kepadatan dilakukan berdasarkan topografi (*topographic wetness index*) dan tipe habitat. Dugaan populasi spesies burung ini di Pulau Komodo adalah 1.113 ekor (95% *CI* 587–2.109), lebih tinggi dari pendugaan populasi sebelumnya. Peta kepadatan (*density surface maps*) menunjukkan bahwa kakatua ini tidak terdapat di sebagian besar pulau, namun dapat ditemukan dengan kepadatan yang tinggi di lembah-lembah berhutan. Kesesuaian antara DSM dan titik pengamatan independen bernilai tinggi (93%). Penghitungan populasi tahunan oleh staf Balai TNK pada lokasi-lokasi terpilih menunjukkan adanya penambahan populasi dari <400 ekor pada tahun 2011 menjadi sekitar 650 ekor pada tahun 2017. Dengan demikian, selain melindungi satwa komodo *Varanus komodoensis,* TNK juga berhasil melindungi populasi *Cacatua sulphurea* dalam jumlah yang signifikan. Penelitian ini merupakan upaya pertama yang menggunakan DSM untuk spesies dengan status Kritis. Metoda ini berpotensi untuk menentukan pusat-pusat kepadatan populasi, mengidentifikasi asosiasi habitat, serta menduga ukuran populasi secara global bagi taksa-taksa yang terancam punah, terutama jika dataset yang independen dapat dipakai untuk memvalidasi prediksi model.

Indonesian keywords (kata kunci): density surface model, distance sampling, kakatua, konservasi, model habitat, spesies terancam

INTRODUCTION

Estimates of population sizes are cornerstones of conservation science at both global and local scales and are instrumental in assessing extinction risks, conservation priorities, and Red List status (Mace et al. 2008, Collen et al. 2011). These essential data are, however, lacking for a great many rare and threatened species (MacKenzie et al. 2005), which are often difficult to survey on account of their biology and/or the areas they inhabit (McDonald 2004). Even for relatively well-known groups such as psittacines (parrots), ~75% of species are lacking abundance estimates (Marsden and Royle 2015), a worrying statistic given that almost one-third of psittacines are currently threatened (IUCN 2019). A variety of methods have been used to calculate population size in parrots. For very rare species it may be possible to count every individual. For others, marked or identifiable individuals allow mark–recapture or mark–resighting methods, but these conditions are not the norm. For most species, roost counts, flyway counts, and distance sampling have been used more or less effectively (Casagrande and Beissinger 1997, Marsden and Royle 2015). Distance sampling, despite difficulties in meeting method assumptions, has become a well-established method for estimating sizes of animal populations generally (Thomas et al. 2010) and parrots in particular (Marsden and Royle 2015).

Estimates derived from distance sampling have become the most commonly used, involving 84% of published parrot abundance estimates (Marsden and Royle 2015), despite question marks over reliability related to lack of records in rare species and idiosyncrasies of parrot behavior (Marsden 1999, Dénes et al. 2018). Alternative methods fail to measure absolute bird abundance (Bibby et al. 2000), face the same (and additional) challenges (Casagrande and Beissinger 1997), or remain largely untested (Dénes et al. 2018).

While there has been considerable work on optimizing distance sampling design, field protocol, and analysis phases (Marsden 1999, Buckland 2006, Bächler and Liechti 2007, Marques et al. 2007, Buckland et al. 2008, Oedekoven et al. 2015), far less attention has been paid to the process of estimating site-based or total population sizes through extrapolation of local abundances at sampled sites to larger areas or even whole ranges of threatened birds. Several extrapolation methods have been used, including simple multiplication of average density by area of study site or range (e.g., Guix et al. 1999, Marques et al. 2007), stratification by habitat type (e.g., Jones et al. 1995, Casagrande and Beissinger 1997), and interpolation across unvisited sites (Koshkin et al. 2016). The best-accepted methods are those which model local density against habitat and other relevant features (Buckland et al. 2016), sometimes along with spatial information, to predict densities in unvisited areas (e.g., Williamson and Homes 1964, Somershoe et al. 2006). Apart from predicting spatial distributions and producing realistic abundance estimates, spatial modeling can also identify factors that affect abundance (Hedley and Buckland 2004), knowledge which can then inform conservation management decisions. The spatial input for the model can either originate from covariates with a spatial distribution (e.g., habitat, elevation, distance from coast) or include the location coordinates directly (usually latitude and longitude). The functional relationships between these covariates and the response variable are rarely linear in reality, and generalized additive models (GAMs) allow this to be reflected in complex nonlinear functions in the modeling process (Zuur et al. 2014).

Density surface modeling (DSM) uses GAMs (Wood 2017) to model the point-specific density at the sampling points (or segment-specific for line transects) in a 2-step approach: first, it accounts for detectability using the distance sampling method; second, it incorporates spatial and/or environmental covariates to explain the variation between sampling points (Hedley and Buckland 2004, Miller et al. 2013). The resultant model can then be used to map predicted population densities within the sampling area and also, with caution, for new unsampled areas (Miller et al. 2013). DSMs are not widely used for population estimates at present but have been successfully applied to marine birds (Petersen et al. 2011, Winiarski et al. 2013, 2014; Bradbury et al. 2014), a peatland bird community (Leivits and Leivits 2016), marine mammals (de Segura et al. 2007, Gilles et al. 2011, Williams et al. 2011, Miller et al. 2013, Bravington et al. 2019), and ungulates (Harihar et al. 2014, Schroeder et al. 2014, La Morgia et al. 2015, Valente et al. 2016). Several of these studies had conservation objectives such as identification of priority areas for protection (Winiarski et al. 2013) or assessment of endangered species (Ibouroi et al. 2019). While the method has been recommended as suitable for parrots (Dénes et al. 2018), we know of no application of DSMs to any parrot, or indeed to any critically endangered species.

The Yellow-crested Cockatoo (*Cacatua sulphurea*) used to occur commonly across the Lesser Sunda Islands, parts of Sulawesi, and its satellites (Figure 1), but habitat alteration and especially excessive trapping for the international pet trade from the 1970s through the 1990s caused severe declines and local extinctions across much of its range. Thus, populations >100 individuals remain at only a handful of sites, rendering the species critically endangered (Broch 1981, Cahyadin et al. 1994a, 1994b; Jones et al. 1995, PHPA/LIPI/BirdLife International 1998, Agista et al. 2001, BirdLife International 2001, Eaton et al. 2015). Some 560–4,000 of the very distinctive subspecies *citrinocristata* are thought to exist in several forest patches on Sumba (Wungo 2011; A. Reuleaux personal observation; Figure 1). The population of Yellow-crested Cockatoos of the subspecies *occidentalis* in Komodo National Park (KNP; Figure 1), in the Lesser Sunda Islands, is also believed to be relatively large, although a survey in 2006 (Imansyah et al. 2016) diagnosed a sharp decline since 2000 (Agista and Rubyanto 2001). Both these surveys obtained minimum numbers for selected coastal valleys by direct sightings from vantage points, which cover <10% of the island's area. Here we used density surface modeling to predict local cockatoo densities across Komodo Island. We validated the models using independent sightings, investigated correlates of local abundance, and estimated the island-wide population size.

METHODS

Study Area

Komodo Island (8.42°S–8.75°S, 119.37°E–119.57°E) is situated between Flores and Sumbawa in the Lesser Sunda Islands, Nusa Tenggara Timur, Indonesia (Figure 1). With an area of 340 km^2 and a maximum elevation of 824 m above sea level (m.a.s.l.), it is the largest and highest of the islands of KNP, which was established in 1980 to protect the Komodo dragon (*Varanus komodoensis*) and the terrestrial and marine biodiversity of the islands (UNESCO World Heritage Committee 1991, Lilley 1997). It now harbors one of the most important remnant populations of Yellow-crested Cockatoos and the most important population of subspecies *C. s. occidentalis* (Collar and Marsden 2014). Komodo is situated in one of the driest areas of Indonesia; streams do not run for most of the year and natural water sources are rare (Monk et al. 1997). Large areas of the island are covered by open grassland (Auffenberg 1980) interspersed with scrubland, palm savanna, small stands of broadleaved trees, and gallery forests along watercourses (Monk et al. 1997). Where larger streams meet the sea, deciduous monsoon forests cover the valley floors (Auffenberg 1980, Monk et al. 1997; Figure 2). Higher altitudes (>500 m) support denser closed-canopy forest (Figure 2), which is often dominated by bamboo or rattan and referred to as "quasi cloud forest" (Auffenberg 1980) or "mossy forest" (Monk et al. 1997); this terrain transitions downhill via sparse forest into scrubland.

Following recommendations based on conservation considerations (Collar et al. 2017), to avoid supplying information to potential trappers, we do not include complete maps of our results. The complete maps are available for *bona fide* researchers or for conservation purposes from the authors. They are replaced in the results section by out-of-context cutouts of exemplary locations.

Point Count Distance Sampling

Komodo Island has a surface area of 340 km^2. We first excluded all 1 × 1 km^2 pixels that contained >50% bare grassland or sea (landcover map by Ministry of Environment and Forestry Indonesia, KLHK 2017), habitat types deemed unsuitable for cockatoos. From the remaining 152 potentially suitable pixels we randomly selected 25 for our point count distance sampling. The survey stations were located 200 m apart on the perimeter of each of these pixels (navigation by GPS). From November 6 to December 14, 2017, one of two experienced observers (AR, BAS) carried out one distance sampling point count at each of 178 stations between 0600 and 1000 hours (Figure 1). Both observers had experience in studying cockatoos (22 and 36 mo, respectively) and distance sampling of cockatoos (each 3 mo, early in 2017). The number of survey stations per pixel varied from 5 to 10 (mean = 7) depending on how many point counts could be finished within the survey time frame. Slow walking speed in rough terrain and large distances from the nearest permitted campsite often hindered maximization of survey effort.

We followed standard methods for point count distance sampling (Buckland et al. 2001, 2008; Thomas et al. 2010). Specifically we adapted the field protocol described by Marsden (1999): (1) 10-min count durations but without a settling-down period, (2) exclusion of encounters in flight,

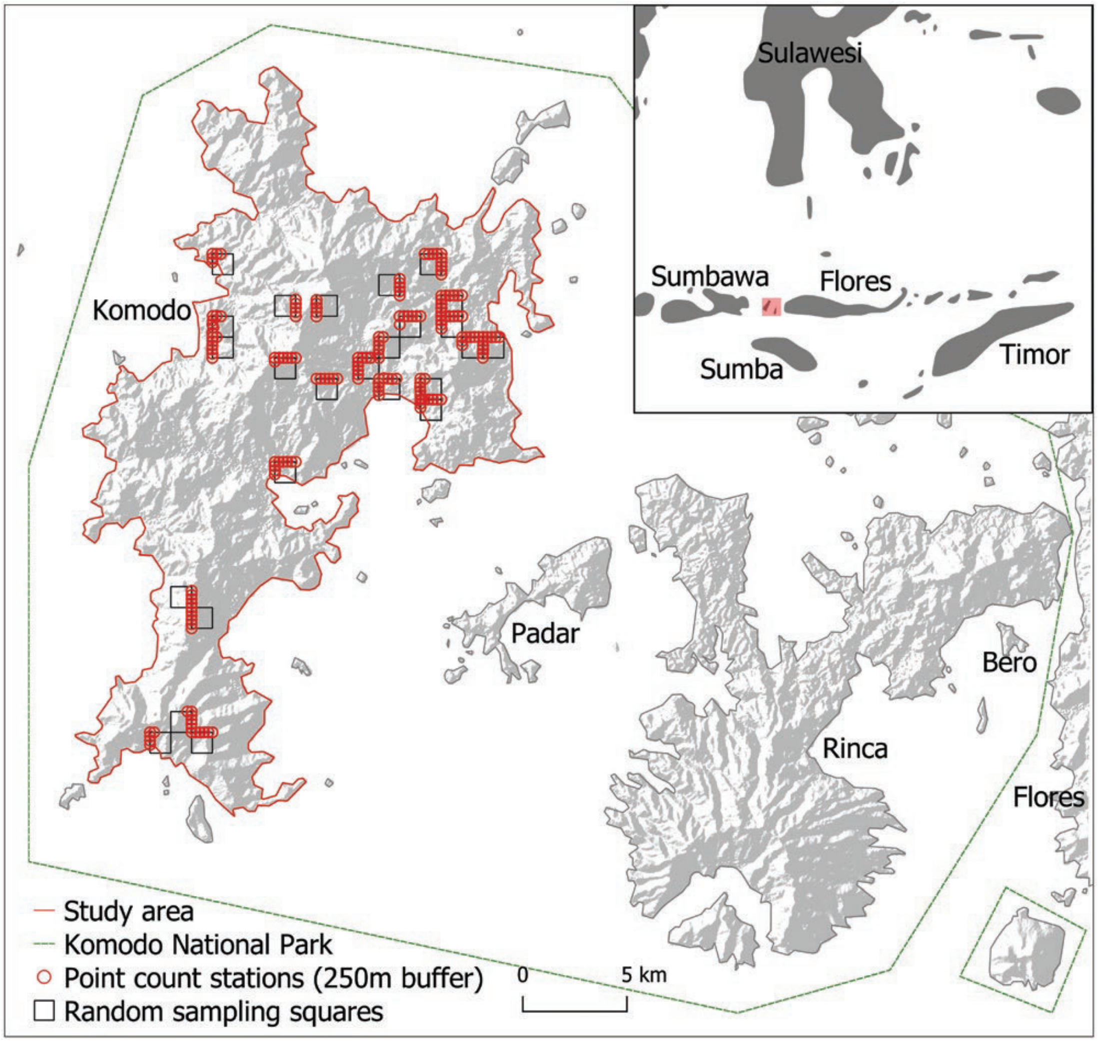

FIGURE 1. Study area Komodo Island situated in Komodo National Park, Indonesia, showing 178 point count stations, nested within 25 sampling squares, with their 250-m radius buffers.

(3) recording of flocks as clusters including the number of their individuals, and (4) replacement of group sizes for purely aural detections with the average size of known groups. To minimize errors in assessing distances, we used laser rangefinders (Nikon Forestry Pro) and followed protocols suggested by Buckland (2006) and Buckland et al. (2008). For example, this included measuring distances to other objects at a similar distance if the detected bird was not directly visible. Our survey period fell in the early part of the breeding season (Agista and Rubyanto 2001). Although all pairs observed near cavities were still prospecting, we checked the surrounding of each survey station for cavities with incubating adults. Analysis followed standard methods recommended in Buckland et al. (2001) and used a truncation distance of 350 m and open vs. enclosed habitat as a 2-level covariate for the detection function. We defined stations as open habitat if palm savanna, scrubland, and grassland made up ≥60% of land cover within a 50-m radius). We carried out distance sampling analysis in R using package *Distance 1.0.0* (Miller et al. 2016, R Core Team 2019). We used ungrouped distances as recorded without manual binning. Cluster size as a covariate was very unstable against truncation distances and did not improve AIC, so no cluster size bias regression was used. Results are reported as means ± SE.

Environmental Variables

We used a wetness index (by System for Automated Geoscientific Analyses, SAGA), a topographic index predicting the soil moisture based solely on a digital elevation grid (Böhner and Selige 2006, Conrad et al. 2015), in our case a Shuttle Radar Topography Mission digital elevation model with ~30 × 30 m resolution. We generated a contemporary raster habitat map based on LANDSAT

FIGURE 2. Habitat types on Komodo Island: (**A**) gallery forest among open grassland; (**B**) gallery forest; (**C**) palm savanna in front of deciduous monsoon forest; (**D**) quasi cloud forest (mossy forest, >500 m.a.s.l.).

8 imagery from September and October 2015–2017 (Appendix Figure 4). After cloud removal and adjustment of burnt areas to the survey period, we used our field observations and Google Maps to generate training data for landcover classification in QGIS with the semi-automatic classification plug-in (Congedo 2016, QGIS Development Team 2019).

