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

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ABSTRACT

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

Keywords: Cacatua sulphurea, conservation, density surface model, distance sampling, habitat model, parrots, Psittaciformes, threatened species

LAY SUMMARY

- Yellow-crested Cockatoos are threatened by extinction due to illegal trapping for the pet trade. Komodo Island in Indonesia supports one of the largest remaining populations. The island is part of Komodo National Park, famous for its Komodo dragons. A 2006 survey indicated cockatoo numbers might have been declining.
- In contrast to previous surveys we sampled the whole island instead of focusing on coastal valleys, which are known to harbor the highest cockatoo densities. We used distance sampling and density surface modeling, which allowed us to estimate how many cockatoos remained undetected and to produce a map of predicted cockatoo densities.
- We estimate there are between 600 and 2,100 cockatoos on Komodo, most likely ~1,100. Komodo National Park authorities also reported an increase in their annual counts of cockatoos from below 400 in 2011 to around 650 in 2017. Thus, the cockatoo population on Komodo Island is large and stable; Komodo National Park is successfully protecting its cockatoos.

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

ABSTRAK (BAHASA INDONESIA)

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

Indonesian keywords (kata kunci): density surface model, distance sampling, kakatua, konservasi, model habitat, spesies terancam

INTRODUCTION

Estimates of population sizes are cornerstones of conservation science at both global and local scales and are instrumental in assessing extinction risks, conservation priorities, and Red List status (Mace et al. 2008, Collen et al. 2011). These essential data are, however, lacking for a great many rare and threatened species (MacKenzie et al. 2005), which are often difficult to survey on account of their biology and/or the areas they inhabit (McDonald 2004). Even for relatively well-known groups such as psittacines (parrots), ~75% of species are lacking abundance estimates (Marsden and Royle 2015), a worrying statistic given that almost one-third of psittacines are currently threatened (IUCN 2019). A variety of methods have been used to calculate population size in parrots. For very rare species it may be possible to count every individual. For others, marked or identifiable individuals allow mark–recapture or mark–resighting methods, but these conditions are not the norm. For most species, roost counts, flyway counts, and distance sampling have been used more or less effectively (Casagrande and Beissinger 1997, Marsden and Royle 2015). Distance sampling, despite difficulties in meeting method assumptions, has become a well-established method for estimating sizes of animal populations generally (Thomas et al. 2010) and parrots in particular (Marsden and Royle 2015).

Estimates derived from distance sampling have become the most commonly used, involving 84% of published parrot abundance estimates (Marsden and Royle 2015), despite question marks over reliability related to lack of records in rare species and idiosyncrasies of parrot behavior (Marsden 1999, Dénes et al. 2018). Alternative methods fail to measure absolute bird abundance (Bibby et al. 2000), face the same (and additional) challenges (Casagrande and Beissinger 1997), or remain largely untested (Dénes et al. 2018).

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

Density surface modeling (DSM) uses GAMs (Wood 2017) to model the point-specific density at the sampling points (or segment-specific for line transects) in a 2-step approach: first, it accounts for detectability using the distance sampling method; second, it incorporates spatial and/or environmental covariates to explain the variation between sampling points (Hedley and Buckland 2004, Miller et al. 2013). The resultant model can then be used to map predicted population densities within the sampling area and also, with caution, for new unsampled areas (Miller et al. 2013). DSMs are not widely used for population estimates at present but have been successfully applied to marine birds (Petersen et al. 2011, Winiarski et al. 2013, 2014; Bradbury et al. 2014), a peatland bird community (Leivits and Leivits 2016), marine mammals (de Segura et al. 2007, Gilles et al. 2011, Williams et al. 2011, Miller et al. 2013, Bravington et al. 2019), and ungulates (Harihar et al. 2014, Schroeder et al. 2014, La Morgia et al. 2015, Valente et al. 2016). Several of these studies had conservation objectives such as identification of priority areas for protection (Winiarski et al. 2013) or assessment of endangered species (Ibouroi et al. 2019). While the method has been recommended as suitable for parrots (Dénes et al. 2018), we know of no application of DSMs to any parrot, or indeed to any critically endangered species.

The Yellow-crested Cockatoo (*Cacatua sulphurea*) used to occur commonly across the Lesser Sunda Islands, parts of Sulawesi, and its satellites (Figure 1), but habitat alteration and especially excessive trapping for the international pet trade from the 1970s through the 1990s caused severe declines and local extinctions across much of its range. Thus, populations >100 individuals remain at only a handful of sites, rendering the species critically endangered (Broch 1981, Cahyadin et al. 1994a, 1994b; Jones et al. 1995, PHPA/LIPI/BirdLife International 1998, Agista et al. 2001, BirdLife International 2001, Eaton et al. 2015). Some 560–4,000 of the very distinctive subspecies *citrinocristata* are thought to exist in several forest patches on Sumba (Wungo 2011; A. Reuleaux personal observation; Figure 1). The population of Yellow-crested Cockatoos of the subspecies *occidentalis* in Komodo National Park (KNP; Figure 1), in the Lesser Sunda Islands, is also believed to be relatively large, although a survey in 2006 (Imansyah et al. 2016) diagnosed a sharp decline since 2000 (Agista and Rubyanto 2001). Both these surveys obtained minimum numbers for selected coastal valleys by direct sightings from vantage points, which cover <10% of the island's area. Here we used density surface modeling to predict local cockatoo densities across Komodo Island. We validated the models using independent sightings, investigated correlates of local abundance, and estimated the island-wide population size.

