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, 2021a). 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, 2021a). Since the establishment of CITES in 1975, the international trade in parrots, of which only four species are not included in its appendices (CITES, 2020), has become increasingly regulated, but evidence of a direct benefit to threatened species is inconclusive (Martin, 2000), not least because of a severe lack of reliable abundance data (Marsden & 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 variably be influenced by traditional beliefs, political circumstances, enforcement activities and conservation interventions (Verissimo et al., 2020). Capture methods vary with local cultures and traditions and can determine the stability of the targeted population (Valle et al., 2018). Identifying the factors correlating with survival at some sites and extinction at others offers important leverage points for conservation policy and management.

The yellow-crested cockatoo Cacatua sulphurea is endemic to the islands of western Wallacea (BirdLife International, 2021b), with the citron-crested cockatoo C. citrinocristata, only recently recognized as a separate species from yellow-crested, restricted to Sumba in the south-west of the same region (BirdLife International, 2022a). Like many other parrots the species are negatively affected by habitat loss and trade, as a consequence of which they have disappeared from almost all of their range and been listed as Critically Endangered all this century (Collar et al., 2001; BirdLife International, 2021b). Once the species were so numerous in parts of their ranges that their flocks made trees appear white, and crops had to be guarded against them (Kendall, 1979; Setiawan, 1996; Collar et al., 2001). As obligate hole-nesters, the cockatoos are highly vulnerable to trapping when breeding or communally roosting (Marsden & Jones, 1997; Walker, Cahill & Marsden, 2005; Imansyah et al., 2016). Consequently, they were trapped and exported in the thousands for the international pet market (Inskip, 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 (Mollo & 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. djameana 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 (Burring 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 (Goldmann 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
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 wild-life 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 diminishing 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; KLIHK & 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, 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

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**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.
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).

| Subspecies/species       | Minimum estimate | Estimated | Sites survived/total | Density on island (ind × km⁻²) | % of island area occupied |
|--------------------------|------------------|-----------|----------------------|--------------------------------|---------------------------|
| *C. s. occidentalis*     | 1207             | 1711      | 22/47                | 0.09                           | 3.5                       |
| *C. s. parvula*          | 431              | 985       | 20/37                | 0.03                           | 5.9                       |
| *C. s. paulandrewi*      | 81               | 172       | 4/4                  | 1.27                           | 10.7                      |
| *C. s. djampeana*        | 61               | 156       | 4/4                  | 0.45                           | 14.7                      |
| *C. s. sulphurea*        | 27               | 105       | 6/26                 | 0.001                          | 0.3                       |
| *C. s. abbotti*          | 17               | 22        | 1/1                  | 7.33                           | 11.2                      |
| *C. citrinocristata*     | 286              | 1400      | 19/25                | 0.11                           | 11.0                      |