We tailored the classification for use as a predictor of cockatoo detectability and density, and distinguished 6 habitat types (Appendix Table 3) following Auffenberg (1980) and Monk et al. (1997): open grassland and scrubland; palm savanna; deciduous monsoon forest including gallery forests and monsoon forests of the coastal plains; mangrove forest; quasi cloud forest >500 m; and sparse forest as a transition zone between quasi cloud forest and open habitat types. After inspection of spectral signature plots of the training units, cutoff values for critical bands were set manually to improve separation of overlapping categories (Congedo 2016); grassland and scrubland were classified separately and pooled afterwards. Mangrove forest was not recognized properly by the classification method, so the Indonesian Ministry of Forestry's landcover data (KLHK 2017) were used instead to correct the extent of this locally rare habitat type. We used the resulting fine-resolution habitat map to calculate percentage cover for each 250-m radius buffer around sampling stations and for each 0.25-km^2 prediction pixel. The 2 classes with the highest cockatoo encounter rates were termed "suitable habitat" and their combined percentages were used as a covariate in the DSM.

For model building we summarized the environmental covariates at the point count locations by averaging the gridded values within overlapping 250-m radius circles (sampling buffers) centered at each location. For our prediction surface, we divided each 1-km^2 pixel of the island into 4, resulting in 1,457 prediction grid pixels containing land. The environmental covariate values obtained at a smaller resolution were averaged within each of these 0.25-km^2 prediction pixels (Figure 3).

Density Surface Modeling (DSM) and Prediction

We used density surface modeling (Miller et al. 2013) to estimate population density within each 0.25-km^2 pixel across the island, involving the distance-based abundance estimates and the 2 environmental covariates. The *dsm* function in R (Miller et al. 2019) is based on generalized additive models (Wood 2017, 2019) and a detection function (Miller et al. 2016), and allows for the uncertainty of detection probability when estimating the variance of this 2-step modeling process. Our full generalized additive mixed model (GAMM) included the explicit spatial term s(x,y) (a smooth function for interaction of latitude and longitude), smooth functions of the log-transformed SAGA wetness index and the arcsine transformed percentage

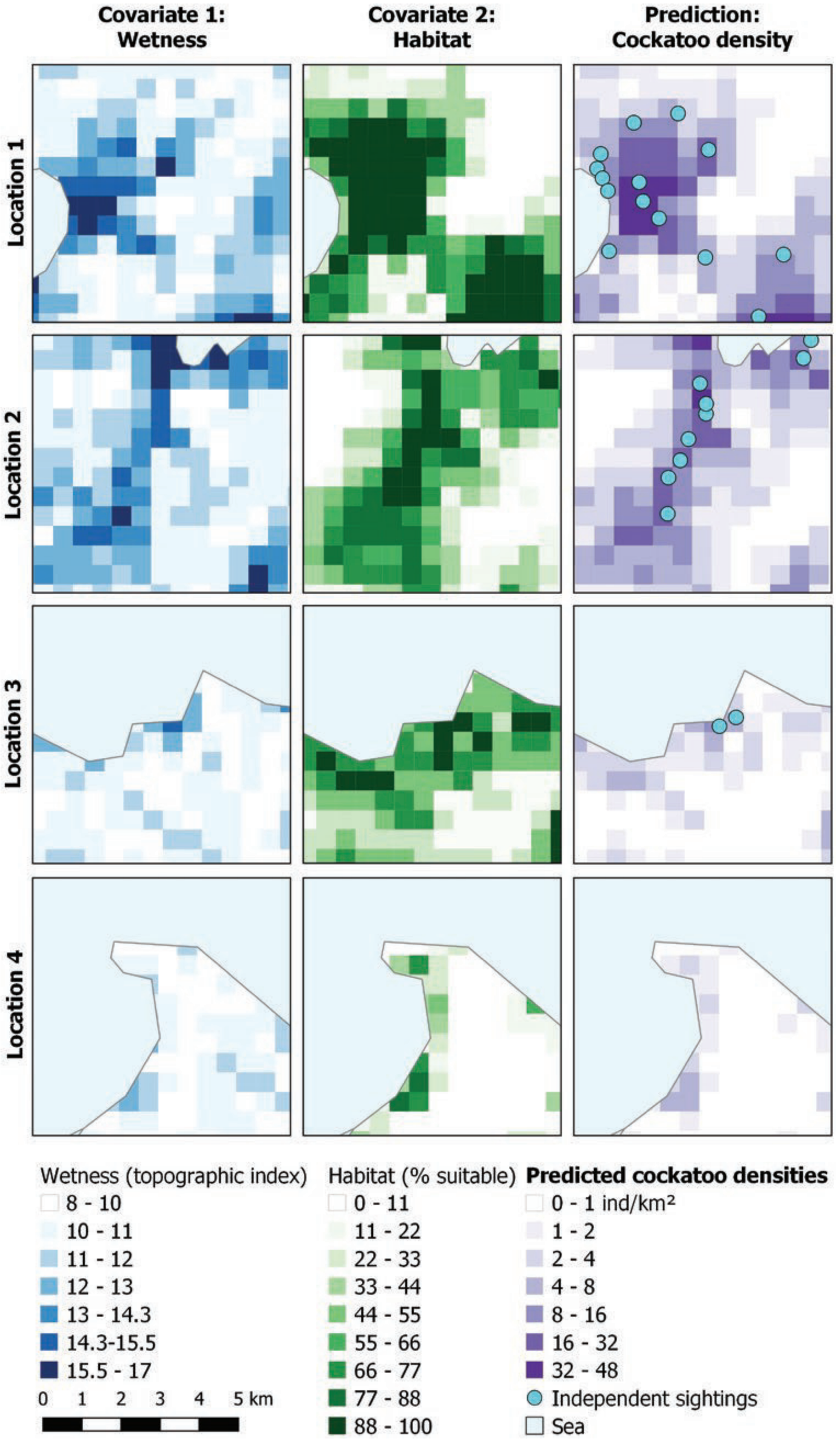

FIGURE 3. Exemplary map details of predictor values (topographic wetness index and percentage of suitable habitat) and densities of Yellow-crested Cockatoos (individuals km^{-2}) predicted by the density surface model, on a 0.25-km^2 grid of Komodo Island; cross-validated with independent sightings of the species (Agista and Rubyanto 2001, Imansyah et al. 2003, 2016; Taman Nasional Komodo 2016, eBird Basic Dataset 2019). To avoid supplying information to potential trappers, locations are provided out of context, with smoothed coastlines and random orientation. The complete maps of the whole island are available for research or conservation purposes from the authors.

of suitable habitat, as well as an autocorrelation structure (AR1 structure with form = ~1|sampling square) to allow for nestedness of the point count stations within the sampling squares. For the spatial term, we used a Duchon spline (Duchon 1977) as recommended for areas with complex borders where misidentification of population hotspots is a potential problem (Miller and Wood 2014). Smooth functions for interactions of these environmental variables were also explored but did not improve model fit. We compared Gaussian, Tweedie, and quasi Poisson distributions. After dropping nonsignificant terms, we selected the best combination of the remaining terms by AIC minimization (Appendix Table 4). Comparison of GAMMs is not straightforward; indicators are still in development (Wood 2017) and the AIC of the lme component of the GAMM is not recommended as an indicator for choice either (Wood 2019). Therefore, we used the AIC of the equivalent GAM for this step. With the GAM component of the chosen GAMM we predicted cockatoo density and coefficient of variation (CV) for each pixel of the prediction grid. To obtain the overall variance and confidence intervals we combined the variance of the detection function and that of the GAM using the Delta method via the *dsm.var.gam* function (Seber 1982, Miller et al. 2019).

Validating DSM Predictions Using Independent Cockatoo Sightings

We used 3 independent sources of cockatoo observations that were not included in our DSM analysis to validate the spatial predictions of our DSM. The first source was annual monitoring by KNP staff on flight paths and roosts (2012–2017, 16 locations; KNP unpublished data). The second source was citizen science observations from eBird (eBird Basic Dataset 2019), from which we selected those records where the observer had specified a precise location on the map instead of allocating it to a predefined hotspot, the national park, or the island in general (2004–2017, 7 locations). The third source was cockatoo records from survey reports, involving 9 locations from valley-floor surveys in 2000 (Agista and Rubyanto 2001) and 10 locations from a general fauna survey in 2002 (Imansyah et al. 2003), which were partly confirmed again by cockatoo valley-floor surveys in 2005 and 2006 (Imansyah et al. 2005, 2016). We used only one independent sighting location per prediction pixel. We checked coincidence of the model's local density predictions against these known positives (regarding densities ≥1 individual km^{-2} as predicted presence).

RESULTS

Cockatoo groups were observed at 48 of the 178 point count locations, with an encounter rate of 0.38 groups per point count (after exclusion of flying individuals and truncation). Encounter rates were highest in deciduous monsoon forest (0.91 ± 0.17, n = 22) and palm savanna (0.62 ± 0.11, n = 86) and lowest in the remaining habitat types (0.19 ± 0.10, n = 26 in grassland and scrubland; 0.06 ± 0.04, n = 32 in sparse forest; 0.00, n = 12 in quasi cloud forest; and no data in mangrove forest). The average number of individuals in each group seen was 2.61 individuals (SE = 0.49, n = 31, before truncation). Detection probabilities were described best by a hazard-rate detection function with habitat openness as a covariate (Table 1, Appendix Figure 5).

The DSM with the best fit contained 2 smooth terms with thin plate regression splines of 2 environmental covariates: SAGA wetness index (log-transformed, F = 8.08, edf = 1, P = 0.005; Appendix Table 4) and percentage cover by suitable habitat (palm savanna and deciduous monsoon forest combined and arcsine transformed, F = 7.70, edf = 1, P = 0.006; Figure 3, Appendix Figure 6). The spatial term was excluded as it was not significant (P > 0.3 regardless of spline base, as long as the model accounted for the autocorrelation structure of the points within sampling squares). This best model predicted high cockatoo densities (>8 individuals km^{-2}, locally up to 48 individuals km^{-2}) for 2 forested valleys (Figure 3) where cockatoos are known to be common and where we had high encounter rates at point counts (2.77 ± 0.49 individuals per station, n = 35, presence at 32, up to 6 groups at one station) and flock sizes up to 60 individuals in incidental observations. High densities were also predicted for a dry river valley and a coastal valley that we did not sample, along with moderate densities for several other unsampled locations (Figure 3). Cross-checking these locations with the independent sightings showed that the model had predicted almost all known cockatoo hotspots, and 93% of the 42 independent presence points. The 3 false negatives were very close (<85 m) to pixels with predicted cockatoo presence. The mapped coefficient of variation showed that CV was high in areas with predicted low densities and low in high-density areas. Totaling the modeled population densities over the whole

TABLE 1. Comparison of half-normal and hazard-rate detection functions with and without habitat openness as a covariate. ΔAIC between the 2 top models was small but visual inspection of the detection function confirmed the choice of a hazard-rate key detection function with openness as 2-level covariate, although resulting confidence intervals were slightly larger than with the equivalent half-normal model. C-vM: Cramér-von Mises goodness-of-fit test. ΔAIC: difference in Akaike Information Criterion compared to best model.

Key function	Formula	df	C-vM *P*-value	Average detectability	SE (average detectability)	ΔAIC
Hazard-rate	~openness	3	0.98	0.247	0.050	0.0
Half-normal	~openness	2	0.77	0.224	0.030	1.0
Half-normal	~1	1	0.63	0.252	0.031	8.4
Hazard-rate	~1	2	0.76	0.248	0.055	9.0

island resulted in a population estimate for Komodo Island of 1,113 individuals (95% CI: 587–2,109; Figure 3).

DISCUSSION

We used density surface modeling (Miller et al. 2013) of local abundance estimates from distance sampling to estimate the population of the critically endangered Yellow-crested Cockatoo on the 340-km^2 island of Komodo. Our estimated population size of 1,113 individuals and the spatial density predictions are in line with independent KNP Authority monitoring, which recorded direct sightings of over 600 individuals (KLHK and DJ KSDAE 2018) when selectively covering <10% (albeit the most suitable areas) of the island. In their preference for palm savanna and deciduous monsoon forest Komodo's cockatoos resemble conspecifics on other islands, whereas their near-complete absence from quasi cloud forest is unexpected, as similar habitat types and altitudes are readily used on other islands (e.g., Jones et al. 1995, Trainor et al. 2008). While the absence from quasi cloud forest could be seasonal, there are no incidental sightings reported for other times of the year. Mangrove forest—an important roosting habitat for cockatoos on Komodo (Agista and Rubyanto 2001)—was not sampled because our survey times were deliberately chosen to avoid daily periods of high cockatoo mobility and commenced after the cockatoos had traveled away from their roosts early in the morning. Although the numbers are not directly comparable, we calculated a local abundance estimate for the pixels overlapping the valley-floor study areas used by Imansyah et al. (2016). For these valleys our model predicts a population size of 397 individuals, which is more than double the number of direct sightings in September and October 2005/2006 (Imansyah et al. 2016) but not far above the 340 individuals sighted in September–October 2000 in those areas (Agista and Rubyanto 2001).

Our results strongly suggest that the population on Komodo Island is substantial, and we found no evidence that the steep decline reported for the early 2000s has continued (Imansyah et al. 2016). Direct counts collected annually by experienced KNP rangers from vantage points overlooking 6 coastal valleys show an increase from <400 recorded cockatoos for Komodo Island in 2011 to 641 in 2017 (Table 2; Taman Nasional Komodo 2016; KNP unpublished data). This is evidence that the population has certainly been stable and probably increasing over the last 6 yr. As such, in addition to providing protection to the iconic Komodo dragon (Purwandana et al. 2014), KNP appears to be working as a long-term stronghold for the cockatoo. This park's population is by far the largest of the subspecies *occidentalis* and would be the largest for the entire species in the likely case that the distinctive *C. s. citrinocristata* is accorded species rank (Collar and Marsden 2014).

The remoteness and topography of Komodo Island and its fear-inducing dragon appear to provide some natural protection from habitat destruction (e.g., fires and conversion to agriculture) and illegal trapping, but enforcement of legal protection for the cockatoo by park authorities has undoubtedly played an important role in the current situation. Poor soils, steep terrain, and lack of water mean that there has never been much incentive for the single community on the island, which traditionally relied almost exclusively on fishing, to convert land for agriculture (Singleton et al. 2002, Pannell 2013). The Komodo dragons attract a stream of paying visitors (~180,000 in 2018; CNN Travel 2019) and, therefore, KNP is relatively well resourced (Hakim 2017, KLHK and DJ KSDAE 2018). It has 13 field stations, 120 staff (including a permanent presence of ~30 rangers on the islands), several speedboats, and provision for regular patrols and ecological monitoring (Taman Nasional Komodo 2016). Although patrols discover a few poaching incidents every year, these mainly concern marine life, and occasionally deer (2 cases of deer 2009–2015; Taman Nasional Komodo 2016). When over 40 young Komodo dragons were discovered in trade in 2019, they turned out to originate from the species' scarce populations outside KNP's borders (Gokkon 2019). The park has the support of local communities (Walpole and Goodwin 2001), which largely depend economically on tourism (Walpole and Goodwin 2000, 2001; Nurilma et al. 2019). Although KNP's fame, protection, visitors, income, and acceptance are mainly owed to Komodo dragons and marine life (UNESCO 1991), the cockatoos clearly benefit from the protection as well. KNP provides a successful model with regard to methods and resources that could be applied in other protected areas where formal protection has yet to increase cockatoo numbers.

Based on just 5 weeks of fieldwork, and despite the poor accessibility of most of the island and a complex mosaic of habitats, we succeeded in modeling the population of this difficult-to-count species with a distribution map that is suitable for conservation practitioners. Local cockatoo densities fall within the range of estimated densities of other cockatoo species (Marsden and Royle 2015) and the confidence intervals of the predicted densities are narrow enough to be used for assessing conservation status and viability. An independent dataset of cockatoo sightings gave us the opportunity to validate our predictions. During the modeling process this validation process in fact prevented us from accepting a candidate model that neglected residual spatial autocorrelation and instead included the spatial term as a predictor (Gaspard et al. 2019). This model, although favored according to information theoretic criteria, scored very poor hit rates on the independent sightings dataset, as it was dominated by the spatial term. This might be important for other researchers, as >80% of

TABLE 2. Minimum estimate of Yellow-crested Cockatoo numbers from annual monitoring by Komodo National Park authorities derived by summing direct encounters from simultaneous valley-floor counts (Taman Nasional Komodo 2016, KLHK and DJ KSDAE 2018; A. Kefi 2019 personal communication).

