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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,

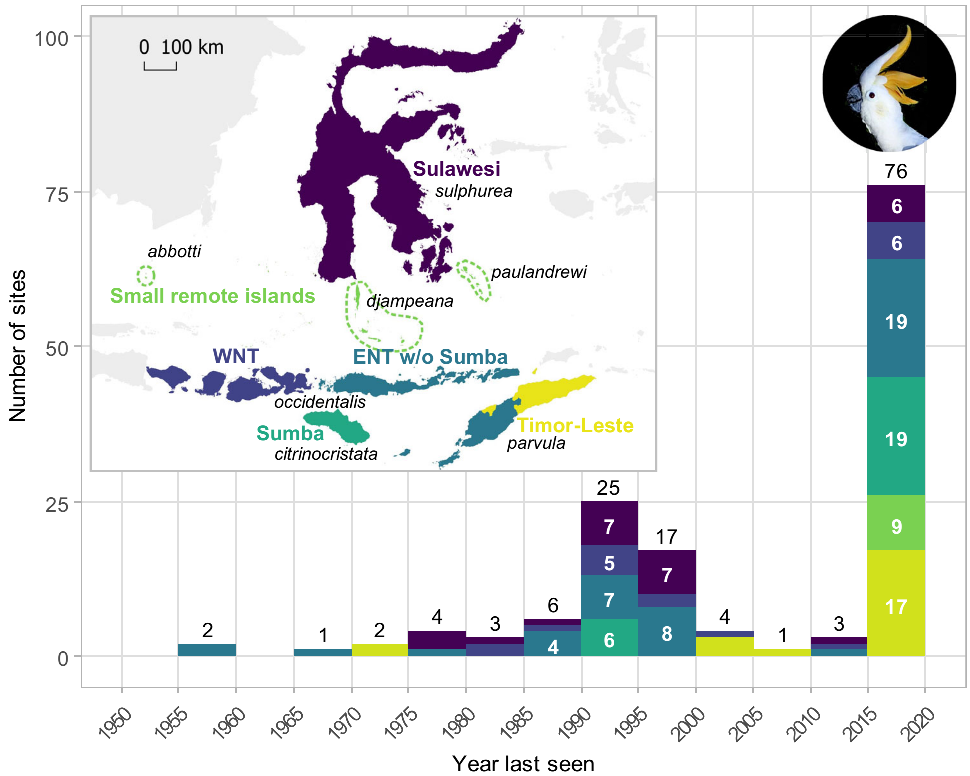

Figure 1 Study area, island grouping and timing of last record at sites with historic and extant yellow-crested cockatoo *Cacatua sulphurea* and citron-crested cockatoo *C. citrinocristata* populations. As a precaution against aiding illegal trapping, we do not show precise location information of extant 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$_{extinct}$	0.221	0.221	0.254	0.242	0.262	0.270	0.288	0.316	0.373	0.486	0.727
Error rate$_{survived}$	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^{-+}

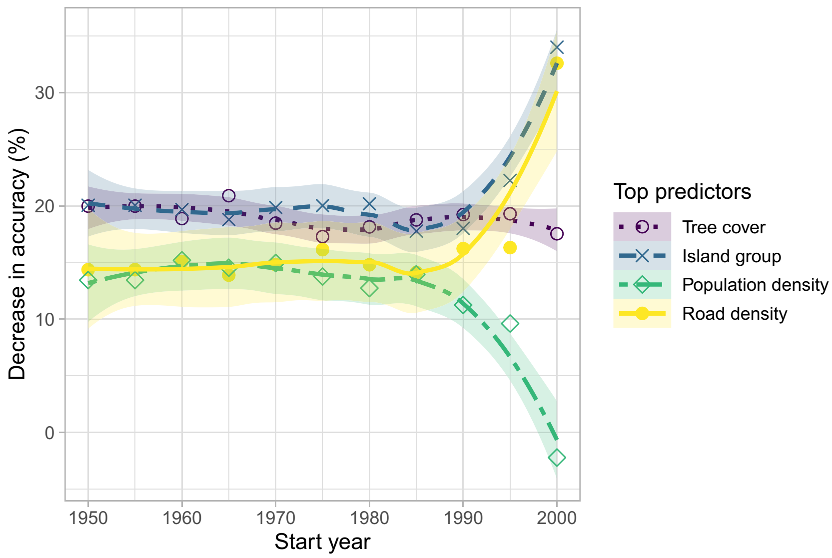

Figure 2 Change of predictor importance in random forest models for different time intervals. Importance is measured in decrease of model accuracy when the respective predictor is removed from the model (i.e. more important predictors would cause a larger decrease in model accuracy when removed). Only 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