METHODS

Study Area

Komodo Island (8.42°S–8.75°S, 119.37°E–119.57°E) is situated between Flores and Sumbawa in the Lesser Sunda Islands, Nusa Tenggara Timur, Indonesia (Figure 1). With an area of 340 km^2 and a maximum elevation of 824 m above sea level (m.a.s.l.), it is the largest and highest of the islands of KNP, which was established in 1980 to protect the Komodo dragon (*Varanus komodoensis*) and the terrestrial and marine biodiversity of the islands (UNESCO World Heritage Committee 1991, Lilley 1997). It now harbors one of the most important remnant populations of Yellow-crested Cockatoos and the most important population of subspecies *C. s. occidentalis* (Collar and Marsden 2014). Komodo is situated in one of the driest areas of Indonesia; streams do not run for most of the year and natural water sources are rare (Monk et al. 1997). Large areas of the island are covered by open grassland (Auffenberg 1980) interspersed with scrubland, palm savanna, small stands of broadleaved trees, and gallery forests along watercourses (Monk et al. 1997). Where larger streams meet the sea, deciduous monsoon forests cover the valley floors (Auffenberg 1980, Monk et al. 1997; Figure 2). Higher altitudes (>500 m) support denser closed-canopy forest (Figure 2), which is often dominated by bamboo or rattan and referred to as "quasi cloud forest" (Auffenberg 1980) or "mossy forest" (Monk et al. 1997); this terrain transitions downhill via sparse forest into scrubland.

Following recommendations based on conservation considerations (Collar et al. 2017), to avoid supplying information to potential trappers, we do not include complete maps of our results. The complete maps are available for *bona fide* researchers or for conservation purposes from the authors. They are replaced in the results section by out-of-context cutouts of exemplary locations.

Point Count Distance Sampling

Komodo Island has a surface area of 340 km^2. We first excluded all 1 × 1 km^2 pixels that contained >50% bare grassland or sea (landcover map by Ministry of Environment and Forestry Indonesia, KLHK 2017), habitat types deemed unsuitable for cockatoos. From the remaining 152 potentially suitable pixels we randomly selected 25 for our point count distance sampling. The survey stations were located 200 m apart on the perimeter of each of these pixels (navigation by GPS). From November 6 to December 14, 2017, one of two experienced observers (AR, BAS) carried out one distance sampling point count at each of 178 stations between 0600 and 1000 hours (Figure 1). Both observers had experience in studying cockatoos (22 and 36 mo, respectively) and distance sampling of cockatoos (each 3 mo, early in 2017). The number of survey stations per pixel varied from 5 to 10 (mean = 7) depending on how many point counts could be finished within the survey time frame. Slow walking speed in rough terrain and large distances from the nearest permitted campsite often hindered maximization of survey effort.

We followed standard methods for point count distance sampling (Buckland et al. 2001, 2008; Thomas et al. 2010). Specifically we adapted the field protocol described by Marsden (1999): (1) 10-min count durations but without a settling-down period, (2) exclusion of encounters in flight,

