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

Anna Reuleaux [a,*], Benny A. Siregar [b], Nigel J. Collar [c], Ani Mardiastuti [d], Stuart J. Marsden [a]

[a] Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK
[b] Burung Indonesia, Bogor, Indonesia
[c] BirdLife International, Cambridge, UK
[d] Bogor Agricultural University (IPB University), Bogor, Indonesia

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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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* Corresponding author.
E-mail addresses: anna.reuleaux@stu.mmu.ac.uk, anna.reuleaux@gmail.com (A. Reuleaux).

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.
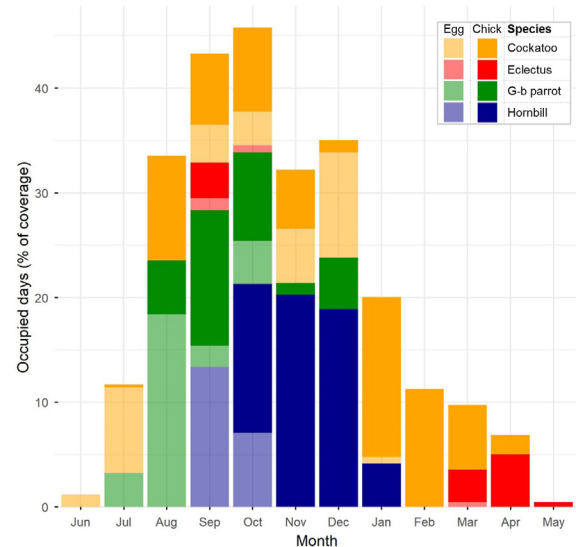
Fig. 3. Seasonality of cavity-nesting monitored by camera-traps over 2.5 years (November 2016–April 2019) in the forested areas of central and western Sumba. Paler colours indicate days at egg stage, darker colours chick stage. Data were pooled across three breeding seasons and twelve cavities that had 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).
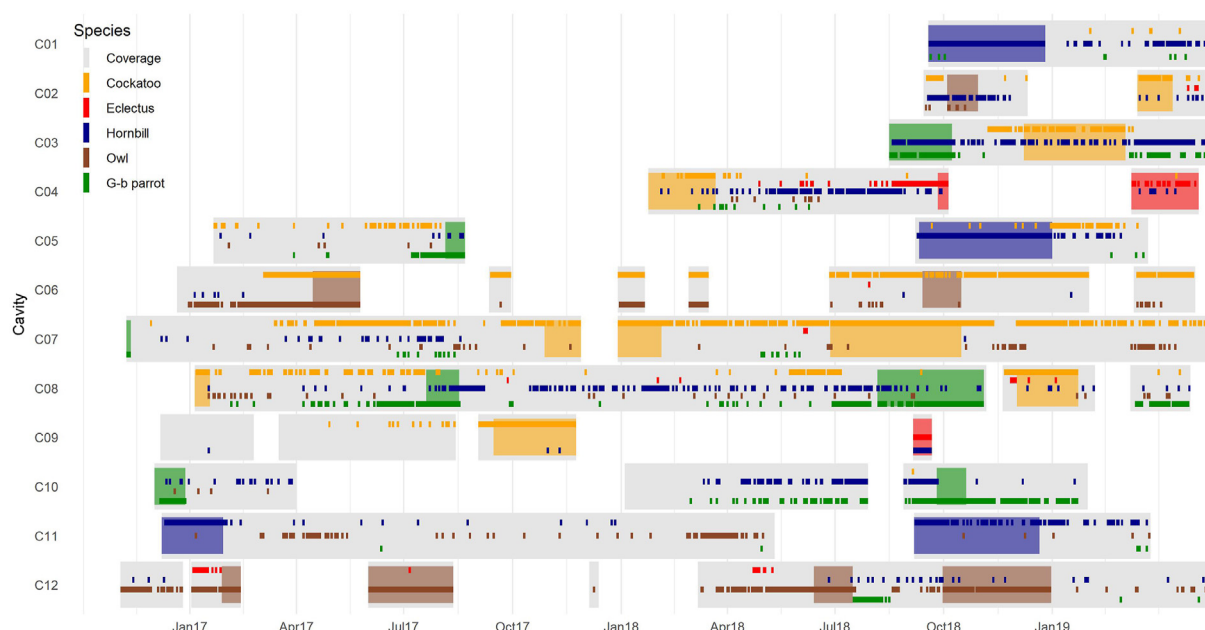
Fig. 4. Visitors and occupants of nesting cavities monitored by camera-traps over three breeding seasons, November 2016–April 2019, in the forested areas of central and western Sumba. Each row represents one of twelve cavities with cockatoo interest. Small narrow, darker bars indicate visits. Broad paler 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-

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

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.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.avrs.2022.100015.

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