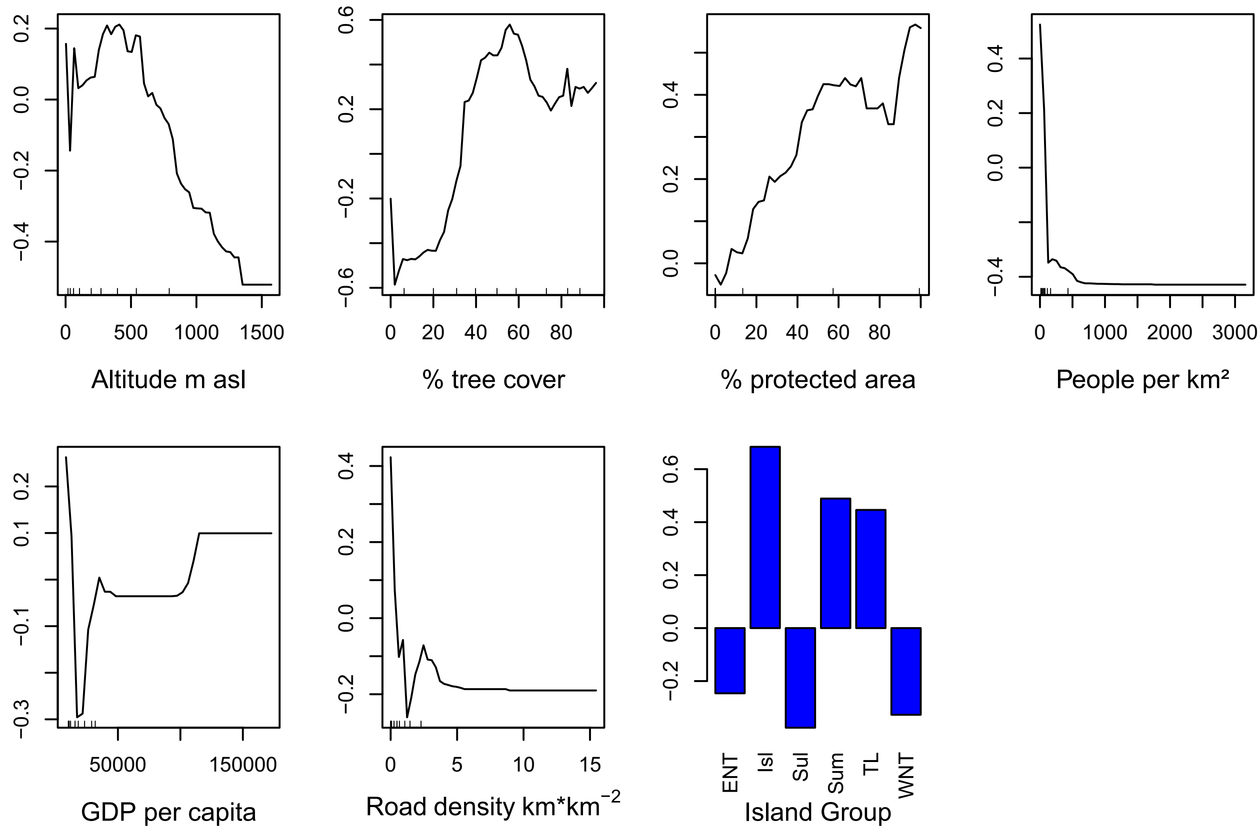

Figure 3 Partial importance of seven predictors for survival of yellow-crested cockatoo and citron-crested cockatoos at 144 sites from 1950 to 2015. ENT, East Nusa Tenggara without Sumba; Isl, small remote islands (see text); Sul, Sulawesi and satellites; Sum, Sumba; TL, Timor-Leste; WNT, West Nusa Tenggara (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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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.