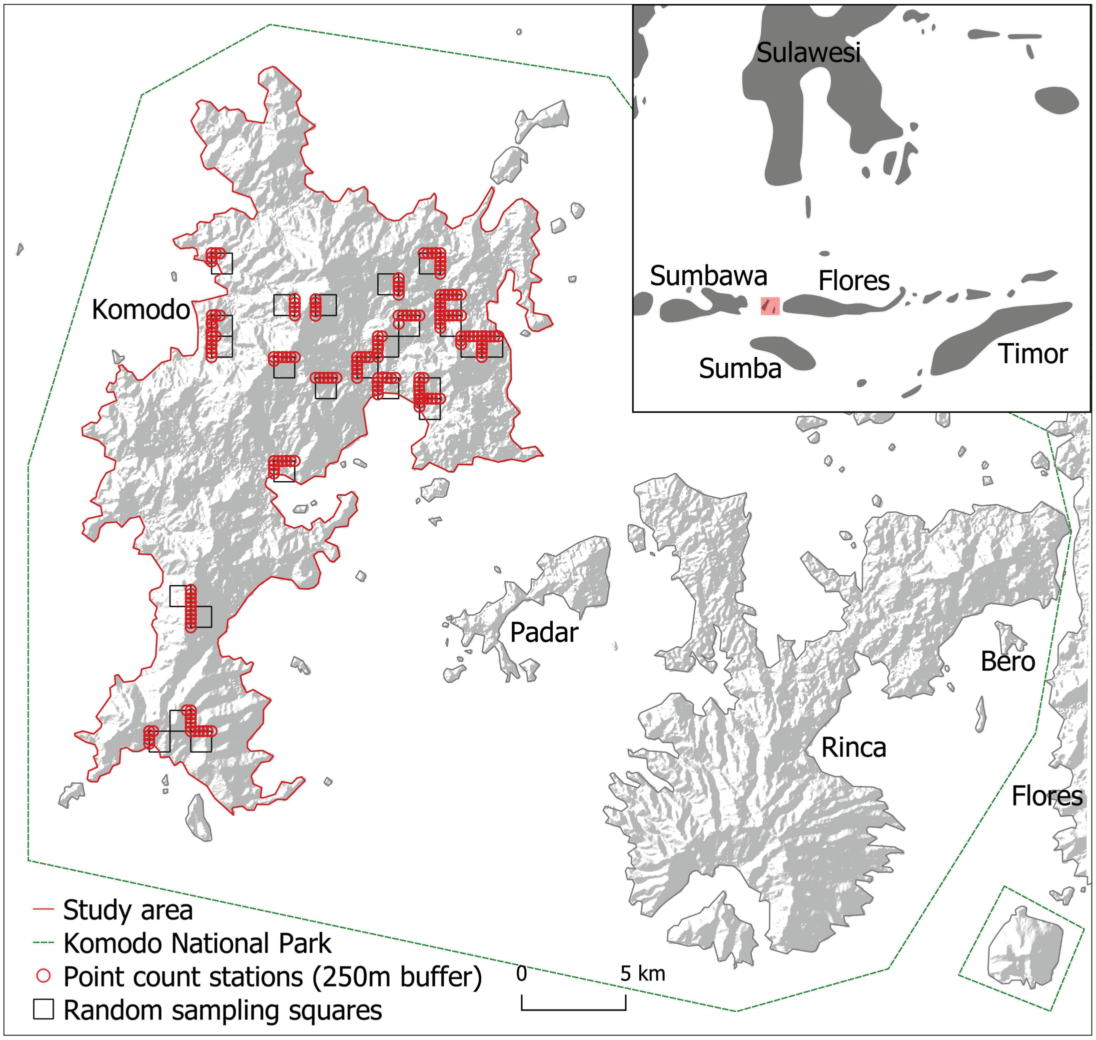

FIGURE 1. Study area Komodo Island situated in Komodo National Park, Indonesia, showing 178 point count stations, nested within 25 sampling squares, with their 250-m radius buffers.

(3) recording of flocks as clusters including the number of their individuals, and (4) replacement of group sizes for purely aural detections with the average size of known groups. To minimize errors in assessing distances, we used laser rangefinders (Nikon Forestry Pro) and followed protocols suggested by Buckland (2006) and Buckland et al. (2008). For example, this included measuring distances to other objects at a similar distance if the detected bird was not directly visible. Our survey period fell in the early part of the breeding season (Agista and Rubyanto 2001). Although all pairs observed near cavities were still prospecting, we checked the surrounding of each survey station for cavities with incubating adults. Analysis followed standard methods recommended in Buckland et al. (2001) and used a truncation distance of 350 m and open vs. enclosed habitat as a 2-level covariate for the detection function. We defined stations as open habitat if palm savanna, scrubland, and grassland made up ≥60% of land cover within a 50-m radius). We carried out distance sampling analysis in R using package *Distance 1.0.0* (Miller et al. 2016, R Core Team 2019). We used ungrouped distances as recorded without manual binning. Cluster size as a covariate was very unstable against truncation distances and did not improve AIC, so no cluster size bias regression was used. Results are reported as means ± SE.

Environmental Variables

We used a wetness index (by System for Automated Geoscientific Analyses, SAGA), a topographic index predicting the soil moisture based solely on a digital elevation grid (Böhner and Selige 2006, Conrad et al. 2015), in our case a Shuttle Radar Topography Mission digital elevation model with ~30 × 30 m resolution. We generated a contemporary raster habitat map based on LANDSAT

FIGURE 2. Habitat types on Komodo Island: (**A**) gallery forest among open grassland; (**B**) gallery forest; (**C**) palm savanna in front of deciduous monsoon forest; (**D**) quasi cloud forest (mossy forest, >500 m.a.s.l.).

8 imagery from September and October 2015–2017 (Appendix Figure 4). After cloud removal and adjustment of burnt areas to the survey period, we used our field observations and Google Maps to generate training data for landcover classification in QGIS with the semi-automatic classification plug-in (Congedo 2016, QGIS Development Team 2019).

We tailored the classification for use as a predictor of cockatoo detectability and density, and distinguished 6 habitat types (Appendix Table 3) following Auffenberg (1980) and Monk et al. (1997): open grassland and scrubland; palm savanna; deciduous monsoon forest including gallery forests and monsoon forests of the coastal plains; mangrove forest; quasi cloud forest >500 m; and sparse forest as a transition zone between quasi cloud forest and open habitat types. After inspection of spectral signature plots of the training units, cutoff values for critical bands were set manually to improve separation of overlapping categories (Congedo 2016); grassland and scrubland were classified separately and pooled afterwards. Mangrove forest was not recognized properly by the classification method, so the Indonesian Ministry of Forestry's landcover data (KLHK 2017) were used instead to correct the extent of this locally rare habitat type. We used the resulting fine-resolution habitat map to calculate percentage cover for each 250-m radius buffer around sampling stations and for each 0.25-km^2 prediction pixel. The 2 classes with the highest cockatoo encounter rates were termed "suitable habitat" and their combined percentages were used as a covariate in the DSM.