| Island groups            | Minimum estimate | Estimated | Sites survived/total | Density on island (ind × km⁻²) | % of island area occupied |
|--------------------------|------------------|-----------|----------------------|--------------------------------|---------------------------|
| 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 *Megapodididae* (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 Kuznets’ 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, 2021b). However, there have undoubtedly been severe declines across the species’ range over the last 40 years (three generations, BirdLife International, 2022b). Although we can only guess the extent of losses before 1950, local extinctions were particularly prominent in the 1990s and 2000s when both trade records and field surveys (Inskipp et al., 1988; PHPA et al., 1998; Cahill et al., 2006) showed that market prices of birds had already risen and remnant populations had fallen victim to further trapping. Considerable time lags between the onset of population decline and extinction are known in long-lived species (Diamond, 1972; Kuussaari et al., 2009), particularly when trappers only target nestlings (Valle et al., 2018). In addition to gauging population changes over long periods, Red List reassessment of the cockatoos is complicated by several other considerations. The recent split of citron-crested cockatoo leaves the resultant two species at higher risk of extinction than when combined, as the population on Sumba remains under pressure from illegal trapping and appears to have low productivity (Reuleaux et al., 2022). The subspecies occidentalis and parvula may seem relatively safe with one stronghold each (Komodo for occidentalis, Timor-Leste for parvula), but the Komodo population depends on intense patrolling and local goodwill, both of which will be under threat if the recently proposed drastic reduction in visitor numbers to Komodo National Park (CNN Travel, 2019) is implemented, or if international travel is curtailed due to unforeseen issues such the current Covid-19 pandemic (Caraka et al., 2020; Leon & 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 pauliandrewi 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 haematotupa. 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, 2022 The Authors. Animal Conservation published by John Wiley & Sons Ltd on behalf of Zoological Society of London. 819
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 (T Turnbull et al., 2015). In this respect, the particularity of the factors behind the species’ local population persistence underlines the value of tailoring conservation efforts to each site and case. Some of these factors can be turned to advantage in differing local contexts and represent exciting opportunities to recover crucial populations through relatively low-cost management interventions. This insight is important not only for the conservation of the yellow-crested and citron-crested cockatoos and other Asian hole-nesters (such as Tenggara hill myna, parrots and hornbills) but also for species in other parts of the world threatened by persecution (brown bears Ursus arctos, Naves et al., 2003; jaguars Panthera onca, De Angelo et al., 2013 and other large carnivores under hunting pressure). The models themselves may yield relevant information, such as the importance of human occupation and infrastructure patterns or the role of protected areas in influencing species persistence. However, the approach of looking beyond the model and examining location-specific factors could be applied to many other species with wide but now fragmented ranges for a better understanding of – and stronger measures against – extinction risk. A network of ‘cockatoo advocates’ (at least one committed individual from each site, such as local residents, protected areas staff, NGO members) would greatly help build local support for the birds’ conservation, reducing trapping and upgrading legal protection. The most urgent conservation actions include improving the conditions for law enforcement in south-east Sulawesi, a mobile awareness campaign aimed at communities near remnant populations in Nusa Tenggara and a detailed study of the status and cultural treatment of the species in Timor-Leste. Without these interventions, the future of the two species, regardless of their Red List status, will remain in the balance.

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References

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

Argeloo, M. & Dekker, R.W.R.J. (1996). Exploitation of megapode eggs in Indonesia: the role of traditional methods in the conservation of megapodes. Oryx 30, 59–64.

Badan Pusat Statistik. (2016). Statistical yearbook of Indonesia. Available at www.bps.go.id

Benitez-Lopez, A., Alkemade, R. & Verweij, P.A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biol. Conserv. 143, 1307–1316.

Bhagwat, S.A. & Rutte, C. (2006). Sacred groves: potential for biodiversity management. Front. Ecol. Environ. 4, 519–524.

BirdLife International. (2018). State of the world’s birds: taking the pulse of the planet. Cambridge: BirdLife International.

BirdLife International. (2021a). Datazone. Available at http://datazone.birdlife.org/

BirdLife International. (2021b). Species factsheet Cacatua sulphurea. Available at http://www.birdlife.org

BirdLife International. (2022a). Species factsheet Cacatua citrinocristata. Available at http://www.birdlife.org

BirdLife International. (2022b). Species factsheet Cacatua sulphurea. Available at http://www.birdlife.org

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

Breme, L. (2001). Random forests. Mach. Learn. 45, 5–32.

Brun, C., Cook, A.R., Lee, J.S.H., Wich, S.A., Koh, L.P. & Carrasso, L.R. (2015). Analysis of deforestation and protected area effectiveness in Indonesia: a comparison of Bayesian spatial models. Glob. Environ. Chang. 31, 285–295.

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

Burung Indonesia. (2011). The behavioural ecology of breeding the yellow-crested Cockatoo in Manupeu Tanahdaru National Park, Sumba Island. Bogor: Burung Indonesia.
Bush, E.R., Baker, S.E. & Macdonald, D.W. (2014). Global trade in exotic pets 2006–2012. *Conserv. Biol.* 28, 663–676.

Butchard, S.H.M., Stattersfield, A.J. & Brooks, T.M. (2006). Going or gone: defining “possibly extinct” species to give a truer picture of recent extinctions. *Bull. Br. Ornithol. Club* 126, 7–24.

Cahill, A.J., Walker, J.S. & Marsden, S.J. (2006). Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea sulphurea* in South Sulawesi Province. Bogor: PHPA/BirdLife International – Indonesia Programme.

Caraka, R.E., Lee, Y., Kurniawan, R., Herliansyah, R., Kaban, P.A., Nasution, B.I., Gia, P.U., Chen, R.C., Toharudin, T. & Pardamean, B. (2020). Impact of COVID-19 large scale restriction on economy and environment in Indonesia. *Glob. J. Environ. Sci. Manag.* 6, 65–84.