Island(s)	2011	2012	2013	2014	2015	2016	2017	2018	2019
Komodo	382	406	500	524	547	522	641	660	733
Rinca & Bero	111	136	149	122	148	160	141	151	150
Total	493	542	649	646	695	682	782	811	883

ecological and biogeographical modeling studies do not account for spatial autocorrelation (Gaspard et al. 2019), which can lead to estimation errors of coefficients of 25% on average (Dormann 2007). Accounting for autocorrelation was particularly important because of our clustered sampling design as opposed to studies where sampling locations are distributed more evenly. However, for parrot species and other rare, highly mobile birds in fragmented rugged habitats, sampling each inhabited patch will often be impractical.

As a 2-step modeling process, the DSM required that we combine the variances of both models (detection function and GAM) to obtain a realistic measure of the variance of our prediction. We used the Delta method (Seber 1982, Miller et al. 2019) for this purpose, ignoring a potential lack of independence between the 2 steps (stemming from the covariate in the detection function), because the more advanced variance propagation method (Williams et al. 2011) is not available for mixed models, and bootstrapping (Hedley and Buckland 2004) should not be used if smooth functions are involved in the model formula (Miller et al. 2013, Bravington et al. 2019). In general, we were forced by the combination of point transects, a covariate in the detection function, and an autocorrelation structure in the DSM to use mixed models (GAMMs instead of GAMs), for which more recent developments in the statistical software have yet to be incorporated. Optimizing adjustments (e.g., use of variance propagation or restricted maximum likelihood) might have increased the precision of our estimates, but spatial density predictions and estimated total population size were so stable across models and modeling engines that final results are unlikely to have differed.

Red List assessments of extinction risk currently rely heavily on population sizes and areas of occupancy (SSC IUCN 2001), but estimating these indicators for threatened species is often problematic as available resources limit precision and reliability of results. DSMs have the potential to provide these data based on limited sampling effort (La Morgia et al. 2015) because they cope well with nonrandom sampling designs (Miller et al. 2013) and can still predict absolute abundances and distributions (Hedley and Buckland 2004). They account for detection probability and utilize spatial environmental information, which is often available remotely. DSMs can also identify habitat associations or other ecological dependencies and predict population hotspots and range limits, which can be cross-validated with independent opportunistic datasets. However, despite their broad applicability for population estimates, DSMs have limitations as well: survey designs still need to cover the study area sufficiently (geographical extent, full range of densities including absence, all relevant habitat types and altitudes; Miller et al. 2013) and reach the minimum number of contacts for reliably estimating a detection function (Buckland et al. 2001). DSMs can only make useful predictions if the population's limiting factors can be captured directly or indirectly by spatially referenced covariates, and the method only reaches its full potential if these data are available remotely. Interpolated densities for unsampled areas between samples are predicted with confidence whereas extrapolation to new areas outside the sample range require more caution (Miller et al. 2013). Consequently, predictions across islands (or functional islands such as protected areas or areas that span biogeographical boundaries) that are not included at the modeling stage are risky, as new areas might be subject to unconsidered influences. In our case we decided against using the model from Komodo Island to estimate the neighboring cockatoo subpopulation on Rinca Island because additional factors such as introduced predators and accessibility for potential trappers from Flores could not be accounted for.

Cockatoos in KNP are a showcase for the potential of a 2-level monitoring approach, where annual trend assessment with relatively simple methods could be used to indicate optimal timing of high-effort abundance surveys like distance sampling with DSM. In the future large gaps in published abundance data, coinciding with suspected population declines as in the decades before our study (Imansyah et al. 2016), could be prevented if annual monitoring data are accessible to conservation practitioners who can then trigger more intensive research as soon as a decline becomes apparent and in time for potential mitigations. We found DSM to be an efficient and effective estimator of population size and distribution in the Yellow-crested Cockatoo, and suggest its use for larger populations of the species (e.g., on Sumba and in Timor-Leste), provided that region-specific limiting factors such as trapping pressure can be accounted for. The useful predictions and broad applicability of DSM give it an edge over alternative methods with similar survey effort and make it a powerful tool for estimating population sizes of threatened island species.

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Data depository: Analyses reported in this article can be reproduced partly using data provided by Reuleaux et al. (2020). Sensitive location information was deleted from the dataset so an analysis cannot be reproduced completely with the data in Dryad. Uncensored data files are available from the authors to bona fide researchers.

LITERATURE CITED

Agista, D., and D. Rubyanto (2001). Telaah awal status, penyebaran, dan populasi kakatua kecil jambul kuning, *Cacatua sulphurea parvula*: di Taman Nasional Komodo, Nusa Tenggara Timur. BirdLife International Indonesia Programme, Bogor, Indonesia.

Agista, D., Sumardin, A. Hamid, F. N. Mallo, S. Alam, Harjun, and C. Mamengko (2001). Telaah awal status, penyebaran dan Populasi Kakatua-kecil Jambul-kuning (*Cacatua sulphurea sulphurea*) di Taman Nasional Rawa Aopa Watumohai, Sulawesi Tenggara dan Pulau Pasoso, Sulawesi Tengah. BirdLife International - Indonesia Programme, Bogor, Indonesia.

Auffenberg, W. (1980). The herpetofauna of Komodo with notes on adjacent areas. Bulletin of Florida State Museum, Biological Sciences 25:39–156.

Bächler, E., and F. Liechti (2007). On the importance of *g* (0) for estimating bird population densities with standard distance sampling: Implications from a telemetry study and a literature review. Ibis 149:693–700.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. Mustoe (2000). Bird Census Techniques, 2nd ed. Academic Press, Amsterdam, The Netherlands.

BirdLife International (2001). Threatened Birds of Asia: The BirdLife International Red Data Book. BirdLife International, Cambridge, UK.

Böhner, J., and T. Selige (2006). Spatial prediction of soil attributes using terrain analysis and climate regionalisation. In SAGA - Analysis and Modelling Applications (J. Böhner, K. R. McCloy, and J. Strobl, Editors). Göttinger Geographische Abhandlungen, Göttingen, Germany. pp. 13–28.

Bradbury, G., M. Trinder, B. Furness, A. N. Banks, R. W. G. Caldow, and D. Hume (2014). Mapping seabird sensitivity to offshore wind farms. PLOS One 9:e106366.

Bravington, M. V., D. L. Miller, and S. L. Hedley (2019). Reliable variance propagation for spatial density surface models. arXiv:1807.07996v4 [stat.ME] https://arxiv.org/pdf/1807.07996

Broch, H. B. (1981). Cultural variation on the islands in the Sea of Flores. Archipel 22:43–53.

Buckland, S. T. (2006). Point-transect surveys for songbirds: Robust methodologies. The Auk 123:345–357.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas (2001). Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.

Buckland, S. T., S. J. Marsden, and R. E. Green (2008). Estimating bird abundance: Making methods work. Bird Conservation International 18:91–108.

Buckland, S. T., C. S. Oedekoven, and D. L. Borchers (2016). Model-based distance sampling. Journal of Agricultural, Biological, and Environmental Statistics 21:58–75.

Cahyadin, Y., P. Jepson, and S. Arif (1994a). The status of *Cacatua sulphurea abbotti* on the Masalembo Islands. PHPA/BirdLife International - Indonesia Programme, Bogor, Indonesia.

Cahyadin, Y., P. Jepson, and M. Syarief (1994b). A rapid status assessment of *Cacatua sulphurea sulphurea* in South Sulawesi Province. PHPA/BirdLife International - Indonesia Programme, Bogor, Indonesia.

Casagrande, D. G., and S. R. Beissinger (1997). Evaluation of four methods for estimating parrot population size. The Condor 99:445–457.

CNN Travel (2019). Indonesia cancels plan to ban tourists from Komodo Island. CNN Travel, October 2. https://edition.cnn.com/travel/article/indonesia-komodo-islands-reverse-tourist-ban-intl-hnk/index.html

Collar, N. J., and S. J. Marsden (2014). The subspecies of Yellow-crested Cockatoo *Cacatua sulphurea*. Forktail 30:23–27.

Collar, N., J. Eaton, and B. Sykes (2017) Conservation and the redaction of locality data. BirdingASIA 28:3–4.

Collen, B., L. McRae, S. Deinet, A. De Palma, T. Carranza, N. Cooper, J. Loh, and J. E. M. Baillie (2011). Predicting how populations decline to extinction. Philosophical Transactions of the Royal Society B 366:2577–2586.

Congedo, L. (2016). Semi-automatic classification plugin documentation. http://dx.doi.org/10.13140/RG.2.2.29474.02242/1

Conrad, O., B. Bechtel, M. Bock, H. Dietrich, E. Fischer, L. Gerlitz, J. Wehberg, V. Wichmann, and J. Böhner (2015). System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. Geoscientific Model Development 8:1991–2007.

Dénes, F. V., J. L. Tella, and S. R. Beissinger (2018). Revisiting methods for estimating parrot abundance and population size. Emu-Austral Ornithology 118:67–79.

de Segura, A. G., P. S. Hammond, A. Cañadas, and J. A. Raga (2007). Comparing cetacean abundance estimates derived from spatial models and design-based line transect methods. Marine Ecology Progress Series 329:289–299.

Dormann, C. F. (2007). Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Global Ecology and Biogeography 16:129–138.

Duchon, J. (1977). Splines minimizing rotation-invariant semi-norms in Sobolev spaces. In Constructive Theory of Functions of Several Variables (W. Schempp and K. Zeller, Editors). Springer, Berlin, Germany. pp. 85–100.

Eaton, J. A., C. R. Shepherd, F. E. Rheindt, J. B. C. Harris, S. B. van Balen, D. S. Wilcove, and N. J. Collar (2015). Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia. Forktail 31:1–12.

eBird Basic Dataset (2019). Version: EBD_relMay-2019. Cornell Lab of Ornithology, Ithaca, NY, USA. https://ebird.org/science/download-ebird-data-products

Gaspard, G., D. Kim, and Y. Chun (2019). Residual spatial autocorrelation in macroecological and biogeographical modeling: A review. Journal of Ecology and Environment 43:Article 19.

Gilles, A., S. Adler, K. Kaschner, M. Scheidat, and U. Siebert (2011). Modelling harbour porpoise seasonal density as a function of the German Bight environment: Implications for management. Endangered Species Research 14:157–169.

Gokkon, B. (2019). Indonesia arrests 7 for allegedly selling Komodo dragons over Facebook. Mongabay, April 5. https://news.mongabay.com/2019/04/

Guix, J. C., M. Martín, and S. Mañosa (1999). Conservation status of parrot populations in an Atlantic rainforest area of southeastern Brazil. Biodiversity and Conservation 8:1079–1088.

Hakim, L. (2017). Managing biodiversity for a competitive ecotourism industry in tropical developing countries: New opportunities in biological fields. AIP Conference Proceedings 1908(1):030008. American Institute of Physics, Malang, Indonesia.

Harihar, A., B. Pandav, and D. C. MacMillan (2014). Identifying realistic recovery targets and conservation actions for tigers in a human-dominated landscape using spatially explicit densities of wild prey and their determinants. Diversity and Distributions 20:567–578.

Hedley, S. L., and S. T. Buckland (2004). Spatial models for line transect sampling. Journal of Agricultural, Biological, and Environmental Statistics 9:181–199.

Ibouroi, M. T., N. A. Hassane, S. Moindjié, M. Ombade, N. Mohamed, M. H. Saidou, K. Abderemane, A. Cheha, and J. Chiffard (2019). The first comprehensive survey of habitat suitability and population size for the endangered Grande Comoro Scops Owl (*Otus pauliani*): Implications for its conservation. Journal of Ornithology 160:1121–1132.

Imansyah, M. J., D. G. Anggoro, N. Yangpatra, A. Hidayat, and Y. J. Benu (2005). Sebaran dan karakteristik pohon sarang kakatua jambul kuning (*Cacatua sulphurea parvula*) di pulau Komodo, Taman Nasional Komodo. CRES Komodo Project, TN Komodo, Denpasar, Indonesia.

Imansyah, M. J., D. Purwandana, A. Ariefiandy, Y. J. Benu, T. S. Jessop, and C. R. Trainor (2016). Valley-floor censuses of the critically endangered Yellow-crested Cockatoo *Cacatua sulphurea occidentalis* on Komodo Island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period. Forktail 32:66–72.

Imansyah, M. J., D. Purwandana, H. Rudiharto, and T. S. Jessop (2003). Survey potensi hidupan liar terestrial di Pulau Komodo, Taman Nasional Komodo 2002. Zoological Society of San Diego, Taman Nasional Komodo, The Nature Conservancy, Labuan Bajo, Indonesia.

IUCN (2019). The IUCN Red List of Threatened Species, version 2019-2. http://www.iucnredlist.org

Jones, M. J., M. D. Linsley, and S. J. Marsden (1995). Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia. Bird Conservation International 5:21–52.

KLHK (2017). Penutupan Lahan Indonesia. Landcover map Indonesia by WebGIS Ministry of Environment and Forestry. http://webgis.menlhk.go.id:8080/kemenhut

KLHK and DJ KSDAE (2018). Statistik Direktorat Jenderal Konservasi Sumber Daya Alam dan Ekosistem Tahun 2017. Kementerian Lingkungan Hidup dan Kehutanan, Jakarta, Indonesia.

Koshkin, M. A., R. J. Burnside, N. J. Collar, J. L. Guilherme, D. A. Showler, and P. M. Dolman (2016). Effects of habitat and land use on breeding season density of male Asian Houbara *Chlamydotis macqueenii*. Journal of Ornithology 157:811–823.

La Morgia, V., R. Calmanti, A. Calabrese, and S. Focardi (2015). Cost-effective nocturnal distance sampling for landscape monitoring of ungulate populations. European Journal of Wildlife Research 61:285–298.

Leivits, A., and M. Leivits (2016). Using density surface modelling for estimating abundance of breeding birds in heterogeneous mire habitats: A case study in Estonia. In BirdNumbers 2016: Birds in a Changing World. Programme and Abstracts of the 20th Conference of the European Bird Census Council (Dachverband Deutscher Avifaunisten, Editor). Halle, Germany.

Lilley, R. J. (1997). Komodo National Park. In The Ecology of Nusa Tenggara and Maluku. (K. Monk, Y. De Fretes and G. Reksodiharjo-Lilley, Editors). eBook. Periplus Editions, Hong Kong. pp. 807–811.

Mace, G. M., N. J. Collar, K. J. Gaston, C. Hilton-Taylor, H. R. Akçakaya, N. Leader-Williams, E. J. Milner-Gulland, and S. N. Stuart (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. Conservation Biology 22:1424–1442.

MacKenzie, D. I., J. D. Nichols, N. Sutton, K. Kawanishi, and L. L. Bailey (2005). Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101–1113.

Marques, T. A., L. Thomas, S. G. Fancy, and S. T. Buckland (2007). Improving estimates of bird density using multiple-covariate distance sampling. The Auk 124:1229–1243.

Marsden, S. J. (1999). Estimation of parrot and hornbill densities using a point count distance sampling method. Ibis 141:327–390.

Marsden, S. J., and K. Royle (2015). Abundance and abundance change in the world's parrots. Ibis 157:219–229.

McDonald, L. L. (2004). Sampling rare populations. In Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters (W. L. Thompson, Editor). Island Press, Washington, DC, USA. pp. 11–42.

Miller, D. L., and S. N. Wood (2014). Finite area smoothing with generalized distance splines. Environmental and Ecological Statistics 21:715–731.

Miller, D. L., M. L. Burt, E. A. Rexstad, and L. Thomas (2013). Spatial models for distance sampling data: Recent developments and future directions. Methods in Ecology and Evolution 4:1001–1010.

Miller, D. L., E. Rexstad, L. Burt, M. V. Bravington, and S. Hedley (2019). dsm: Density Surface Modelling of Distance Sampling Data. https://cran.r-project.org/package=dsm

Miller, D. L., E. Rexstad, L. Thomas, L. Marshall, and J. L. Laake (2016). Distance sampling in R. BioRxiv:63891.