For model building we summarized the environmental covariates at the point count locations by averaging the gridded values within overlapping 250-m radius circles (sampling buffers) centered at each location. For our prediction surface, we divided each 1-km^2 pixel of the island into 4, resulting in 1,457 prediction grid pixels containing land. The environmental covariate values obtained at a smaller resolution were averaged within each of these 0.25-km^2 prediction pixels (Figure 3).

Density Surface Modeling (DSM) and Prediction

We used density surface modeling (Miller et al. 2013) to estimate population density within each 0.25-km^2 pixel across the island, involving the distance-based abundance estimates and the 2 environmental covariates. The *dsm* function in R (Miller et al. 2019) is based on generalized additive models (Wood 2017, 2019) and a detection function (Miller et al. 2016), and allows for the uncertainty of detection probability when estimating the variance of this 2-step modeling process. Our full generalized additive mixed model (GAMM) included the explicit spatial term s(x,y) (a smooth function for interaction of latitude and longitude), smooth functions of the log-transformed SAGA wetness index and the arcsine transformed percentage

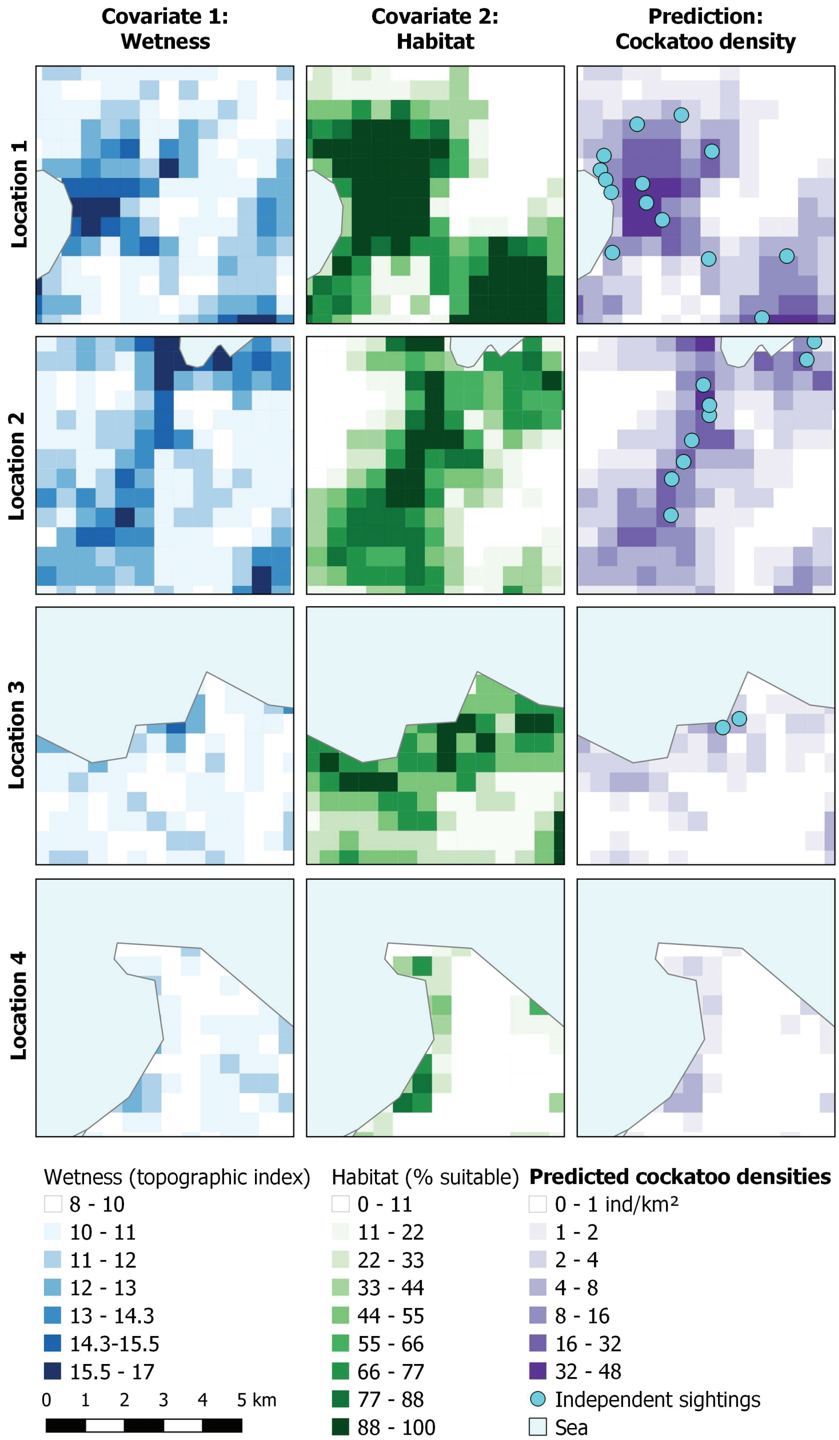

FIGURE 3. Exemplary map details of predictor values (topographic wetness index and percentage of suitable habitat) and densities of Yellow-crested Cockatoos (individuals km^{-2}) predicted by the density surface model, on a 0.25-km^2 grid of Komodo Island; cross-validated with independent sightings of the species (Agista and Rubyanto 2001, Imansyah et al. 2003, 2016; Taman Nasional Komodo 2016, eBird Basic Dataset 2019). To avoid supplying information to potential trappers, locations are provided out of context, with smoothed coastlines and random orientation. The complete maps of the whole island are available for research or conservation purposes from the authors.