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

Cazalis, V., Princé, K., Mihoub, J.B., Kelly, J., Butchert, S.H.M. & Rodrigues, A.S.L. (2020). Effectiveness of protected areas in conserving tropical forest birds. *Nat. Commun.* 11, 1–8.

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

CITES. (2020). *Convention on international trade in endangered species of wild fauna and flora – appendices*. Available at https://cites.org/eng/app/appendices.php

CNN Travel. (2019). *Indonesia cancels plan to ban tourists from Komodo Island*. CNN Travel. Available at https://edition.cnn.com/travel/article/indonesia-komodo-islands-reverse-tourist-ban-inll-hnk/index.html

Collar, N.J., Andreev, A.V., Chan, S., Crosby, M.J., Subramanya, S. & Tobias, J.A. (2001). *Threatened birds of Asia: the BirdLife International red data book* (Collar, N.J., Andreev, A.V., Chan, S., Crosby, M.J., Subramanya, S. & Tobias, J.A., Eds). Cambridge: BirdLife International.

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

Collar, N.J. & Marsden, S.J. (2014). The subspecies of yellow-crested cockatoo *Cacatua sulphurea*. *Forktail* 30, 23–27.

De Angelo, C., Paviolo, A., Wiegand, T., Kanagaraj, R. & Di Bitetti, M.S. (2013). Understanding species persistence for defining conservation actions: a management landscape for jaguars in the Atlantic Forest. *Biol. Conserv.* 159, 422–433.

Devenish, C., Junaid, A.R., Saryanthi, R., van Balen, S.B., Kaprawi, F., Aprianto, G.C., Stanley, R., Poole, O., Owen, A., Collar, N.J. & Marsden, S.J. (2021). Biological richness of Gunung Slamet, Central Java, and the need for its protection. *Oryx*. https://doi.org/10.1017/S0030605320001222

Diamond, J.M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific islands. *Proc. Natl. Acad. Sci. USA* 69, 3199–3203.

Diamond, J.M. (1987). Extant unless proven extinct? Or, extinct unless proven extant? *Conserv. Biol.* 1, 77–79.

Douglas-Hamilton, I., Krink, T. & Völlrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften* 92, 158–163.

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

Erb, M. (2016). Mining and the conflict over values in Nusa Tenggara Timur province, eastern Indonesia. *Extr. Ind. Soc.* 3, 370–382.

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

Froese, G.Z.L. & Mustari, A.H. (2019). Assessments of Maleo *Macrocephalon maleo* nesting grounds in south-East Sulawesi reveal severely threatened populations. *Bird Conserv. Int.* 29, 497–502.

Garland, K.A. & Cathy, R.R. (2010). Changing taste preferences, market demands and traditions in pearl lagoon, Nicaragua: a community reliant on green turtles for income and nutrition. *Conserv. Soc.* 8, 55–72.

Garnier, S. (2018). viridis: default color maps from "matplotlib". *R* package version 0.5.1. Available at https://cran.r-project.org/package=viridis

Geary, M., Brailsford, C.J., Hough, L.I., Baker, F., Guererro, S., Leon, Y.M., Collar, N.J. & Marsden, S.J. (2021). Street-level green spaces support a key urban population of the threatened Hispaniolan parakeet *Psittacula chloropus*. *Urban Ecosyst.* 24, 1–8.

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

Geofabrik. (2021). *OpenStreetMap data for Indonesia (with East Timor)*. Geofabrik Download Serv. Available at https://download.geofabrik.de/asia/indonesia.html

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

Hansen, M.C., Potapov, P.V., Moore, R., Hansen, M., Turubanova, S., Tyukavina, A., Thau, D., Stheiman, S.V., Goetz, S.J. & Loveland, T.R. (2013). High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853.

Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, Sa., Tyukavina, A., Thau, D., Stehman, S. V,
Correlates of persistence in cockatoo populations

A. Reuleaux et al.

Goetz, S. J. & Loveland, T. R. (2020). Global forest change 2000–2019 dataset Hansen/UMD/Google/USGS/NASA. Available at http://earthenginepartners.appspot.com/science-2013-global-forest

Harris, J.B.C., Tingley, M.W., Hua, F., Yong, D.L., Adeney, J.M., Lee, T.M., Marthy, W., Prawiradilaga, D.M., Sekercioğlu, C.H., Suyadi, Winarni, N. & Wilcove, D.S. (2017). Measuring the impact of the pet trade on Indonesian birds. Conserv. Biol. 31, 394–405.