Monk, K., Y. De Fretes, and G. Reksodiharjo-Lilley (1997). Ecology of Nusa Tenggara and Maluku, 1st ed. Oxford University Press, Oxford, UK.

Nurilma, A. D., A. Sjarmidi, and Y. Yustiana (2019). Economic valuation of Komodo dragon (*Varanus komodoensis*, Ouwens 1912) and its contribution to locally-generated revenue of West Manggarai Regency, East Nusa Tenggara Province. In IOP Conference Series: Earth and Environmental Science, Bandung Indonesia.

Oedekoven, C. S., J. L. Laake, and H. J. Skaug (2015). Distance sampling with a random scale detection function. Environmental and Ecological Statistics 22:725–737.

Pannell, S. (2013). Nature and culture in a global context: A case study from World Heritage Listed Komodo National Park, Eastern Indonesia. Terra Australis 36:53–63.

Petersen, I. K., M. L. MacKenzie, E. Rexstad, M. S. Wisz, and A. D. Fox (2011). Comparing pre- and post-construction distributions of Long-tailed Ducks *Clangula hyemalis* in and around the Nysted Offshore Wind Farm, Denmark : A quasi-designed experiment accounting for imperfect detection, local surface features and autocorrelation. University of St Andrews, St Andrews, UK.

PHPA/LIPI/BirdLife International (1998). Species Recovery Plan Yellow-crested Cockatoo. PHPA/LIPI/BirdLife International - Indonesia Programme, Bogor, Indonesia.

Purwandana, D., A. Ariefiandy, M. J. Imansyah, H. Rudiharto, A. Seno, C. Ciofi, D. A. Fordham, and T. S. Jessop (2014). Demographic status of Komodo dragons populations in Komodo National Park. Biological Conservation 171:29–35.

QGIS Development Team (2019). QGIS geographic information system. Open Source Geospatial Foundation Project, Zanzibar, Tanzania. http://qgis.org

R Core Team (2019). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/

Reuleaux, A., B. A. Siregar, N. J. Collar, M. R. Panggur, A. Mardiastuti, M. J. Jones, and S. J. Marsden (2020). Data from: Protected by dragons: Density surface modeling confirms large population of the critically endangered Yellow-crested Cockatoo (*Cacatua sulphurea*) on Komodo Island. The Condor: Ornithological Applications 122:1–15. doi:10.5061/dryad.47d7wm3b9

Schroeder, N. M., S. D. Matteucci, P. G. Moreno, P. Gregorio, R. Ovejero, P. Taraborelli, and P. D. Carmanchahi (2014). Spatial and seasonal dynamic of abundance and distribution of guanaco and livestock: Insights from using density surface and null models. PLOS One 9:e85960.

Seber, G. A. F. (1982). The Estimation of Animal Abundance and Related Parameters, 2nd ed. McMillan Publishing Company, New York, NY, USA.

Singleton, J., R. Sulaiman, and TNC staff (2002). Environmental assessment study – Komodo National Park Indonesia. The Nature Conservancy-SE Asia Center for Marine Protected Areas, Bali, Indonesia.

Somershoe, S. G., D. J. Twedt, and B. Reid (2006). Combining Breeding Bird Survey and distance sampling to estimate density of migrant and breeding birds. The Condor 108:691–699.

SSC IUCN (2001). IUCN Red List categories and criteria: version 3.1. https://portals.iucn.org/library/node/10315

Taman Nasional Komodo (2016). Statistik Balai Taman Nasional Komodo tahun 2009–2015. Kementerian Lingkungan Hidup dan Kehutanan, Labuan-Bajo, Indonesia.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Trainor, C. R., F. Santana, P. Pinto, A. F. Xavier, R. Safford, and R. Grimmett (2008). Birds, birding and conservation in Timor-Leste. Birding Asia 9:16–45.

UNESCO World Heritage Committee (1991). Convention concerning the protection of the World Cultural and Natural Heritage. https://whc.unesco.org/en/list/609/

Valente, A. M., T. A. Marques, C. Fonseca, and R. T. Torres (2016). A new insight for monitoring ungulates: Density surface modelling of roe deer in a Mediterranean habitat. European Journal of Wildlife Research 62:577–587.

Walpole, M. J., and H. J. Goodwin (2000). Local economic impacts of dragon tourism in Indonesia. Annals of Tourism Research 27:559–576.

Walpole, M. J., and H. J. Goodwin (2001). Local attitudes towards conservation and tourism around Komodo National Park, Indonesia. Environmental Conservation 28:160–166.

Williams, R., S. L. Hedley, T. A. Branch, M. V. Bravington, A. N. Zerbini, and K. P. Findlay (2011). Chilean blue whales as a case study to illustrate methods to estimate abundance and evaluate conservation status of rare species. Conservation Biology 25:526–535.

Williamson, K., and R. C. Homes (1964). Methods and preliminary results of the Common Birds Census, 1962–63. Bird Study 11:240–256.

Winiarski, K. J., D. L. Miller, P. W. C. Paton, and S. R. McWilliams (2013). Spatially explicit model of wintering Common Loons: Conservation implications. Marine Ecology Progress Series 492:273–283.

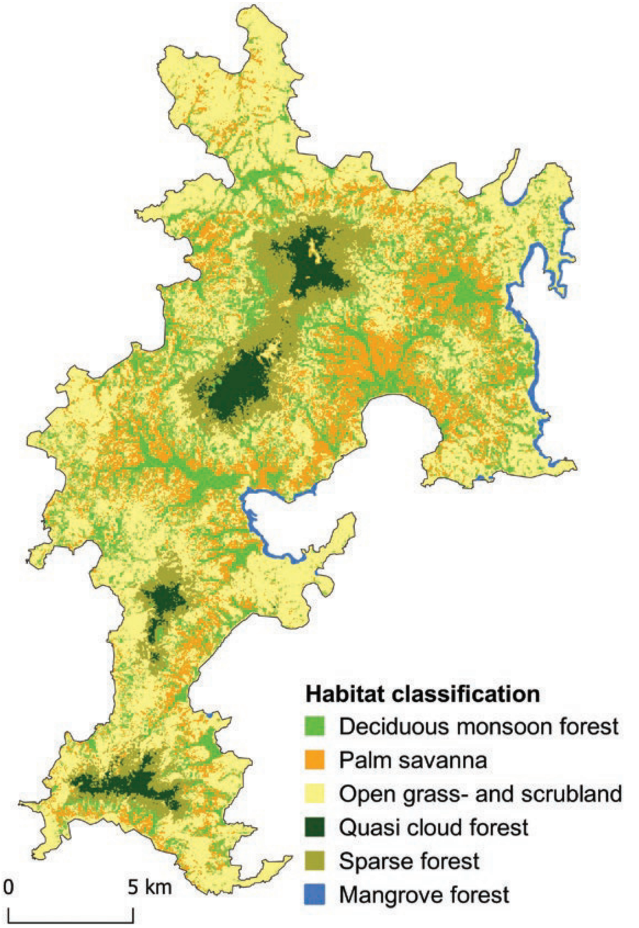
Winiarski, K. J., D. L. Miller, P. W. C. Paton, and S. R. McWilliams (2014). A spatial conservation prioritization approach for protecting marine birds given proposed offshore wind energy development. Biological Conservation 169:79–88.

Wood, S. N. (2017). Generalized Additive Models: An Introduction with R, 2nd ed. Chapman and Hall/CRC, London, UK.

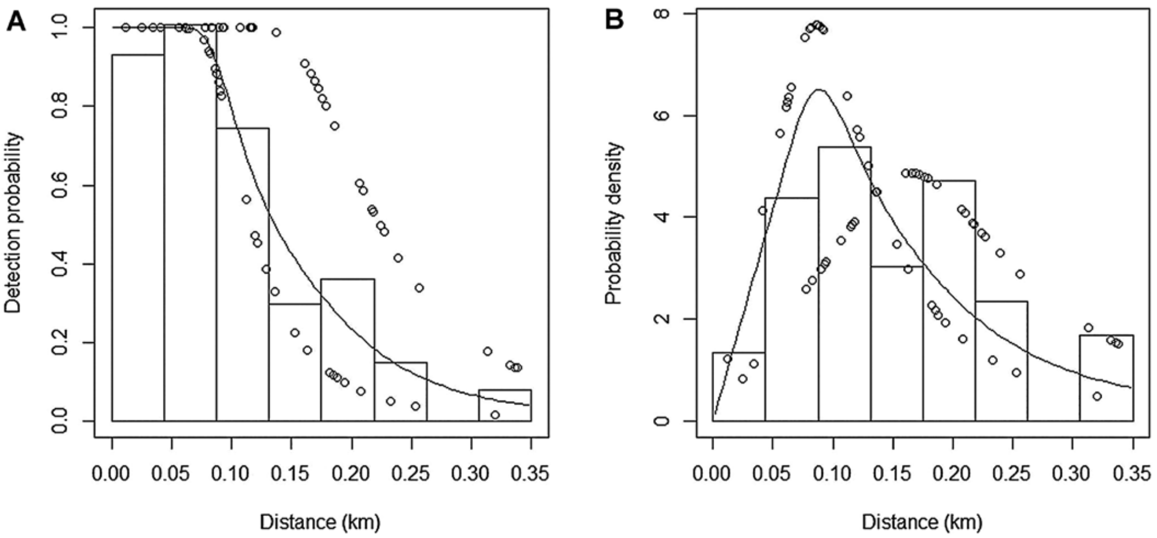
Wood, S. N. (2019). mgcv: Mixed GAM computation vehicle with automatic smoothness estimation. R-project, https://cran.r-project.org/package=mgcv

Wungo, E. (2011). Laporan survei populasi paruh bengkok terancam punah *Cacatua sulphurea citrinocristata*, Sumba, Nusa Tenggara Timur. Burung Indonesia, Bogor, Indonesia.

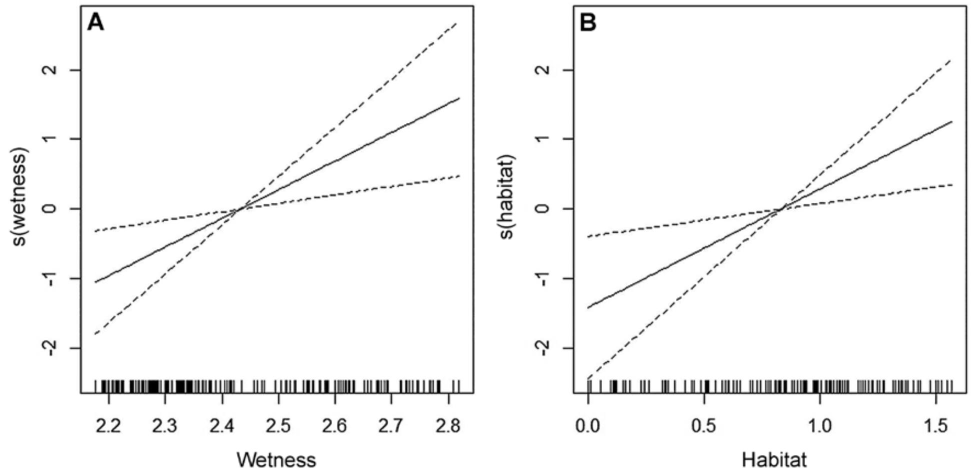
Zuur, A., E. N. Ieno, and A. A. Saveliev (2014). A Beginner's Guide to Generalized Additive Mixed Models with R. Highland Statistics Ltd., Newburgh, UK.



APPENDIX FIGURE 4. Komodo Island habitat classification derived from supervised classification of LANDSAT 8 satellite images with training data from Google Maps. Forest types follow Auffenberg (1980) and Monk et al. (1997) with addition of sparse forest as a transitional zone between quasi cloud forest and open habitat types. Mangrove forest was not distinguished in the supervised classification and was added afterwards (KLHK 2017).



APPENDIX FIGURE 5. Hazard-rate key detection function (**A**) and detection probability density function (**B**) with openness of the habitat as 2-level covariate. Open circles represent individual detections and show the influence of the covariate: in open habitats detection probabilities remained high farther away from the observer (points above the line in [**A**], slopes shallower than the line in [**B**]) than in other habitats (points below the line in [**A**], slopes steeper than the line in [**B**]).



APPENDIX FIGURE 6. Shape of the smooth functions used as environmental predictors for Yellow-crested Cockatoo densities in the GAMM. "Wetness" is the log-transformed SAGA wetness index and "habitat" is the percentage cover by suitable habitat (palm savanna and deciduous monsoon forest combined and arcsine transformed). Ticks on the *x*-axis indicate the sample distribution.

APPENDIX TABLE 3. Habitat type classification on Komodo Island modified from Auffenberg (1980) and Monk et al. (1997).

Habitat class (this study)	Class in Auffenberg 1980	Class in Monk et al. 1997	Location	Main characteristics	Cockatoo observations at point counts [a]	Cover on Komodo Island
Open grassland & scrubland	Steppe	Savanna	Mostly lowlands	Treeless	6	51.5%
Palm savanna	Savanna forest	Savanna	Large lowland areas and many small fragments	Open with tall *Borassus* and *Corypha* palms	37	18.6%
Deciduous monsoon forest	Deciduous monsoon forest	Gallery forest, dry monsoon forest, moist deciduous monsoon forest	Along rivers and in coastal valleys	Closed canopy, *Tamarindus*, *Sterculia*, and *Bredelia*	25	16.5%
Mangrove forest	Mangrove forest	Mangrove forest	Tidal zone	Mangrove species	0	0.5%
Quasi cloud forest	Quasi cloud forest	Mossy forest	>500 m	Moss and lichen on trees, bamboo, rattan	0	3.7%
Sparse forest	Transitional zone to quasi cloud forest	Not mentioned	<500 m, transition zone from quasi cloud forest to scrubland	No closed canopy, bamboo groves	0	9.2%

[a] Number of encounters in our distance sampling survey during point counts.

APPENDIX TABLE 4. Model choice for the density surface model. In model names **S** stands for spatial term (a smoother to the Duchon spline base of the interaction of geographic coordinates s(x,y)), **W** for wetness index (log transformed, s(wetness)), and **H** for the cumulative percentage cover by suitable habitat types (with an arcsine transformation, s(habitat)); edf = effective degrees of freedom, AIC(GAM) = AIC of the equivalent Generalized Additive Model.

Predictors	edf	CI	*P*	AIC(GAM)
W + H [a]				**468**
(Intercept)	1.25	0.55–1.95	**0.001**	
s(wetness)	1		**0.005**	
s(habitat)	1		**0.006**	
S + W + H				**468**
(Intercept)	1.27	0.58–1.96	**<0.001**	
s(x,y)	0		0.445	
s(wetness)	1		**0.003**	
s(habitat)	1		**0.005**	
W				**473**
(Intercept)	1.6	1.03–2.17	**<0.001**	
s(wetness)	1		**<0.001**	
H				**474**
(Intercept)	1.44	0.75–2.13	**<0.001**	
s(habitat)	1		**<0.001**	

[a] Chosen model.

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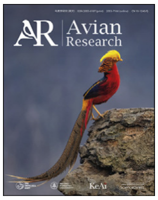

Productivity constraints on Citron-crested Cockatoos in a rich community of large hole-nesting birds

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ABSTRACT

Knowledge of breeding success and its limiting factors is crucial in assessing species' conservation needs. As cavity-nesters, parrots are particularly influenced by the availability of suitable cavities and low breeding output, whether due to natural processes or trapping. On the island of Sumba, Indonesia, the Critically Endangered Citron-crested Cockatoo (*Cacatua citrinocristata*) has the added problem of co-existing with an unusually rich hole-nesting bird community in a forested environment much constrained by habitat loss. We monitored 95 nesting cavities of cockatoos and their competitors and potential nest-predators, over one to four breeding seasons, using a combination of camera-traps, direct checks on nest contents, and observations from the ground. Competition for suitable cavities was intense among three large parrot species, two owls and a hornbill. Visitation rates by potential competitors were higher at unoccupied cavities than at those containing active nests, reflecting the guarding behaviour of the occupants. The Endangered Sumba Hornbill (*Rhyticeros everetti*) dominated observed direct confrontations and was the most frequent visitor to active parrot nests, suggesting a further role as a potential nest-predator. Cockatoos prospected many cavities but rarely then attempted to nest: instead the sites were usually occupied by other cavity-nesters, or by bees. At the few cavities where cockatoos did breed, predation pressure was likely low, and observed success rate high (10 successful of 15 nests), although the low number of nests found early in the breeding cycle suggests that some may have failed before detection. Intense competition for cavities suggests a shortage of suitable nest-sites, the need for preservation of old hole-bearing trees and a role for nestboxes. Accessible, known, safe artificial nest-sites would also provide opportunities to assess the scale of nest-site shortage, allow camera placements to study productivity, exclude some competitors and predators, and prevent illegal trapping. Especially given continued trapping pressure, the species would benefit from targeted local awareness-raising and law enforcement, with the whole endeavour backed up by longer-term forest restoration.