of suitable habitat, as well as an autocorrelation structure (AR1 structure with form = ~1|sampling square) to allow for nestedness of the point count stations within the sampling squares. For the spatial term, we used a Duchon spline (Duchon 1977) as recommended for areas with complex borders where misidentification of population hotspots is a potential problem (Miller and Wood 2014). Smooth functions for interactions of these environmental variables were also explored but did not improve model fit. We compared Gaussian, Tweedie, and quasi Poisson distributions. After dropping nonsignificant terms, we selected the best combination of the remaining terms by AIC minimization (Appendix Table 4). Comparison of GAMMs is not straightforward; indicators are still in development (Wood 2017) and the AIC of the lme component of the GAMM is not recommended as an indicator for choice either (Wood 2019). Therefore, we used the AIC of the equivalent GAM for this step. With the GAM component of the chosen GAMM we predicted cockatoo density and coefficient of variation (CV) for each pixel of the prediction grid. To obtain the overall variance and confidence intervals we combined the variance of the detection function and that of the GAM using the Delta method via the *dsm.var.gam* function (Seber 1982, Miller et al. 2019).

Validating DSM Predictions Using Independent Cockatoo Sightings

We used 3 independent sources of cockatoo observations that were not included in our DSM analysis to validate the spatial predictions of our DSM. The first source was annual monitoring by KNP staff on flight paths and roosts (2012–2017, 16 locations; KNP unpublished data). The second source was citizen science observations from eBird (eBird Basic Dataset 2019), from which we selected those records where the observer had specified a precise location on the map instead of allocating it to a predefined hotspot, the national park, or the island in general (2004–2017, 7 locations). The third source was cockatoo records from survey reports, involving 9 locations from valley-floor surveys in 2000 (Agista and Rubyanto 2001) and 10 locations from a general fauna survey in 2002 (Imansyah et al. 2003), which were partly confirmed again by cockatoo valley-floor surveys in 2005 and 2006 (Imansyah et al. 2005, 2016). We used only one independent sighting location per prediction pixel. We checked coincidence of the model's local density predictions against these known positives (regarding densities ≥1 individual km^{-2} as predicted presence).

RESULTS

Cockatoo groups were observed at 48 of the 178 point count locations, with an encounter rate of 0.38 groups per point count (after exclusion of flying individuals and truncation). Encounter rates were highest in deciduous monsoon forest (0.91 ± 0.17, n = 22) and palm savanna (0.62 ± 0.11, n = 86) and lowest in the remaining habitat types (0.19 ± 0.10, n = 26 in grassland and scrubland; 0.06 ± 0.04, n = 32 in sparse forest; 0.00, n = 12 in quasi cloud forest; and no data in mangrove forest). The average number of individuals in each group seen was 2.61 individuals (SE = 0.49, n = 31, before truncation). Detection probabilities were described best by a hazard-rate detection function with habitat openness as a covariate (Table 1, Appendix Figure 5).

The DSM with the best fit contained 2 smooth terms with thin plate regression splines of 2 environmental covariates: SAGA wetness index (log-transformed, F = 8.08, edf = 1, P = 0.005; Appendix Table 4) and percentage cover by suitable habitat (palm savanna and deciduous monsoon forest combined and arcsine transformed, F = 7.70, edf = 1, P = 0.006; Figure 3, Appendix Figure 6). The spatial term was excluded as it was not significant (P > 0.3 regardless of spline base, as long as the model accounted for the autocorrelation structure of the points within sampling squares). This best model predicted high cockatoo densities (>8 individuals km^{-2}, locally up to 48 individuals km^{-2}) for 2 forested valleys (Figure 3) where cockatoos are known to be common and where we had high encounter rates at point counts (2.77 ± 0.49 individuals per station, n = 35, presence at 32, up to 6 groups at one station) and flock sizes up to 60 individuals in incidental observations. High densities were also predicted for a dry river valley and a coastal valley that we did not sample, along with moderate densities for several other unsampled locations (Figure 3). Cross-checking these locations with the independent sightings showed that the model had predicted almost all known cockatoo hotspots, and 93% of the 42 independent presence points. The 3 false negatives were very close (<85 m) to pixels with predicted cockatoo presence. The mapped coefficient of variation showed that CV was high in areas with predicted low densities and low in high-density areas. Totaling the modeled population densities over the whole

TABLE 1. Comparison of half-normal and hazard-rate detection functions with and without habitat openness as a covariate. ΔAIC between the 2 top models was small but visual inspection of the detection function confirmed the choice of a hazard-rate key detection function with openness as 2-level covariate, although resulting confidence intervals were slightly larger than with the equivalent half-normal model. C-vM: Cramér-von Mises goodness-of-fit test. ΔAIC: difference in Akaike Information Criterion compared to best model.

Key function	Formula	df	C-vM *P*-value	Average detectability	SE (average detectability)	ΔAIC
Hazard-rate	~openness	3	0.98	0.247	0.050	0.0
Half-normal	~openness	2	0.77	0.224	0.030	1.0
Half-normal	~1	1	0.63	0.252	0.031	8.4
Hazard-rate	~1	2	0.76	0.248	0.055	9.0

island resulted in a population estimate for Komodo Island of 1,113 individuals (95% CI: 587–2,109; Figure 3).