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

Indraswari, K., Friedman, R.S., Noske, R., Shepherd, C.R., Biggs, D., Susilawati, C. & Wilson, C. (2020). It’s in the news: characterising Indonesia’s wild bird trade network from media-reported seizure incidents. Biol. Conserv. 243, 108431.

Inskipp, T., Broad, S. & Luxmoore, R. (1988). Significant trade in wildlife – a review of selected species in CITES appendix II, vol. 3: birds. Cambridge: IUCN Conservation Monitoring Centre.

IUCN. (2021). Protected area categories. Available at https://www.iucn.org/theme/protected-areas/about/protected-area-categories

Jeon, C.-Y. & Yang, H.-W. (2021). The structural changes of a local tourism network: comparison of before and after COVID-19. Curr. Issues Tour. 24, 3324–3338.

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

Kendall, S.B. (1979). Citron-crested cockatoos in Sumba. Avic. Mag 85, 93–94.

KLHK & DJ KSDAE. (2018). Statistik Direktorat Jenderal Konservasi Sumber Daya Alam dan Ekosistem Tahun 2017. Jakarta: Kementerian Lingkungan Hidup dan Kehutanan. Available at http://ksdae.menlhk.go.id/assets/publikasi.

Kociolek, A.V., Clevenger, A.P., St. Clair, C.C. & Proppe, D.S. (2011). Effects of road networks on bird populations. Conserv. Biol. 25, 241–249.

Kummu, M., Taka, M. & Guillaume, J.H.A. (2018). Gridded global datasets for gross domestic product and human development index over 1990–2015. Sci. Data 5, 1–15.

Kuusaaari, M., Bonmarroo, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Roda, F., Stefanescu, C., Teder, T., Zobel, M. & Steffen-Dewenter, I. (2009). Extinction debt: a challenge for biodiversity conservation. Trends Ecol. Evol. 24, 564–571.

Liaw, A. & Wiener, M. (2002). Classification and regression by randomForest. R news 2, 18–22.

Liévan-Latorre, L.F., Brum, F.T. & Loyola, R. (2021). How effective have been guerrilla occupation and protected areas in avoiding deforestation in Colombia? Biol. Conserv. 253, 108916.

Lunstrum, E. & Givá, N. (2020). What drives commercial poaching? From poverty to economic inequality. Biol. Conserv. 245, 108505.

Luo, S.J., Kim, J.H., Johnson, W.E., Van Der Walt, J., Martenson, J., Yuhki, N., Miquelle, D.G., Uphyrkina, O., Goodrich, J.M., Quigley, H.B., Tilson, R., Brady, G., Martelli, P., Subramaniam, V., McDougal, C., Hean, S., Huang, S.Q., Pan, W., Karanth, U.K., Sunquist, M., Smith, J.L.D. & O’Brien, S.J. (2004). Phylogeography and genetic ancestry of tigers (Panthera tigris). PLoS Biol. 2, e42.

Mallo, F.N. & Setiawan, I. (1996). Telaah status Cacatua sulphurea sulphurea di Sulawesi Tengah. Bogor: PHPA/BirdLife International.

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

Marsden, S.J. & Jones, M.J. (1997). The nesting requirements of the parrots and hornbill of Sumba, Indonesia. Biol. Conserv. 82, 279–287.

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

Martin, R.B. (2000). When CITES works and when it does not. In Endangered species, threatened convention: the past, present and future of CITES, the Convention on international trade in endangered species of wild fauna and flora: 29–37. Hutton, J. & Dickson, B. (Eds). London: Earthscan.

McCauley, D.J., Power, E.A., Bird, D.W., McInturff, A., Dunbar, R.B., Durham, W.H., Micheli, F. & Young, H.S. (2013). Conservation at the edges of the world. Biol. Conserv. 165, 139–145.

Mephorson, M.A. & Nieswiadomy, M.L. (2005). Environmental Kuznets curve: threatened species and spatial effects. Ecol. Econ. 55, 395–407.