1. Introduction

A great variety of bird species nest in tree cavities (van der Hoek et al., 2017). Cavities provide clear advantages over open nesting in terms of shelter from weather and protection from predators, but have the considerable disadvantage of limited availability, either of the holes themselves or of the substrates in which to make them (Lack, 1968; Nilsson, 1986; Brightsmith, 2005; Olah et al., 2016). In contrast to primary cavity-nesters, such as woodpeckers (Picidae), secondary cavity-nesters, such as most parrots (Psittaciformes), are particularly constrained by availability, commonly resulting in much intra- or interspecific competition for favoured sites (Collias, 1964). Availability can further decline, and competition increases, in circumstances where much the most important cavity-bearing substrate—larger, older trees—is itself reduced by forestry practices such as selective logging (van Balen et al., 1982; Nilsson, 1986; Cockle et al., 2010; Schaaf et al., 2021). For this reason, the plight of secondary cavity-nesters represents a particular conservation concern (Cockle et al., 2010; Altamirano et al., 2017; Gutzat and Dormann, 2018; Schaaf et al., 2020, 2021). In the case of parrots, owing to their unique appeal as pets, this concern is greatly amplified by the fact that trappers learn where the birds' favoured cavities are and take their nestlings year after year, thereby greatly

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suppressing productivity and recruitment (Marsden and Jones, 1997; González, 2003; Martin et al., 2014; Valle et al., 2018). Parrots are long-lived birds, and population size may be a poor correlate of population health if breeding success and other demographic rates are not taken into account (Shoemaker et al., 2013). Certainly a knowledge of productivity and its limiting factors is essential for assessing population viability and urgently needed for many poorly known and threatened parrots (Monterrubio et al., 2002; Spoon, 2006; Heinsohn et al., 2009; Olah et al., 2016). The difficult task of acquiring such knowledge has recently been made somewhat easier by advances in camera technology for checking nest contents (e.g. Reuleaux et al., 2014; Bonaparte and Cockle, 2017), observing behaviour at the nest (e.g. Sanders and Maloney, 2002; Richardson et al., 2009) and monitoring predation (e.g. Clout and Merton, 1998; Masello et al., 2006; Ribeiro-Silva et al., 2018).

The Citron-crested Cockatoo (*Cacatua citrinocristata*) is endemic to the island of Sumba, East Nusa Tenggara, Indonesia, having recently been elevated to species rank from the Wallacean region's Yellow-crested Cockatoo (*C. sulphurea*) (Collar and Marsden, 2014; Eaton et al., 2016). Despite being larger than Sumba (11,000 km^2), the adjacent islands of Sumbawa (15,400 km^2), Flores (13,500 km^2) and Timor (29,700 km^2) have just one or two large parrots (Sumba has three), no hornbills (Sumba has one) and one or two large owls (Sumba has two); thus in total Sumba has six large hole-nesters, Timor four, Flores three and Sumbawa just two. Studies of the Yellow-crested Cockatoo's breeding biology in the wild have been very limited and most were just side notes in studies of population size, usually involving $<$10 nests whose contents were not investigated (Agista and Rubyanto, 2001; Hidayat, 2012; Nandika and Agustina, 2012; Imansyah et al., 2016; Ihsannudin et al., 2020; Nandika et al., 2020). Studies of the Citron-crested Cockatoo have been slightly more extensive (Marsden, 1995; Marsden and Jones, 1997), even including some nest access (Walker et al., 2005; Djawarai et al., 2014), but owing to the difficulties in locating active nests the sample sizes still remained low (Marsden and Jones, 1997; Walker et al., 2001, 2005; Djawarai et al., 2014).

After decades of intense pressure from the international pet trade and resultant dramatic declines in numbers, the trapping of cockatoos has been illegal on Sumba since 1992/93 (Marsden, 1995; PHPA and BirdLife International-IP, 1998). In 2002, evidence of increased densities (2.0 individuals/ha in 1995 to 4.3 in 2002, Jones et al., 1995; Cahill et al., 2006) gave hope that populations were recovering. However, current estimated numbers are not significantly higher than those immediately before the ban (Jones et al., 1995; Wungo, 2011; A.R., unpubl. data). The only published total population estimate based on field work remains the 1992 figure of 3200 individuals (Jones et al., 1995). In the absence of reports of trapping, this apparent failure to recover significantly has been suspected to relate to low productivity (Djawarai et al., 2014).

Here, therefore, we aim to assess the recent productivity of Citron-crested Cockatoos and the factors that might affect it. Typically, breeding success in parrots is limited by lack of suitable nest sites, competition for these sites (e.g. Heinsohn et al., 2003), nest predation (Moorhouse et al., 2003; Harper and Bunbury, 2015) and taking chicks and adults for the pet trade (e.g. Pires, 2012; Valle et al., 2018). Natural productivity in Citron-crested Cockatoos may always have been low even without human interference, but an understanding of the current limiting factors may nevertheless be crucial for identifying conservation interventions that might improve the status of the species (e.g. predator management, provision of artificial nest-sites, exclusion of competitors from current nest-sites) at least until sufficient habitat can be restored. We investigated the occupancy and fate of potential cockatoo nest sites, seasonal cavity use across the community of large hole-nesters, and visitation rates to nests by potential competitors and predators, and present new knowledge on the Citron-crested Cockatoo's breeding behaviour in the wild.

2. Materials and methods

2.1. Study area

The island of Sumba (9.3–10.3°S, 118.9–120.8°E) is an important centre of endemism which, in the taxonomy of the late 1990s, supported seven bird species known nowhere else (Stattersfield et al., 1998). To this tally the elevation of Citron-crested Cockatoo (Critically Endangered), Sumba Eclectus (*Eclectus cornelia*, Endangered) and—depending on taxonomy—up to four other avian taxa to species rank has added further evidence of the island's high biological significance. Sumba is dominated by relatively low limestone hills reaching up to 1200 m a.s.l., with a dry season from May to November and a rainy season from December to April. With one of Indonesia's lowest per capita incomes and large numbers of livestock, it has lost most of its forest cover to pasture and agriculture, on which many of its 650,000 inhabitants rely for subsistence (Monk et al., 1997; Badan Pusat Statistik, 2016). By 2020 the number of inhabitants had risen to 779,000 (Badan Pusat Statistik, 2021). We undertook fieldwork in the forested areas of central and western Sumba, mostly in Matalawa National Park (the 501 km^2 portion formerly called Manupeu Tanah Daru National Park), but we also included four smaller forest patches in the centre of the island. Following recommendations on conservation considerations (Collar et al., 2017), we omit all details on locations here and do not present maps to avoid supplying information to potential trappers and traders. The locations and maps are however available for bona-fide researchers or conservation purposes from the authors.

2.2. Survey methods

The entire study period was June 2015–May 2019, encompassing four breeding seasons, but with effort varying between years and seasons. Our methods for locating nest-sites were: checking all cavities recorded as parrot nests in the past (Djawarai et al., 2014); long watches from vantage points over areas with cockatoo activity; checking trees with potentially suitable cavities; searching for twigs snapped off large trees by cockatoos during nest-prospecting; and following tip-offs from forest users and information from former trappers about once-occupied cavities. At the start of the study in 2015, we knew, from previous work by the non-governmental organisation Burung Indonesia, of twelve cavities with past cockatoo activity. We learnt of a further 53 nests from former trappers at various points in time throughout the study period. In addition, we located 30 prospected cavities by following cockatoo activity. Nests were difficult to find in the dense forest, particularly when no good vantage points were present. Even cavities we repeatedly observed being entered by cockatoos had only a small chance of being nests, as less than a quarter of prospected sites became active (Table 1). Ethical and legal issues prohibited cooperation with any of the few trappers who were still active. The former trappers we consulted had, by then, not raided nests for over ten years, and most sites they identified (47 out of 53) were not occupied by cockatoos in the study period.

Once we located a cavity with cockatoo activity, we watched it from a distance of 300–1000 m with optics or from a hide near the tree to determine breeding stage. If the cavity was accessible (i.e. in a living tree, with no dead branches at or directly above it and not beyond the reach of safe rope placement points), we checked its contents using a single-rope climbing technique. We inspected the contents visually or using a compact camera, a mobile phone camera or an endoscopic camera attached to a mobile phone. We deployed camera-traps sporadically within the period November 2016–May 2019. Where possible, a camera-trap (Acorn 5210A or Bushnell Natureview) was installed 1–2 m above the entrance with a metal brace (Fig. 1), following a method developed in the New Zealand Department of Conservation (J. Malham *in litt.*, 2016).

Table 1
Number of potential nests found and monitored per season. Cavities are split by method of finding them: B, cavity was part of the Burung Indonesia (BI) dataset before 2014, O, cavity found by own fieldwork, T, cavity shown by former trappers or other forest users. Breeding season headings contain two years because they span the turn of the year. Data for monitoring by the BI team in 2014/15 are not included here.

	2015–2016	2016–2017	2017–2018	2018–2019	All seasons
No. potential nests monitored (B/O/T)	42 (11/21/10)	62 (12/21/29)	68 (11/19/38)	68 (10/17/41)	95 (12/30/53)
First monitored that year (O/T)	31 (21/10)	23 (2/21)	20 (6/14)	9 (1/8)	83 (30/53)
No. cavities occupied by cockatoos (B/O/T)	3 (1/2/0)	3 (1/0/2)	4 (0/3/1)	5 (1/1/3)	12 (1/6/5)
Working period	Aug–Apr	Nov–Feb	Dec–Mar	Jun–Oct, Mar, May	–

Fig. 1. (A) Nest tree in deciduous forest, (B) rope access at emergent nest tree in closed-canopy forest, (C) camera set-up above nest-cavity in *Tetrameles nudiflora* tree occupied by a Barn Owl (*Tyto alba*), (D) camera-trap with brace and rain protection, (E) camera above a cavity with upwards-facing entrance. (Photos A,C: AR; B: Romy ND Limu with permission; D,E: BAS).

In the absence of branches or suitably positioned trunk, cameras had to be installed nearer or further away from the entrance and/or to the side instead of above. We set the cameras to be triggered by motion at the nest entrance and to take still photographs during the day and infra-red photographs with an invisible IR flash at night (a series of three photos was taken automatically each time the motion sensor was triggered), with medium motion sensitivity, 50–80% of IR-LED blocked with tape to reduce over-exposure depending on distance from the nest. We serviced the cameras every two weeks when a cavity was hosting nesting birds, and otherwise every 2–6 months. Camera malfunctions due to various factors (ants, moisture, falling branches, false triggers by newly grown foliage, rapid battery depletion from unexpected nocturnal activity) were frequent. We compiled camera data by viewing photographs with each day as a datapoint and recording each species that visited or occupied the cavity. For clarity, figures only show the visiting five taxa that also appeared as occupants in our study (three large parrots, two owls, here combined, and a hornbill) and the potential predators are grouped into hornbill, owls, hawks, reptiles and mammals.

We sought always to avoid disturbance to breeding birds. Nests were watched from as far away as visibility of the cavity entrance permitted. If cockatoos started alarm-calling without another discernible cause, the observers left the area and later tried to approach it undetected from another direction. We watched nests from early in the morning and accessed them when both parents had left the cavity. Disturbance was limited to 30 min from the time the climber was noticed by a guarding parent to his or her leaving the area. Eggs of unknown age were examined in place by candling without moving them, to determine if they were old enough to be handled. If candling in place was not possible, we waited for 7–10 days to ensure the egg was sufficiently developed to be handled without risk to the embryo. Eggs older than seven days were candled more thoroughly by handling them within the dark of the cavity to determine fertility, age and any problems, following Delany et al. (1999). We did not access nests during the suspected laying period (to prevent potential abandonment), the calculated hatching period (to avoid disrupting a delicate process) or the week before anticipated fledging (to eliminate the chance of accidental force-fledging).

We included a cavity in our dataset if cockatoos ever showed an interest in it, as defined by at least one cockatoo entering it with its whole body at least once (referred to hereafter as 'prospected'). We also included cavities that were reported by former trappers to have been prospected by cockatoos in the past. Cavities reportedly once used by cockatoos but subsequently destroyed, filled by termites (Termitoidae) or blocked by epiphytes were recorded as 'unusable' and excluded from the dataset. We defined cavities as 'occupied/active nests' if we confirmed eggs or broods through direct access or had strong behavioural evidence that the adult cockatoos had eggs or chicks (e.g. swift changeover between partners attending the nest). Older chicks (>30 days) were often fed in the entrance and could therefore be observed directly.

2.3. Statistical analysis

To assess differences between occupied and unoccupied cavities in terms of visitation rates (daily and weekly) by nest-competitors and potential nest-predators, we used generalized linear mixed models (GLMM with package lme4 v1.1-26) fit by maximum likelihood with logit link and cavity as random effect (Bates et al., 2015; R Core Team, 2021). We created four competing models for each species combination: one with a random intercept and a random slope, one with only a random intercept, one without a random effect and one with only the random effect. We used AIC to choose between the models, and checked significance of the random effect with an ANOVA. We report the coefficient $\beta \pm$ standard error. For the comparisons between occupied and unoccupied cavities, we excluded the occupying species as visitors for the duration of the nesting attempt including a period of one month before and after use unless this overlapped with the exclusion period of a different species' nesting attempt. In case of overlap, the species to be excluded changed half-way between the occupied periods.

3. Results

3.1. Nest trees and cameras

In total, we investigated 95 cavities as cockatoo nest-sites over the four-year period (with 266 monitored cavity-seasons). Of these, 36 cavities with repeated cockatoo activity were monitored more intensively, for a total of 128 cavity-seasons, with 103 occupied by cockatoos or their competitors, 13 unusable and 12 apparently available but unused. All investigated cavities were in large mature trees (minimum diameter at breast height = 82 cm, minimum height = 27 m), with 67% in *Tetrameles* sp. (Tetramelaceae), 13% in *Chisocheton* sp. (Meliaceae), and 8% in *Palaquium* sp. (Sapotaceae) (Fig. 2). Only 11% were in dead trees.

Over 30 months spanning three breeding seasons, a total of 5675 camera-days of monitoring were undertaken at twelve cavities (range 115–889 days). We excluded three other, unoccupied cavities (381 camera-days) owing to poor cavity quality, unmonitored alternative entrances and safety reasons. A total of 27 animal species—five parrots, a hornbill, three owls, four raptors, a dove, five passerines, three reptiles and five mammals—were photographed near the cavity entrances. Of these, 16 were hole-nesters, so we considered them for the role of cavity-competitors. Eggs or chicks featured in the diets of 14 of these species, which we therefore investigated as potential nest-predators of parrots.