DISCUSSION

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

Our results strongly suggest that the population on Komodo Island is substantial, and we found no evidence that the steep decline reported for the early 2000s has continued (Imansyah et al. 2016). Direct counts collected annually by experienced KNP rangers from vantage points overlooking 6 coastal valleys show an increase from <400 recorded cockatoos for Komodo Island in 2011 to 641 in 2017 (Table 2; Taman Nasional Komodo 2016; KNP unpublished data). This is evidence that the population has certainly been stable and probably increasing over the last 6 yr. As such, in addition to providing protection to the iconic Komodo dragon (Purwandana et al. 2014), KNP appears to be working as a long-term stronghold for the cockatoo. This park's population is by far the largest of the subspecies *occidentalis* and would be the largest for the entire species in the likely case that the distinctive *C. s. citrinocristata* is accorded species rank (Collar and Marsden 2014).

The remoteness and topography of Komodo Island and its fear-inducing dragon appear to provide some natural protection from habitat destruction (e.g., fires and conversion to agriculture) and illegal trapping, but enforcement of legal protection for the cockatoo by park authorities has undoubtedly played an important role in the current situation. Poor soils, steep terrain, and lack of water mean that there has never been much incentive for the single community on the island, which traditionally relied almost exclusively on fishing, to convert land for agriculture (Singleton et al. 2002, Pannell 2013). The Komodo dragons attract a stream of paying visitors (~180,000 in 2018; CNN Travel 2019) and, therefore, KNP is relatively well resourced (Hakim 2017, KLHK and DJ KSDAE 2018). It has 13 field stations, 120 staff (including a permanent presence of ~30 rangers on the islands), several speedboats, and provision for regular patrols and ecological monitoring (Taman Nasional Komodo 2016). Although patrols discover a few poaching incidents every year, these mainly concern marine life, and occasionally deer (2 cases of deer 2009–2015; Taman Nasional Komodo 2016). When over 40 young Komodo dragons were discovered in trade in 2019, they turned out to originate from the species' scarce populations outside KNP's borders (Gokkon 2019). The park has the support of local communities (Walpole and Goodwin 2001), which largely depend economically on tourism (Walpole and Goodwin 2000, 2001; Nurilma et al. 2019). Although KNP's fame, protection, visitors, income, and acceptance are mainly owed to Komodo dragons and marine life (UNESCO 1991), the cockatoos clearly benefit from the protection as well. KNP provides a successful model with regard to methods and resources that could be applied in other protected areas where formal protection has yet to increase cockatoo numbers.

Based on just 5 weeks of fieldwork, and despite the poor accessibility of most of the island and a complex mosaic of habitats, we succeeded in modeling the population of this difficult-to-count species with a distribution map that is suitable for conservation practitioners. Local cockatoo densities fall within the range of estimated densities of other cockatoo species (Marsden and Royle 2015) and the confidence intervals of the predicted densities are narrow enough to be used for assessing conservation status and viability. An independent dataset of cockatoo sightings gave us the opportunity to validate our predictions. During the modeling process this validation process in fact prevented us from accepting a candidate model that neglected residual spatial autocorrelation and instead included the spatial term as a predictor (Gaspard et al. 2019). This model, although favored according to information theoretic criteria, scored very poor hit rates on the independent sightings dataset, as it was dominated by the spatial term. This might be important for other researchers, as >80% of

TABLE 2. Minimum estimate of Yellow-crested Cockatoo numbers from annual monitoring by Komodo National Park authorities derived by summing direct encounters from simultaneous valley-floor counts (Taman Nasional Komodo 2016, KLHK and DJ KSDAE 2018; A. Kefi 2019 personal communication).

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

ecological and biogeographical modeling studies do not account for spatial autocorrelation (Gaspard et al. 2019), which can lead to estimation errors of coefficients of 25% on average (Dormann 2007). Accounting for autocorrelation was particularly important because of our clustered sampling design as opposed to studies where sampling locations are distributed more evenly. However, for parrot species and other rare, highly mobile birds in fragmented rugged habitats, sampling each inhabited patch will often be impractical.

As a 2-step modeling process, the DSM required that we combine the variances of both models (detection function and GAM) to obtain a realistic measure of the variance of our prediction. We used the Delta method (Seber 1982, Miller et al. 2019) for this purpose, ignoring a potential lack of independence between the 2 steps (stemming from the covariate in the detection function), because the more advanced variance propagation method (Williams et al. 2011) is not available for mixed models, and bootstrapping (Hedley and Buckland 2004) should not be used if smooth functions are involved in the model formula (Miller et al. 2013, Bravington et al. 2019). In general, we were forced by the combination of point transects, a covariate in the detection function, and an autocorrelation structure in the DSM to use mixed models (GAMMs instead of GAMs), for which more recent developments in the statistical software have yet to be incorporated. Optimizing adjustments (e.g., use of variance propagation or restricted maximum likelihood) might have increased the precision of our estimates, but spatial density predictions and estimated total population size were so stable across models and modeling engines that final results are unlikely to have differed.