Mills, J.H. & Waite, T.A. (2009). Economic prosperity, biodiversity conservation, and the environmental Kuznets curve. Ecol. Econ. 68, 2087–2095.

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

Mortelliti, A. & Boitani, L. (2007). Estimating species’ absence, colonization and local extinction in patchy landscapes: an application of occupancy models with rodents. J. Zool. 273, 244–248.

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

Naves, J., Wiegand, T., Revilla, E. & Delibes, M. (2003). Endangered species constrained by natural and human factors: the case of Brown bears in northern Spain. Conserv. Biol. 17, 1276–1289.
Olah, G., Blanchet, S.H.M., Symes, A., Guzmán, I.M., Cunningham, R., Brightsmith, D.J. & Heinsohn, R. (2016). Ecological and socio-economic factors affecting extinction risk in parrots. *Biodivers. Conserv.* 25, 205–223.

OpenStreetMap Contributors. (2021). *OpenStreetMap data.* Available at https://www.openstreetmap.org/copyright

Pain, D.J., Martins, T.L.F., Boussekey, M., Diaz, S.H., Downs, C.T., Ekstrom, J.M.M., Garnett, S., Gilardi, J.D., McNiven, D. & Primot, P. (2006). Impact of protection on nest take and nesting success of parrots in Africa, Asia and Australasia. *Anim. Conserv.* 9, 322–330.

Peres, C.A. & Lake, I.R. (2003). Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon Basin. *Conserv. Biol.* 17, 521–535.

Persulessy, Y.E., Djawaray, Y.B. & Marut, R. (2003). *Survei populasi dan distribusi kakatua-kecil jambul-kuning Gatucatua sulphurea cristinocrissata dan empat jenis paruh bengkok lain di Pulau Sumba.* Bogor: BirdLife Indonesia/ZGAP.

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

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

Pires, S.F. & Clarke, R.V. (2011). Sequential foraging, itinerant fences and parrot poaching in Bolivia. *Br. J. Criminol.* 51, 314–335.

Pires, S.F., Olah, G., Nandika, D., Agustina, D. & Heinsohn, R. (2021). What drives the illegal parrot trade? Applying a criminological model to market and seizure data in Indonesia. *Biol. Conserv.* 257, 109098. https://doi.org/10.1016/j.biocon.2021.109098.

Plieenier, T., Quintas-Soriano, C., Torralba, M., Mohammadi Samani, K. & Shakeri, Z. (2020). Social dynamics of values, taboos and perceived threats around sacred groves in Kurdistan, Iran. *People Nat.* 2, 1237–1250.

QGIS Development Team. (2021). *QGIS geographic information system.* Hannover: Open Source Geospatial Foundation Project.

R Core Team. (2021). *R: a language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing.

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

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

Reuleaux, A., Siregar, B.A., Collar, N.J., Mardiastuti, A. & Marsden, S.J. (2022). Productivity constraints on citron-crested cockatoos in a rich community of large hole-nesting birds. *Avian Res.* 13, 100015. https://doi.org/10.1016/J.AVR.2022.100015.

Reuleaux, A., Siregar, B.A., Collar, N.J., Panggur, M.R., Mardiastuti, A., Jones, M.J. & Marsden, S.J. (2020). Protected by dragons: density surface modeling confirms large population of the critically endangered yellow-crested cockatoo on Komodo Island. *Condor* 122, duaa042.

Robinson, J.G. & Bodmer, R.E. (1999). Towards wildlife management in tropical forests. *J. Wildl. Manage.* 63, 1–13.

Romero-Vidal, P., Hiraldo, F., Rosseto, F., Blanco, G., Carrete, M. & Tella, J.L. (2020). Opportunistic or non-random wildlife crime? Attractiveness rather than abundance in the wild leads to selective parrot poaching. *Diversity* 12, 314.

Rowley, I., Sharpe, C. & Boesman, P. (2017). Yellow-crested Cockatoo (*Cacatua sulphurea*) – HBW Alive. In *Handbook of the birds of the world alive.* del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (Eds). Barcelona: Lynx Edicions. Available at https://www.hbw.com

Rutte, C. (2011). The sacred commons: conflicts and solutions of resource management in sacred natural sites. *Biol. Conserv.* 144, 2387–2394.

Ryder, O.A. (1986). Species conservation and systematics: the dilemma of subspecies. *Trends Ecol. Evol.* 1, 9–10.