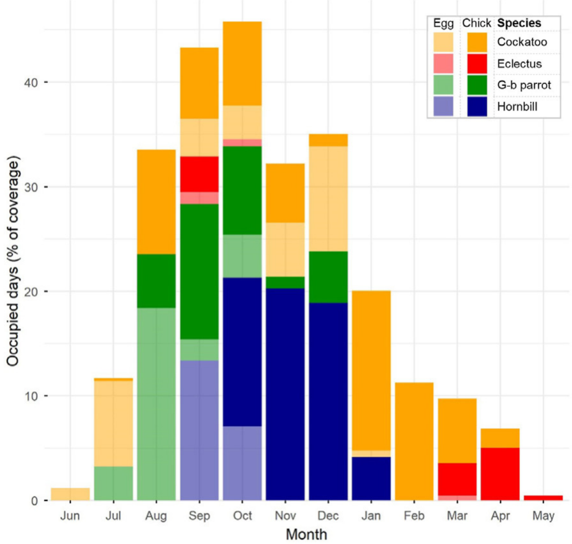

Fig. 3. Seasonality of cavity-nesting monitored by camera-traps over 2.5 years (November 2016–April 2019) in the forested areas of central and western Sumba. Paler colours indicate days at egg stage, darker colours chick stage. Data were pooled across three breeding seasons and twelve cavities that had cockatoos prospecting them at some point. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 2. (A) Cockatoo nest tree found with traditional climbing set-up prepared for harvest by illegal trappers in 2018; (B) guide demonstrating traditional Sumba cockatoo tree-climbing method in 2017; (C) twig with nylon nooses left behind by cockatoo trappers after use at a cockatoo roost site in 2018. (Photos A,B: Charles U. Daula used with permission, C: AR).

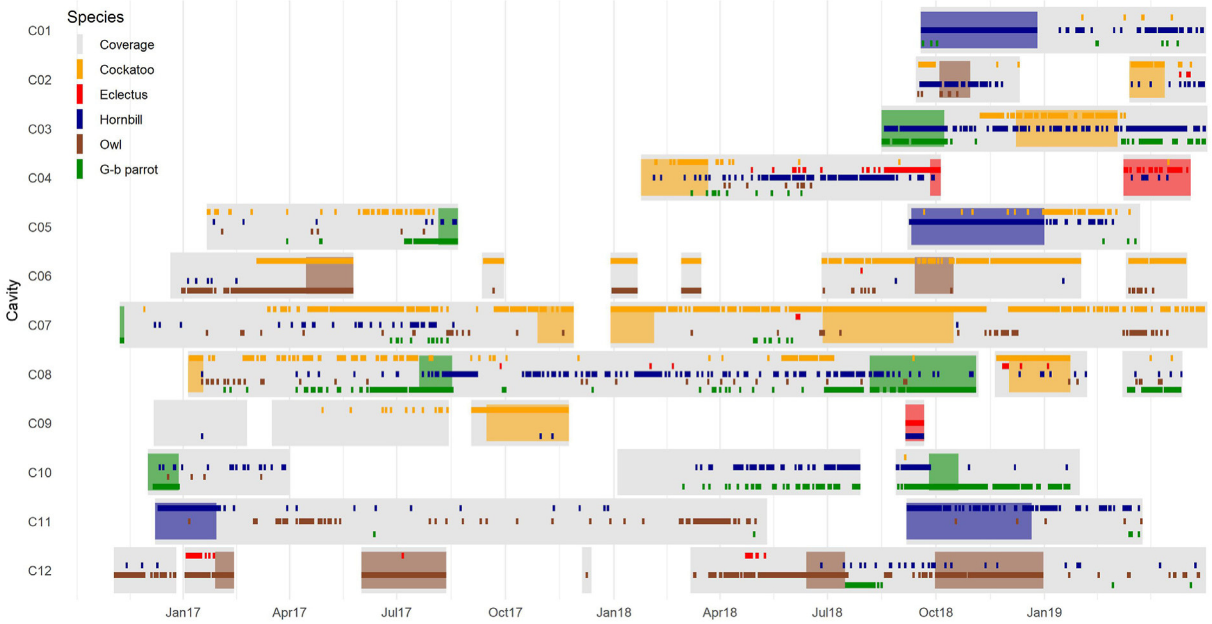

Fig. 4. Visitors and occupants of nesting cavities monitored by camera-traps over three breeding seasons, November 2016–April 2019, in the forested areas of central and western Sumba. Each row represents one of twelve cavities with cockatoo interest. Small narrow, darker bars indicate visits. Broad paler bars indicate that the respective species occupied the cavity, i.e. had either eggs or chicks within. Grey background indicates the days covered by camera footage.

3.2. *Seasonal cavity use across the community*

Cockatoo breeding activity was observed in almost every month of the year, but the laying stage was limited to late June to early December and fledging only occurred from January to April (Fig. 3). Most chicks fledged during the rainy season. Owls, although not included in the graph, were found breeding in every month of the year (Fig. 4).

3.3. *Visitation rates and competition*

Overall visitation rates and species visiting varied considerably across cavities (Fig. 4, $\chi^2 = 54.3$, df = 3, $p < 0.001$). Six of the twelve cavities were occupied by two different species during the study period, and all of them were visited by at least three of the five large cavity-nesters (Fig. 4). Competing species visited occupied cavities less often than unoccupied ones (GLMM fit by maximum likelihood, $\beta = -0.29 \pm 0.05$ [SE], $p < 0.001$).

Direct confrontations between competing hole-nesting species caught by the camera-traps were relatively rare (30 occasions in 5675 cavity-days monitored, Table 2, Fig. 5), as many directly observed conflicts took place in the tops of the nest trees and were often decided vocally without the intruders approaching the cavities. The majority of camera-trapped confrontations were won by Sumba Hornbill (*Rhyticeros everetti*) (two against cockatoos, one against Sumba Eclectus, one against a conspecific and three against Great-billed Parrots *Tanygnathus megalorynchos*) and by owls (five against cockatoos and one against Sumba Eclectus). Confrontations between cockatoos and Great-billed Parrots were the most common of all observed confrontations, with cockatoos dominating in 14 of 16 interactions. Great-billed Parrots were the species to lose most confrontations.

Table 2
Tallies of wins and losses in direct confrontations between nest-cavity competitors captured by camera-traps at 12 cavities in 5675 camera-days. Interspecific confrontations in other parts of the tree were not captured by the cameras aimed at the cavity entrances and are therefore not included here.

Displaced taxon	Dominant taxon					
	Hornbill	Cockatoo	Eclectus	Great-billed Parrot	Owls	Total losses
Sumba Hornbill	1	0	0	0	0	1
Citron-crested Cockatoo	2	0	0	2	9	13
Sumba Eclectus	1	0	1	0	0	2
Great-billed Parrot	3	14	0	1	0	18
Owl spp.	0	1	0	0	0	1
Total wins	7	15	1	3	9	35

3.4. *Predation*

Among the animals that could theoretically prey on the monitored nests, 14 taxa were captured by our cameras near the nest entrances (Fig. 6): the Sumba Hornbill visitation rate was 5.8 (i.e. birds visited on average 5.8 days per monitored 30 days), Brown Goshawk (*Accipiter fasciatus*; including other *Accipiter* spp.) 0.1; Eastern Buzzard (*Buteo japonicus*) 0.01; two falcons (Spotted Kestrel *Falco moluccensis*, Australian Hobby *F. longipennis*) 0.65; three owls (Sumba Boobook *Ninox rudolfi* 1.1, Least Boobook *N. sumbaensis* 0.01, Barn Owl *Tyto alba* 2.8); three mammals (Long-tailed Macaque *Macaca fascicularis* 0.4; Common Palm Civet *Paradoxurus hermaphroditus* 0.01, and rats *Rattus* spp. 0.06); and three reptiles (Tokay Gecko *Gecko gecko* 0.6, Emerald Tree Skink *Lamprolepis smaragdina* 0.4, Lesser Sundas Bronzeback Snake *Dendrelaphis inornatus* 0.01) (Marini and Melo, 1998). Among these, the hornbill, owls and falcons likely have a dual potential as both nest competitors and nest predators. Hornbills visited nests occupied by owls and parrots as often as unoccupied nests (GLMM $\beta = -0.05 \pm 0.20$ [SE], $p = 0.77$), whereas hawks visited unoccupied nests more frequently than occupied owl and parrot nests ($\beta = -0.48 \pm 0.18$, $p = 0.007$). Geckos and skinks visited unoccupied cavities more often than those occupied by parrots or owls ($\beta = -1.15 \pm 0.33$, $p < 0.001$). While we found no evidence for predation by reptiles, eggs of both lizard species often occurred in cavities unused by birds. Similarly, owls visited active parrot nests less than unoccupied cavities ($\beta = -0.69 \pm 0.28$, $p = 0.001$). Weekly predator visit rates varied between cavities (Fig. 6), and cavity identity featured as a significant

Fig. 5. Direct evidence of competitive interaction at Citron-crested Cockatoo cavities: (A) Sumba Eclectus attempting to take over a cockatoo cavity; (B) Sumba Hornbill and Great-billed Parrot competing for a cavity used by Citron-crested Cockatoos in the previous season; (C) Sumba Hornbill displacing a cockatoo from its prospected cavity; (D) a cockatoo repeatedly evicting a Great-billed Parrot from its cavity before either laid eggs; (E) Sumba Hornbill attempting to take over an active Great-billed Parrot nest; (F) cockatoo finding a Barn Owl inside the cavity the cockatoo pair had been prospecting for weeks, while a second cavity occupied by a different cockatoo pair can be seen below bordering the top left edge of the image. (Photos: camera-traps deployed, programmed, serviced and collected by team AR, BAS, Romy ND Limu, used with permission).

random factor in all GLMMs above. Mammals were not recorded visiting any active nests and only appeared on 20 occasions at the entrances of unoccupied nests. During nest watches we often encountered troupes of macaques in the vicinity, which triggered alarm calls from parrots on three occasions, but no predation attempts were observed. According to incidental direct observations and camera-trap footage of direct confrontations, only hornbills and hawks are a threat to active parrot nests.

3.5. Cockatoo nesting attempts

Among the 95 monitored cavities, 12 nest-sites became active cockatoo nests during the study period (five found from trapper reports, six from own fieldwork and one cavity from Burung Indonesia's records, the latter occupied thrice). Fifteen nest attempts took place in these cavities, 10 successful and five not (Table 1, Table 3). Eggs were laid between the last week of June and first week of December (median date = 14 November). Chicks fledged between October and April (median date = 24 January), aged 55–70 days ($n = 3$ cavities with lay dates known to ± 2 days). Causes of nest failure were uncertain but evidence suggested nest takeover by a hornbill during incubation, interference by a Sumba Boobook at chick stage, falling of a dead cavity tree soon after laying, unknown predation shortly before fledging, and trapping of parents and chick.

Although most cavities not claimed early in the season by competitors were prospected by cockatoos (49 of 79 monitored cavity-seasons), repeated occupancy of cavities was low for cockatoos: only one cavity hosted active cockatoo nests in two consecutive years (the first year's nest having failed, Table 4). Cockatoos tended to nest only once in individual cavities, whereas other species nested multiple times in the same cavity, although the difference was not significant ($\chi^2 = 2.0$, df = 1, $p = 0.15$).

4. Discussion

Productivity in the Citron-crested Cockatoo was very difficult to detect, and may be alarmingly low. During around 300 person-days spent searching within approximately 60% of the former Manupeu Tanah Daru National Park and the other remnant forest patches with known cockatoo presence in Central and West Sumba, just ten successful nests of the species were found, involving just twelve fledged young. No doubt we missed nesting attempts within the study area, but this was not due to a lack of search effort. Similar patterns of strikingly low output despite seemingly high opportunity have been found in previous studies: 47 nests found, 16 'occupied' (Marsden and Jones, 1997); 62 sites monitored, 24 visited by cockatoos, 8 with repeated activity and only 1 successful nest (Walker et al., 2005); and 10 trees monitored, 7 with cockatoo activity and 2 active nests (Djawarai et al., 2014). Even allowing that cockatoos

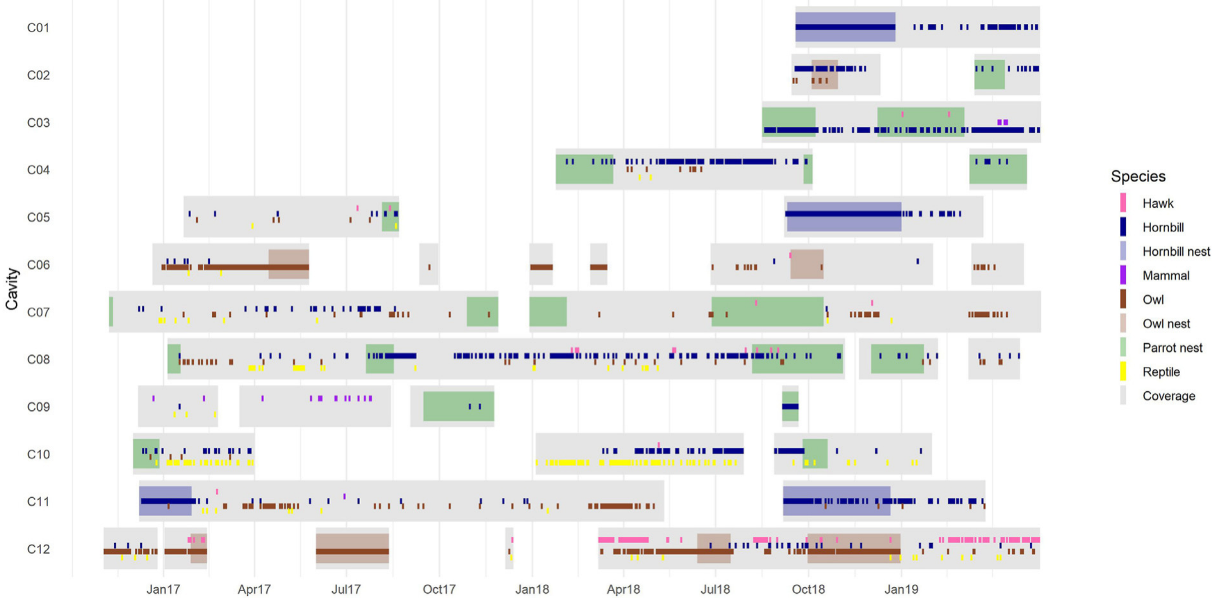

Fig. 6. Visits to nest-cavities by potential predators recorded by 12 camera-traps at cavity entrances. Grey background indicates days monitored by camera-traps; periods with active nests (with eggs or chicks) are shaded in the colour of the occupying species. Species recorded as occupants or predators include (parrots): Citron-crested Cockatoo (*Cacatua citrinocristata*), Sumba Eclectus (*Eclectus cornelia*) and Great-billed Parrot (*Tanygnathus megalorynchos*); (owls): Sumba Boobook (*Ninox rudolfi*), Least Boobook (*Ninox sumbaensis*) and Barn Owl (*Tyto alba*); (hornbill) Sumba Hornbill (*Rhyticeros everetti*); (hawks): Eastern Buzzard (*Buteo japonicus*), Brown Goshawk (*Accipiter fasciatus*) (and other *Accipiter* spp.), Spotted Kestrel (*Falco moluccensis*) and Australian Hobby (*F. longipennis*); (mammals): Long-tailed Macaque (*Macaca fascicularis*), Common Palm Civet (*Paradoxurus hermaphroditus*) and rats *Rattus* sp.; (reptiles): Tokay Gecko (*Gecko gecko*) and Emerald Tree Skink (*Lamprolepis smaragdina*), Lesser Sundas Bronzeback Snake (*Dendrelaphis inornatus*). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Summary of Citron-crested Cockatoo (*Cacatua citrinocristata*) nest success and timing over four breeding seasons on Sumba.

	2015–2016	2016–2017	2017–2018	2018–2019	All 4 seasons
No. successful nests	1	3	3	3	10
No. fledglings	2	4	5	4	12
Observed nest failures	4	0	1	0	5
No. nests found at egg stage	2	0	1	2	5
Laying period (calculated)	Sep–Nov	Nov	Oct–Jan	Jun–Dec	Jun–Jan
Last fledging date	Mar	Mar	Apr	Mar	Apr

are K-selected species which offset low breeding rates against long life-spans (Murphy et al., 2003), this circumstance appears too extreme to represent a stable balance between these two parameters. The possible factors underlying the situation therefore needed to be examined. These clearly involve the natural pressures from nest competition and the anthropogenic pressures from exploitation for trade and habitat degradation.