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

Cockatoos in KNP are a showcase for the potential of a 2-level monitoring approach, where annual trend assessment with relatively simple methods could be used to indicate optimal timing of high-effort abundance surveys like distance sampling with DSM. In the future large gaps in published abundance data, coinciding with suspected population declines as in the decades before our study (Imansyah et al. 2016), could be prevented if annual monitoring data are accessible to conservation practitioners who can then trigger more intensive research as soon as a decline becomes apparent and in time for potential mitigations. We found DSM to be an efficient and effective estimator of population size and distribution in the Yellow-crested Cockatoo, and suggest its use for larger populations of the species (e.g., on Sumba and in Timor-Leste), provided that region-specific limiting factors such as trapping pressure can be accounted for. The useful predictions and broad applicability of DSM give it an edge over alternative methods with similar survey effort and make it a powerful tool for estimating population sizes of threatened island species.

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Data depository: Analyses reported in this article can be reproduced partly using data provided by Reuleaux et al. (2020). Sensitive location information was deleted from the dataset so an analysis cannot be reproduced completely with the data in Dryad. Uncensored data files are available from the authors to bona fide researchers.

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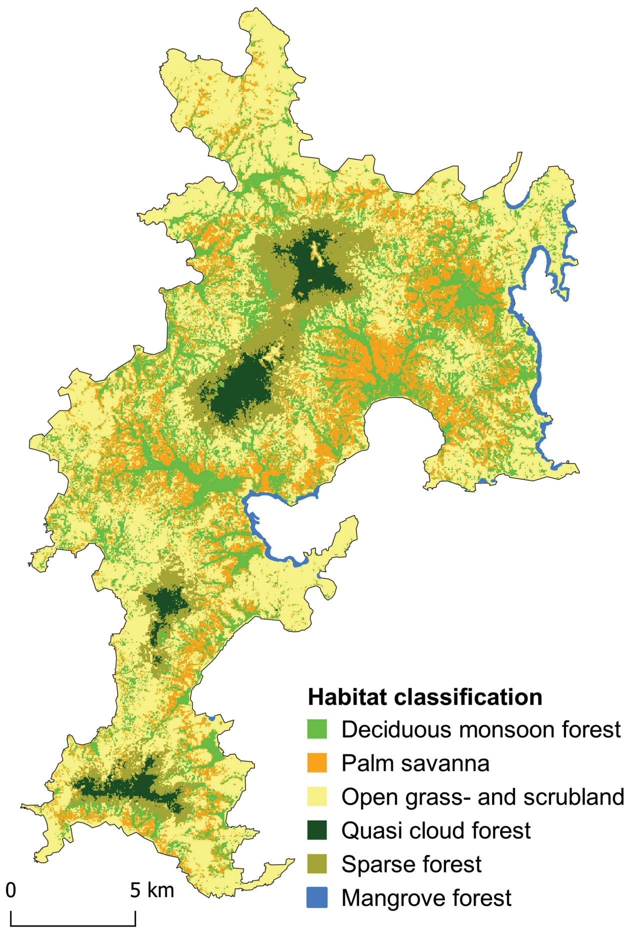
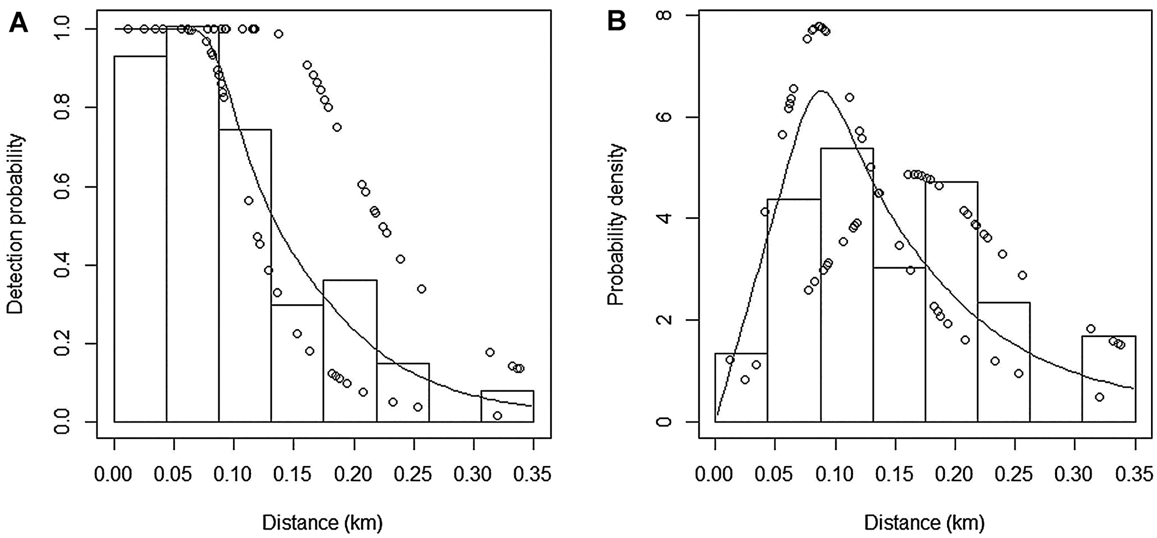
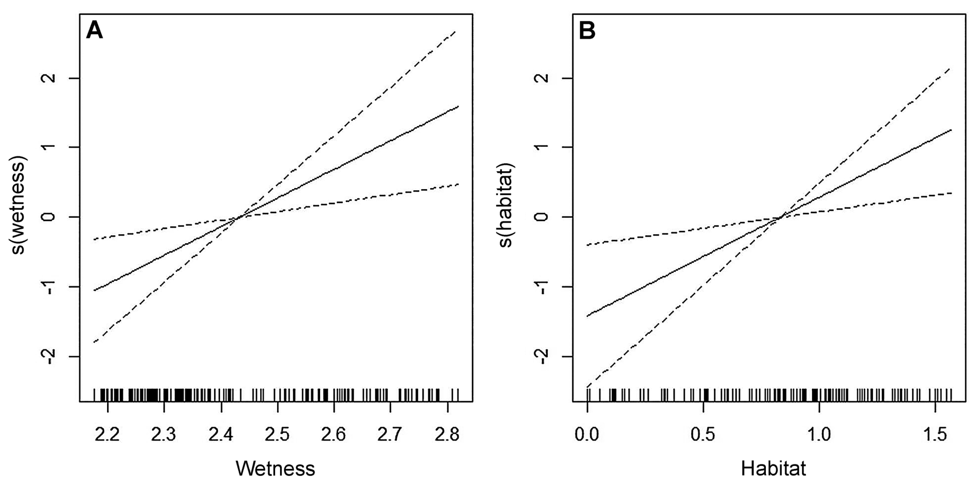