Samudro, B.R., Bloch, H. & Salim, R. (2015). The uneven regional pattern of ecological capital in Indonesia: a political economy perspective. *Int. J. Green Econ.* 9, 258–272.

Setiawan, I. (1996). *The status of Cacatua sulphurea parvula in Nusa Penida, Bali, and Sumbawa,* Vol. 6. Bogor: PHPA/BirdLife International. Available at http://www.nusapenida.nl/index.php/biology/birding/sulphur-crested-cockatoo-setiawan-1996

Shepherd, C.R. & Nijman, V. (2008). The trade in bear parts from Myanmar: an illustration of the ineffectiveness of enforcement of international wildlife trade regulations. *Biodivers. Conserv.* 17, 35–42.

Snodgrass, J.G. & Tiedje, K. (2008). Indigenous nature reverence and conservation. *J. Study Relig. Nat. Cult.* 2, 6–29.

Sodhi, N.S., Posa, M.R.C., Lee, T.M., Bickford, D., Koh, L.P. & Brook, B.W. (2010). The state and conservation of southeast Asian biodiversity. *Biodivers. Conserv.* 19, 317–328.

Sonter, L.J., Ali, S.H. & Watson, J.E.M. (2018). Mining and enforcement of international wildlife trade regulations. *Biodivers. Conserv.* 17, 35–42.

Sopian, N.L. (2015). Informal dispute resolution based on Adat law: a case study of land dispute in Flores, East Nusa Tenggara, Indonesia. *Indon. L. Rev.* 5, 106.

Steaman, A.M. (2000). A pound of flesh: social change and modernization as factors in hunting sustainability among neotropical indigenous societies. In *Hunting for sustainability in tropical forests.* 1st edn: 233–250.
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A. Reuleaux et al.

Robinson, J. & Bennett, E.L. (Eds). New York: Columbia University Press.

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

Thu, P.M. (2012). Access to land and livelihoods in post-conflict Timor-Leste. *Aust. Geogr.* 43, 197–214.

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

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

Van Zyl, J.J. (2001). The shuttle radar topography Mission (SRTM): a breakthrough in remote sensing of topography. *Acta Astronaut.* 48, 559–565.

Verissimo, D., Vieira, S., Monteiro, D., Hancock, J. & Nuno, A. (2020). Audience research as a cornerstone of demand management interventions for illegal wildlife products: demarking sea turtle meat and eggs. *Conserv. Sci. Pract.* 2, e164.

Walker, J.S., Cahill, A.J. & Marsden, S.J. (2005). Factors influencing nest-site occupancy and low reproductive output in the Critically Endangered yellow-crested cockatoo *Cacatua sulphurea* on Sumba, Indonesia. *Bird Conserv. Int.* 15, 347–359.

Webb, R.A.F.P. (1986). Adat and Christianity in Nusa Tenggara Timur: reaction and counteraction: traditional custom and modern development in eastern Indonesia. *Philipp. Q. Cult. Soc.* 14, 339–365.

Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., Woo, K., Yutani, H. & Dunnington, D. (2021). Package ‘ggplot2’. Create elegant data visualisations using the grammar of graphics. Version 3.3.5. Available at https://cran.r-project.org/web/packages/ggplot2/index.html

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

Wilkie, D.S., Starkey, M., Abernethy, K., Effa, E.N., Telfer, P. & Godoy, R. (2005). Role of prices and wealth in consumer demand for bushmeat in Gabon, Central Africa. *Conserv. Biol.* 19, 268–274.

Worldpop. (2018). Global high resolution population denominators project. Southampton: School of Geography and Environmental Science, University of Southampton.

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

Zhang, L., Hua, N. & Sun, S. (2008). Wildlife trade, consumption and conservation awareness in southwest China. *Biodivers. Conserv.* 17, 1493–1516.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Sources for presence and absence of yellow-crested cockatoos and citron-crested cockatoos used in this study.

Table S2. Broad locations with surviving cockatoo populations despite random forest model predictions of extinction between 1950 and 2015.

Table S3. Accuracy and variable importance (measured in decrease in model accuracy when the predictor is removed) compared between three different measures of area protection as predictors of yellow-crested and citron-crested cockatoo site-specific survival from 1950 to 2015 in a random forest model.