Nest competition appears to be intense in terms of both the richness of the cavity-nesting community and our direct observations of nest uptake. A more species-rich community of large cavity-nesting species exists on Sumba than on nearby islands. Our work and earlier studies on Sumba (Marsden and Jones, 1997; Walker et al., 2005; Hidayat, 2012) found many instances of multiple nests in the same tree—both multiple cavities frequented by different cockatoo pairs and mixed ‘colonies’ involving Sumba Eclectus and Great-billed Parrot. Competition between the three large parrots was intense in the prospecting phase, as in other communities of large parrots (Saunders et al., 1982, 2020; Heinsohn et al., 2003; Igag et al., 2019), but there was no evidence that any parrot nests failed due to interference from other parrots. We also saw no intraspecific competition among cockatoos although two pairs attempted to nest in two cavities in the same tree, which would have led to aggression in some other parrot species (e.g. Renton, 2004). The synergies of joint nest site guarding may be an advantage for all neighbouring parrot pairs once cavity ownership has been established (Danchin and Wagner, 1997; Rolland et al., 1998), and indeed, colonial nesting may have evolved in other parrot species to reduce predation risk (Masello and Quillfeldt, 2002; Heinsohn and Legge, 2003). However, it is still unclear what happens when parrots and owls prospect the same cavity alternately each day and night; in the four cases we observed (one monitored by camera), none of the species managed to establish an active nest. Hornbill interference at cockatoo nests, whether for competition or predation (as in other hornbill species: Pierce and Pobprasert, 2013; Loong et al., 2021), appeared to cause nest failure and stress in cockatoos.

By contrast, the threat of predation at cockatoo nests on Sumba appears surprisingly low. Mammals, reptiles and hawks seem to have minor roles as predators at most, and even hornbills rarely destroyed nest contents despite very frequent visits to parrots nests. Cockatoos are known to protect their nest sites well (e.g. Rowley, 1990; Rowley and Chapman, 1991; Murphy et al., 2003), and our observations confirmed this: during incubation and early brooding, one parent usually stayed in the nest until the other arrived to take over duties, and once the chicks were older (> ca 3 weeks) we frequently found the guarding parent perched near the nest. Moreover, cockatoos remove foliage around the entrance of potential nest holes, and vines and small branches connecting theirs to neighbouring trees (Walker et al., 2005; Djawarai et al., 2014; Hidayat and Kayat, 2020), presumably thereby

Table 4

Fate of monitored cavities with past or present cockatoo interest. **ID** cavity identification number, **C p** prospected by cockatoos, **C s** successful cockatoo nest attempt, **C f** failed cockatoo nest attempt, **E** occupied by Sumba Eclectus, **H** occupied by Sumba Hornbill, **B** occupied by Sumba Boobook, **T** occupied by Barn Owl, **G** occupied by Great-billed Parrot, **K** occupied by Spotted Kestrel, **u** cavity was unusable due to e.g. structural damage, epiphytes, termites, bees, **X** no occupation detected despite some monitoring, **grey cell** site not checked, or not sufficiently to determine status; **Camera**: camera-trap installed on the tree (yes/no), **Climbed:** nest contents checked directly by climbing (yes/no), **Found**: **BI** cavity was part of Burung Indonesia's dataset before 2014, **OF** cavity found by own fieldwork, **FT** cavity shown by former trappers; Breeding season headings contain two years because they span the turn of the year. The 2014/15 breeding season data collected by the BI team are included here to show prospected and failed sites that were subsequently included in regular monitoring. The totals given in the text only cover the four seasons 2015–2019.

ID	2014/15	2015/16	2016/17	2017/18	2018/19	Camera	Climbed	Found
1[1]	C p	C f	C s	C p/G	C s	y	y	BI
2[2]	C f	B	K	G	T	y	y	BI
3[2]	C p	u	u	u	u	n	n	BI
4[3]	C p	u	u	u	u	n	y	BI
5[2]	C p	u	u	u	u	n	n	OF
6[2]	C p	H/E	H/E	H/E	H/E	n	y	BI
7[1]		C s	C p/G	G	E	y	y	OF
8[2]		C f	H	G/H	H	y	y	OF
9[1]		C p/B	C p/T	C p/T	C p/B	y	y	OF
10[2]		C p	C p	X	C p	y	y	OF
11[2]		C p	C p	G	X	n	n	OF
12[2]		C p	G	G	G	y	y	OF
13[4]		X	C p/G	C p	X	n	n	BI
14[1]		G	G	G	G	n	y	BI
15[1]		T	T	T	T	n	n	OF
16[5]		C p/T	X	T		y	y	BI
17[2]		C p	X	X		n	n	OF
18[2]		C p				n	n	FT
19[2]		C p				n	n	OF
20[2]		C p				n	y	OF
21[2]			C s	G	G/C f	y	y	FT
22[6]			C s	G	G	n	n	FT
23[2]			C p/E	C s	C p	n	n	OF
24[2]			C p	C p	C p	n	y	FT
25[6]			C p	X	X	n	y	FT
26[2]			C p	X		n	y	FT
27[2]				C s	X	n	n	OF
28[7]				C f	u	n	n	OF
29[2]				C s	E	y	y	FT
30[8]				C p	C s	y	y	FT
31[6]				H/C p	C p	y	y	OF
32[2]				C p/K	C p/H	y	y	FT
33[2]				X	C p	y	y	FT
34[2]				C p/T		n	n	FT
35[2]					B/C s	y	y	OF
36[2]					C f	n	n	FT

Tree species: [1]*Chisocheton* sp., [2]*Tetrameles* sp., [3]*Millingtonia hortensis*, [4]*Glochidion* sp., [5]*Syzygium* sp., [6]*Palaquium* sp., [7]unknown, [9]*Artocarpus elasticus*

reducing access for potential predators (Koenig et al., 2007; Britt et al., 2014).

Considering that introduced mammals are one of the commonest causes of extinctions of island species (Howald et al., 2007; Harper and Bunbury, 2015), and that rodents, macaques and civets are all known to predate parrot nests elsewhere (e.g. Jones, 1987; Clout and Merton, 1998; Jones et al., 2013; Pierce and Pobprasert, 2013; Reuleaux et al., 2014), the lack of evidence for predation at our monitored nests is remarkable. All three mammal species were camera-trapped near (and even looking into) previously cockatoo-occupied cavities, but they never entered any cavities or disrupted any active nests monitored by cameras. By their size and body:tail ratio, the rodents were likely Pacific Rats (*Rattus exulans*) or possibly Ricefield Rats (*R. argentiventer*), both of which arrived on Sumba with early seafarers in the Holocene (Heinsohn, 2003). Long-tailed Macaques, which are common in Sumba's forests (pers. obs.), were introduced prehistorically or historically to the Lesser Sunda Islands by humans (Heinsohn, 2001; Murphy et al., 2003), suggesting that the avifauna has had time to adapt (e.g. by nest guarding) to the threat to nests that they pose. We encountered troupes of monkeys during most nest watches and during 150 (38%) of 393 bird survey point counts in forest (AR unpublished data). Macaques have been shown to predate cavity nests almost as often as open-cup nests in other contexts (Kaisin et al., 2018), so the absence of predation events in our camera-monitored cavities is interesting. A possible explanation is that *Tetrameles* sp., the preferred species for nesting (Marsden and Jones, 1997), grows very tall, often becoming emergent, and has a smooth bark, rendering access, at least by mammals, difficult.

The combination of direct and indirect evidence suggests that anthropogenic factors have a decisive limiting influence on cockatoo numbers, although this is hard to establish unequivocally. In the dense tall forests of our study area we found nests very hard to find, in large part because the behaviour of breeding cockatoos was so discreet. This may have been due to decades of trapping: Yellow-crested Cockatoo populations under known trapping pressure, e.g. on Sumbawa and Alor (Setiawan, 1996; Trainor et al., 2012), showed similar behaviour, whereas populations without recent trapping pressure, e.g. on Komodo and at one West Timor site, were almost indifferent to human presence (Imansyah et al., 2016; Reuleaux et al., 2020). On Sumba, nests higher up in the tree were less likely to be exploited by trappers than lower ones (Marsden and Jones, 1997), which could over decades select for the use of higher cavities (Eggers et al., 2005; Chen et al., 2011; Linhart et al., 2012). It is possible, however, that higher cavities are both less suitable and less abundant than lower ones, and these factors may help explain the cockatoo's pronounced fastidiousness over nest-site selection in what may be for them suboptimal breeding habitat: the ratio of prospected sites to active nests found shows that cockatoos spend much time exploring and preparing cavities before eventually rejecting them (or being displaced).

Apart from these potential indirect effects of exploitation, we also found evidence of recent cockatoo trapping (climbing set-ups, nooses and bunches of flight feathers at roosts and nests; Fig. 2) in at least twelve cases, and investigations confirmed that trapping of adults and young, although at low levels, appears to have been increasing since 2017. We saw fewer fledglings accompanying their parents to communal roosts than would be expected after a productive breeding season (Matuzak and Brightsmith, 2007; Widmann and Lacerna-Widmann, 2008). If other typical limiting factors of nest productivity—predation, infertile eggs, embryo death, malnutrition, parasites (Clout and Merton, 1998; Arendt, 2000; White et al., 2015; Stojanovic et al., 2017; Vigo-Trauco et al., 2021)—were frequent, we would expect to have found some evidence for them. Their absence leaves nest site availability and human interference as the likeliest causes for concern.

Forest loss and degradation throughout the 20th century on Sumba has certainly played a role in the cockatoo's decline (Jones et al., 1995) and constrains its current population as is common for most parrot species (e.g. Snyder et al., 2000; BirdLife International, 2021). Cavities of sufficient size for cockatoos and their competitors only form in certain tree species at maturity or in senescence. If selective logging targets the same trees for timber, forest quality as nesting habitat may be much lower than forest cover would suggest. The majority of cockatoo nests were in *Tetrameles* trees. Whether this is out of preference or a consequence of cavity availability was not examined. During field work we found no signs of *Tetrameles* logging inside the park but there was evidence for it outside the park in the other surveyed forests. Although *Tetrameles* trees are not ideal for traditional house-building, the wood is used for walls and boats (Karande, 1967; Monk et al., 1997; Djawarai et al., 2014). Sumba's long history of selective logging and forest clearance (Monk et al., 1997) may have so greatly depleted preferred timber trees that local communities now exploit suboptimal species. This may have an undetected but important effect on the cockatoo and some monitoring of *Tetrameles* utilisation may be warranted.

5. Conclusion

Based on the evidence for nest site competition and ongoing trapping accruing here, conservation actions for the Citron-crested Cockatoo should target the prevention of both trapping and further habitat deterioration or loss of old hole-bearing trees, and the provision of safe artificial nest-sites. Past conservation interventions on Sumba (Persulessy et al., 2003; Djawarai et al., 2014) and elsewhere (Ihsannudin et al., 2020; Indraswari et al., 2020; Pires et al., 2021; Sánchez-Mercado et al., 2021) show that trapping can be reduced locally by raising awareness among communities who control access to the habitat and increasing law enforcement against middlemen and traders. The most sustainable way to address nest-site shortage in the long term is the protection, restoration and re-creation of forest with large cavity-forming trees (Newton, 1994; van der Hoek et al., 2017). To date no extensive nestbox trial has been done on Sumba, so in the short term, we recommend provision of artificial nest-sites as a bridging solution. Wild parrots sometimes ignore nestboxes (e.g. Jones, 1980; Walker et al., 2001; Brightsmith and Bravo, 2006; Tatayah et al., 2007; Rocamora and Laboudallon, 2013), but there are many cases where appropriately designed and positioned nestboxes are successfully supporting threatened parrot species through a period of nest-site shortage (e.g. White et al., 2006; Cockle et al., 2010; Jones et al., 2013; Saunders et al., 2020). Accessible, known, safe nestboxes could also provide opportunities to assess the scale of nest-site shortage, allow camera placements to study productivity, exclude some competitors, and prevent illegal trapping.

Ethics statement

This research was conducted in compliance with the ethics guidelines of Manchester Metropolitan University.

Author contributions

SJM and AR conceived the idea, formulated the questions and secured the funding; AR and BAS developed the field protocol and collected the data; AR analysed the data and wrote the manuscript; SJM, NJC, and AM supervised research and contributed to the manuscript. All authors read and approved the final manuscript.

Declarartion of competing interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

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References

Agista, D., Rubyanto, D., 2001. Telaah awal status, penyebaran, dan populasi kakatua kecil jambul kuning, *Cacatua sulphurea parvula*: di Taman Nasional Komodo, Nusa Tenggara Timur. Birdlife International Indonesia Programme, Bogor, Indonesia.

Altamirano, T.A., Ibarra, J.T., Martin, K., Bonacic, C., 2017. The conservation value of tree decay processes as a key driver structuring tree cavity nest webs in South American temperate rainforests. Biodivers. Conserv. 26, 2453–2472.

Arendt, W.J., 2000. Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery. Ornitol. Neotrop. 11, 13–63.

Badan Pusat Statistik, 2016. Statistical Yearbook of Indonesia. https://www.bps.go.id. (Accessed 17 October 2017).

Badan Pusat Statistik, 2021. Statistical Yearbook of Indonesia. https://www.bps.go.id. (Accessed 20 December 2021).

van Balen, J.H., Booy, C.J.H., van Franeker, J.A., Osieck, E.R., 1982. Studies on hole-nesting birds in natural nest sites. Ardea 70, 1–24.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67, 1–48.

BirdLife International, 2021. Datazone. http://datazone.birdlife.org/. (Accessed 11 March 2021).

Bonaparte, E.B., Cockle, K.L., 2017. Nest niche overlap among the endangered Vinaceous-breasted Parrot (*Amazona vinacea*) and sympatric cavity-using birds, mammals, and social insects in the subtropical Atlantic Forest, Argentina. Condor 119, 58–72.

Brightsmith, D., Bravo, A., 2006. Ecology and management of nesting blue-and-yellow macaws (*Ara ararauna*) in mauritia palm swamps. Biodivers. Conserv. 15, 4271–4287.

Brightsmith, D.J., 2005. Competition, predation and nest niche shifts among tropical cavity nesters: phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes). J. Avian Biol. 36, 64–73.

Britt, C.R., García Anleu, R., Desmond, M.J., 2014. Nest survival of a long-lived psittacid: scarlet macaws (*Ara macao cyanoptera*) in the maya biosphere reserve of Guatemala and chiquibul forest of Belize. Condor 116, 265–276.

Cahill, A.J., Walker, J.S., Marsden, S.J., 2006. Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea citrinocristata* in Indonesia after 10 years of international trade control. Oryx 40, 161–167.

Chen, J.-N., Liu, N.-F., Yan, C., An, B., 2011. Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance. J. Ornithol. 152, 603–608.

Clout, M.N., Merton, D.V., 1998. Saving the kakapo: the conservation of the world's most peculiar parrot. Bird. Conserv. Int. 8, 281–296.

Cockle, K.L., Martin, K., Drever, M.C., 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biol. Conserv. 143, 2851–2857.

Collar, N.J., Eaton, J.A., Sykes, B., 2017. Conservation and the redaction of locality data. BirdingASIA 28, 3–4.

Collar, N.J., Marsden, S.J., 2014. The subspecies of yellow-crested cockatoo *Cacatua sulphurea*. Forktail 30, 23–27.

Collias, N.E., 1964. The evolution of nests and nest-building in birds. Am. Zool. 4, 175–190.

Danchin, E., Wagner, R.H., 1997. The evolution of coloniality: the emergence of new perspectives. Trends Ecol. Evol. 12, 342–347.

Delany, M.E., Tell, L.A., Millam, J.R., Preisler, D.M., 1999. Photographic candling analysis of the embryonic development of orange-winged amazon parrots (*Amazona amazonica*). J. Avian Med. Surg. 13, 116–123.

Djawarai, Y., Bashari, H., Siregar, B., Widyanto, A., 2014. The breeding ecology of Sumba Cockatoo *Cacatua Sulphurea Citrinocristata* in Manupeu Tanadaru National Park and surrounding, Sumba. Burung Indonesia. Bogor, Indonesia.

Eaton, J.A., van Balen, S.B., Brickle, N.W., Rheindt, F.E., 2016. Birds of the Indonesian Archipelago Greater Sundas and Wallacea. Lynx Ediciones, Barcelona.

Eggers, S., Griesser, M., Nystrand, M., Ekman, J., 2005. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. Proc. R. Soc. B. Biol. Sci. 273, 701–706.

González, J.A., 2003. Harvesting, local trade, and conservation of parrots in the Northeastern Peruvian Amazon. Biol. Conserv. 114, 437–446.