APPENDIX FIGURE 4. Komodo Island habitat classification derived from supervised classification of LANDSAT 8 satellite images with training data from Google Maps. Forest types follow Auffenberg (1980) and Monk et al. (1997) with addition of sparse forest as a transitional zone between quasi cloud forest and open habitat types. Mangrove forest was not distinguished in the supervised classification and was added afterwards (KLHK 2017).



APPENDIX FIGURE 5. Hazard-rate key detection function (**A**) and detection probability density function (**B**) with openness of the habitat as 2-level covariate. Open circles represent individual detections and show the influence of the covariate: in open habitats detection probabilities remained high farther away from the observer (points above the line in [**A**], slopes shallower than the line in [**B**]) than in other habitats (points below the line in [**A**], slopes steeper than the line in [**B**]).



APPENDIX FIGURE 6. Shape of the smooth functions used as environmental predictors for Yellow-crested Cockatoo densities in the GAMM. "Wetness" is the log-transformed SAGA wetness index and "habitat" is the percentage cover by suitable habitat (palm savanna and deciduous monsoon forest combined and arcsine transformed). Ticks on the *x*-axis indicate the sample distribution.

APPENDIX TABLE 3. Habitat type classification on Komodo Island modified from Auffenberg (1980) and Monk et al. (1997).

Habitat class (this study)	Class in Auffenberg 1980	Class in Monk et al. 1997	Location	Main characteristics	Cockatoo observations at point counts [a]	Cover on Komodo Island
Open grassland & scrubland	Steppe	Savanna	Mostly lowlands	Treeless	6	51.5%
Palm savanna	Savanna forest	Savanna	Large lowland areas and many small fragments	Open with tall *Borassus* and *Corypha* palms	37	18.6%
Deciduous monsoon forest	Deciduous monsoon forest	Gallery forest, dry monsoon forest, moist deciduous monsoon forest	Along rivers and in coastal valleys	Closed canopy, *Tamarindus*, *Sterculia*, and *Bredelia*	25	16.5%
Mangrove forest	Mangrove forest	Mangrove forest	Tidal zone	Mangrove species	0	0.5%
Quasi cloud forest	Quasi cloud forest	Mossy forest	>500 m	Moss and lichen on trees, bamboo, rattan	0	3.7%
Sparse forest	Transitional zone to quasi cloud forest	Not mentioned	<500 m, transition zone from quasi cloud forest to scrubland	No closed canopy, bamboo groves	0	9.2%

[a] Number of encounters in our distance sampling survey during point counts.

APPENDIX TABLE 4. Model choice for the density surface model. In model names **S** stands for spatial term (a smoother to the Duchon spline base of the interaction of geographic coordinates s(x,y)), **W** for wetness index (log transformed, s(wetness)), and **H** for the cumulative percentage cover by suitable habitat types (with an arcsine transformation, s(habitat)); edf = effective degrees of freedom, AIC(GAM) = AIC of the equivalent Generalized Additive Model.

Predictors	edf	CI	*P*	AIC(GAM)
W + H [a]				**468**
(Intercept)	1.25	0.55–1.95	**0.001**	
s(wetness)	1		**0.005**	
s(habitat)	1		**0.006**	
S + W + H				**468**
(Intercept)	1.27	0.58–1.96	**<0.001**	
s(x,y)	0		0.445	
s(wetness)	1		**0.003**	
s(habitat)	1		**0.005**	
W				**473**
(Intercept)	1.6	1.03–2.17	**<0.001**	
s(wetness)	1		**<0.001**	
H				**474**
(Intercept)	1.44	0.75–2.13	**<0.001**	
s(habitat)	1		**<0.001**	

[a] Chosen model.