Gutzat, F., Dormann, C.F., 2018. Decaying trees improve nesting opportunities for cavity-nesting birds in temperate and boreal forests: a meta-analysis and implications for retention forestry. Ecol. Evol. 8, 8616–8626.

Harper, G.A., Bunbury, N., 2015. Invasive rats on tropical islands: their population biology and impacts on native species. Glob. Ecol. Conserv. 3, 607–627.

Heinsohn, R., Legge, S., 2003. Breeding biology of the reverse-dichromatic, co-operative parrot *Eclectus roratus*. J. Zool. 259, 197–208.

Heinsohn, R., Murphy, S., Legge, S., 2003. Overlap and competition for nest holes among eclectus parrots, palm cockatoos and sulphur-crested cockatoos. Aust. J. Zool. 51, 81–94.

Heinsohn, R., Zeriga, T., Murphy, S., Igag, P., Legge, S., Mack, A.L., 2009. Do Palm Cockatoos (*Probosciger aterrimus*) have long enough lifespans to support their low reproductive success? Emu 109, 183–191.

Heinsohn, T.E., 2001. Human influences on vertebrate zoogeography: animal translocation and biological invasions across and to the east of Wallace's Line. In: Metcalfe, I., Smith, J.M.B., Morwood, M., Davidson, I. (Eds.), Faunal and Floral Migrations and Evolution in SE Asia-Australasia. CRC Press, Boca Raton, US, pp. 153–170.

Heinsohn, T.E., 2003. Animal translocation: long-term human influences on the vertebrate zoogeography of Australasia (natural dispersal versus ethnophoresy). Austral. Zool. 32, 351–376.

Hidayat, O., 2012. Lubang masa depan. Biodivers. Indon. 2, 110–118.

Hidayat, O., Kayat, K., 2020. Pendekatan preferensi habitat dalam penyusunan strategi konservasi in situ Kakatua Sumba (*Cacatua sulphurea citrinocristata*, Fraser 1844). J. Penelit. Hutan dan Konserv. Alam. 17, 113–126.

van der Hoek, Y., Gaona, G.V., Martin, K., 2017. The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world. Divers. Distrib. 23, 1120–1131.

Howald, G., Donlan, C.J., Galván, J.P., Russell, J.C., Parkes, J., Samaniego, A., et al., 2007. Invasive rodent eradication on islands. Conserv. Biol. 21, 1258–1268.

Igag, P., Mack, A.L., Legge, S., Heinsohn, R., 2019. Breeding biology of three large, sympatric rainforest parrots in New Guinea: Palm Cockatoo, Pesquet's Parrot and Eclectus Parrot. Emu 119, 196–204.

Ihsannudin, I., Hidayat, K., Sukesi, K., Yuliati, Y., 2020. Perception of the local community toward the yellow-crested cockatoo (*Cacatua sulphurea abbotti*), a critically endangered species in Masakambing Island, Indonesia. Geografia 16, 1–14.

Imansyah, M.J., Purwandana, D., Ariefiandy, A., Benu, Y.J., Jessop, T.S., Trainor, C.R., 2016. Valley-floor censuses of the critically endangered yellow-crested cockatoo *Cacatua sulphurea occidentalis* on Komodo island, East Nusa Tenggara province, Indonesia, point to a steep population decline over a six-year period. Forktail 32, 66–72.

Indraswari, K., Friedman, R.S., Noske, R., Shepherd, C.R., Biggs, D., Susilawati, C., et al., 2020. It's in the news: characterising Indonesia's wild bird trade network from media-reported seizure incidents. Biol. Conserv. 243, 108431.

Jones, C.G., 1980. Parrot on the way to extinction. Oryx 15, 350–354.

Jones, C.G., 1987. The larger native landbirds of Mauritius. In: Diamon, A.W. (Ed.), Studies of Mascarene Island Birds. Cambridge University Press, Cambridge, UK, pp. 271–300.

Jones, C.G., Malham, J., Reuleaux, A., Richards, H.A., Raisin, C., Tollington, S., et al., 2013. Echo parakeet *Psittacula eques* perruche de Maurice. In: Safford, R., Hawkins, F. (Eds.), The Birds of Africa. Vol. VIII. Birds of the Malagasy Region. A&C Black, Madagascar, pp. 433–438.

Jones, M.J., Linsley, M.D., Marsden, S.J., 1995. Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia. Bird. Conserv. Int. 5, 21–52.

Kaisin, O., Gazagne, E., Savini, T., Huynen, M.-C., Brotcorne, F., 2018. Foraging strategies underlying bird egg predation by macaques: a study using artificial nests. Am. J. Primatol. 80, e22916.

Karande, A.A., 1967. Timber, *Tetrameles nudiflora* R., resistant to teredid borers in Bombay Harbour. Nature 213, 105.

Koenig, S.E., Wunderle, J.M., Enkerlin-Hoeflich, E.C., 2007. Vines and canopy contact: a route for snake predation on parrot nests. Bird. Conserv. Int. 17, 79–91.

Lack, D., 1968. Ecological Adaptations for Breeding in Birds. Methuen & Co Ltd, London, UK.

Linhart, P., Fuchs, R., Poláková, S., Slabbekoorn, H., 2012. Once bitten twice shy: long-term behavioural changes caused by trapping experience in willow warblers *Phylloscopus trochilus*. J. Avian Biol. 43, 186–192.

Loong, S., Sin, Y.C.K., Johns, P., Plowden, T., Yong, D.L., Lee, J., et al., 2021. Nest predation by oriental pied hornbills *Anthracoceros albirostris* in urban Singapore. BirdingASIA 35, 86–91.

Marini, M.Â., Melo, C., 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. Condor 100, 395–399.

Marsden, S.J., 1995. The Ecology and Conservation of the Parrots of Sumba, Buru and Seram, Indonesia. Ph.D thesis. Manchester Metropolitan University, Manchester, UK.

Marsden, S.J., Jones, M.J., 1997. The nesting requirements of the parrots and hornbill of Sumba, Indonesia. Biol. Conserv. 82, 279–287.

Martin, R.O., Perrin, M.R., Boyes, R.S., Abebe, Y.D., Annorbah, N.D., Asamoah, A., et al., 2014. Research and conservation of the larger parrots of Africa and Madagascar: a review of knowledge gaps and opportunities. Ostrich 85, 205–233.

Masello, J.F., Pagnossin, M.L., Sommer, C., Quillfeldt, P., 2006. Population size, provisioning frequency, flock size and foraging range at the largest known colony of Psittaciformes: the Burrowing Parrots of the north-eastern Patagonian coastal cliffs. Emu 106, 69–79.

Masello, J.F., Quillfeldt, P., 2002. Chick growth and breeding success of the Burrowing Parrot. Condor 104, 574–586.

Matuzak, G.D., Brightsmith, D.J., 2007. Roosting of Yellow-naped Parrots in Costa Rica: estimating the size and recruitment of threatened populations. J. Field Ornithol. 78, 159–169.

Monk, K., De Fretes, Y., Reksodiharjo-Lilley, G., 1997. Ecology of Nusa Tenggara and Maluku. Oxford University Press, Oxford, UK.

Monterrubio, T., Enkerlin-Hoeflich, E., Hamilton, R.B., 2002. Productivity and nesting success of thick-billed parrots. Condor 104, 788–794.

Moorhouse, R., Greene, T., Dilks, P., Powlesland, R., Moran, L., Taylor, G., et al., 2003. Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: reversing the decline of a threatened New Zealand parrot. Biol. Conserv. 110, 33–44.

Murphy, S., Legge, S., Heinsohn, R., 2003. The breeding biology of palm cockatoos (*Probosciger aterrimus*): a case of a slow life history. J. Zool. 261, 327–339.

Nandika, D., Agustina, D., 2012. Few and far between. Saving the yellow-crested cockatoos. Psitta Scene 24, 130–134.

Nandika, D., Mulyani, Y.A., Prawiradilaga, D.M., Agustina, D., 2020. Monitoring of *Cacatua sulphurea abbotti* in Masakambing island, Indonesia. Biotropia Southeast Asian J. Trop. Biol. 27, 271–281.

Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biol. Conserv. 70, 265–276.

Nilsson, S.G., 1986. Evolution of hole-nesting in birds: on balancing selection pressures. Auk 103, 432–435.

Olah, G., Butchart, S.H.M., Symes, A., Guzmán, I.M., Cunningham, R., Brightsmith, D.J., et al., 2016. Ecological and socio-economic factors affecting extinction risk in parrots. Biodivers. Conserv. 25, 205–223.

Persulessy, Y.E., Djawarai, Y.B., Marut, R., 2003. Survei populasi dan distribusi kakatua-kecil jambul-kuning *Cacatua sulphurea citrinocristata* dan empat jenis paruh bengkok lain di Pulau Sumba. BirdLife Indonesia/ZGAP, Bogor, Indonesia.

PHPA, L.I.P.I., BirdLife International-IP, 1998. Species Recovery Plan Yellow-Crested Cockatoo. PHPA/LIPI/BirdLife International-Indonesia Programme, Bogor, Indonesia.

Pierce, A.J., Pobprasert, K., 2013. Nest predators of southeast Asian evergreen forest birds identified through continuous video recording. Ibis 155, 419–423.

Pires, S.F., 2012. The illegal parrot trade: a literature review. Global Crime 13, 176–190.

Pires, S.F., Olah, G., Nandika, D., Agustina, D., Heinsohn, R., 2021. What drives the illegal parrot trade? Applying a criminological model to market and seizure data in Indonesia. Biol. Conserv. 257, 109098.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Renton, K., 2004. Agonistic interactions of nesting and nonbreeding macaws. Condor 106, 354–362.

Reuleaux, A., Richards, H., Payet, T., Villard, P., Waltert, M., Bunbury, N., 2014. Breeding ecology of the Seychelles black parrot *Coracopsis barklyi*. Ostrich 85, 255–265.

Reuleaux, A., Siregar, B.A., Collar, N.J., Panggur, M.R., Mardiastuti, A., Jones, M.J., et al., 2020. Protected by dragons: density surface modeling confirms large population of the critically endangered Yellow-crested Cockatoo on Komodo Island. Condor 122, duaa042.

Ribeiro-Silva, L., Perrella, D.F., Biagolini Jr., C.H., Zima, P.V.Q., Piratelli, A.J., Schlindwein, M.N., et al., 2018. Testing camera traps as a potential tool for detecting nest predation of birds in a tropical rainforest environment. Zoologia 35, 1–8.

Richardson, T.W., Gardali, T., Jenkins, S.H., 2009. Review and meta-analysis of camera effects on avian nest success. J. Wildl. Manag. 73, 287–293.

Rocamora, G., Laboudallon, V., 2013. Seychelles black parrot *Coracopsis barklyi*. In: Safford, R., Hawkins, F. (Eds.), The Birds of Africa. Vol. VIII. Birds of the Malagasy Region. Madagascar, Seychelles, Comoros, Mascarenes. A&C Black, Madagascar, pp. 445–447.

Rolland, C., Danchin, E., de Fraipont, M., 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. Am. Nat. 151, 514–529.

Rowley, I., 1990. Behavioural Ecology of the Galah, *Eolophus roseicapillus*. Surrey Beatty & Sons, New South Wales, Australia.

Rowley, I., Chapman, G., 1991. The breeding biology, food, social organisation, demography and conservation of the Major Mitchell or Pink Cockatoo, *Cacatua leadbeateri*, on the margin of the Western Australian Wheatbelt. Aust. J. Zool. 39, 131–142.

Sánchez-Mercado, A., Ferrer-Paris, J.R., Rodríguez, J.P., Tella, J.L., 2021. A literature synthesis of actions to tackle illegal parrot trade. Diversity 13, 191.

Sanders, M.D., Maloney, R.F., 2002. Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. Biol. Conserv. 106, 225–236.

Saunders, D.A., Dawson, R., Mawson, P.R., Cunningham, R.B., 2020. Artificial hollows provide an effective short-term solution to the loss of natural nesting hollows for Carnaby's Cockatoo *Calyptorhynchus latirostris*. Biol. Conserv. 245, 108556.

Saunders, D.A., Smith, G.T., Rowley, I., 1982. The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. Wildl. Res. 9, 541–556.

Schaaf, A.A., García, C.G., Ruggera, R.A., Tallei, E., Vivanco, C.G., Rivera, L., et al., 2021. Influence of logging on nest density and nesting microsites of cavity-nesting birds in the subtropical forests of the Andes. Forestry 95, 73–82.

Schaaf, A.A., Ruggera, R.A., Vivanco, C.G., Tallei, E., Benavidez, A., Albanesi, S., et al., 2020. Tree use, niche breadth and overlap for excavation by woodpeckers in subtropical piedmont forests of northwestern Argentina. Acta Ornithol 55, 111–119.

Setiawan, I., 1996. The Status of *Cacatua Sulphurea Parvula* in Nusa Penida, Bali, and Sumbawa. PHPA/BirdLife International, Bogor, Indonesia.

Shoemaker, K.T., Breisch, A.R., Jaycox, J.W., Gibbs, J.P., 2013. Reexamining the minimum viable population concept for long-lived species. Conserv. Biol. 27, 542–551.

Snyder, N.F.R., McGowan, P., Gilardi, J., Grajal, A., 2000. Parrots. Status Survey and Conservation Action Plan 2000-2004. IUCN, Oxford, UK.

Spoon, T.R., 2006. Parrot reproductive behavior, or who associates, who mates, and who cares. In: Luescher, A. (Ed.), Manual of Parrot Behavior. Blackwell Publishing Ltd, Ames, Iowa US, pp. 63–78.

Stattersfield, A.J., Crosby, M.J., Long, A.J., Wege, D.C., 1998. Endemic bird areas of the world: priorities for biodiversity conservation. BirdLife Conservation Series 7. BirdLife International.

Stojanovic, D., Alves, F., Cook, H., Crates, R., Heinsohn, R., Peters, A., et al., 2017. Further knowledge and urgent action required to save Orange-bellied Parrots from extinction. Emu 118, 126–134.

Tatayah, R.V.V., Malham, J., Haverson, P., Reuleaux, A., Van de Wetering, J., 2007. Design and provision of nest boxes for echo parakeets *Psittacula eques* in Black River Gorges National Park, Mauritius. Conserv. Evid. 4, 16–19.

Trainor, C.R., Verbelen, P., Johnstone, R.E., 2012. The avifauna of Alor and Pantar, Lesser Sundas, Indonesia. Forktail 28, 77–92.

Valle, S., Collar, N.J., Harris, W.E., Marsden, S.J., 2018. Trapping method and quota observance are pivotal to population stability in a harvested parrot. Biol. Conserv. 217, 428–436.

Vigo-Trauco, G., Garcia-Anleu, R., Brightsmith, D.J., 2021. Increasing survival of wild macaw chicks using foster parents and supplemental feeding. Diversity 13, 121.

Walker, J.S., Cahill, A.J., Marsden, S.J., 2001. The nesting ecology of Yellow-crested Cockatoo *Cacatua Sulphurea* on Sumba and the potential for using artificial nest sites to increase recruitment. Preliminary Report 2001. Manchester Metropolitan University, Manchester, UK.

Walker, J.S., Cahill, A.J., Marsden, S.J., 2005. Factors influencing nest-site occupancy and low reproductive output in the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea* on Sumba, Indonesia. Bird. Conserv. Int. 15, 347–359.

White, K.L., Eason, D.K., Jamieson, I.G., Robertson, B.C., 2015. Evidence of inbreeding depression in the critically endangered parrot, the kakapo. Anim. Conserv. 18, 341–347.

White, T.H.J., Brown, G.G., Collazo, J.A., 2006. Artificial cavities and nest site selection by Puerto Rican Parrots: a multiscale assessment. Avian Conserv. Ecol. 1, 5.

Widmann, P., Lacerna-Widmann, I.D., 2008. The cockatoo and the community: ten years of Philippine Cockatoo Conservation Programme. BirdingASIA 10, 23–29.

Wungo, E., 2011. Laporan survei populasi paruh bengkok terancam punah *Cacatua sulphurea citrinocristata*, Sumba, Nusa Tenggara Timur. Burung Indonesia, Bogor, Indonesia.