



# Degree of egg-taking by humans determines the fate of maleo (*Macrocephalon maleo*) nesting grounds across Sulawesi

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## Abstract

The maleo (*Macrocephalon maleo*) of Sulawesi, Indonesia, is culturally iconic and Critically Endangered, but the causes of its decline have never been systematically analyzed nor its nesting grounds comprehensively surveyed. We visited 122 previously known and 58 previously unrecorded sites, collecting data and interviewing local people at each site. We used ordinal logistic regression to fit models with combinations of 18 different predation, habitat, and nesting ground variables to determine the strongest predictors of nesting ground success, as represented by maleo numbers. At least 56% of known nesting grounds are now inactive (abandoned), and 63% of remaining active sites host  $\leq 2$  pairs/day at peak season. Egg-taking by humans is the single biggest driver of maleo decline. Protecting eggs in situ predicts higher maleo numbers than protecting eggs through hatchery methods. After egg-taking, quality (not length) of the travel corridor connecting nesting ground to primary forest best predicts nesting ground success. Being inside a federally protected area is not a primary driver of success, and does not ensure persistence: 28% of federally protected nesting grounds have become inactive. Local conservation efforts protected nesting grounds 2–3 times better than federal protection. We update the methodology for assessing nesting ground status, and recommend five measures for maleo conservation, the foremost being to protect nesting grounds from egg-taking by humans at all remaining active sites.

**Keywords** Poaching · Protection · In-situ conservation · Local conservation · Megapode · Indonesia

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## Introduction

The maleo (*Macrocephalon maleo*) is a highly imperiled megapode endemic to, and once common throughout, Indonesia's major island of Sulawesi (BirdLife International 2021). This striking black, white, and salmon-pink chicken-sized bird does not incubate its own eggs: pairs travel from their rainforest habitat to a communal nesting ground, usually a beach or hot spring area, to dig a hole up to a meter deep in which a single large egg is laid and then re-covered with sand or soil. The egg, which is 5–6 times the size of a chicken egg, is incubated by solar or geothermal heat for 2–3 months before the fully-developed chick hatches, burrows to the surface, disperses into adjacent forest and matures completely independent of parental care (Collar et al. 2001).

For centuries humans across Sulawesi have exploited the maleo's egg as a prized delicacy (Dekker 1990). In some areas, traditional (*adat*) law regulated egg exploitation, but in recent decades, with the growth of human populations and gradual weakening of *adat* authority, maleos have declined or disappeared even in areas with strong local *adat* traditions (Argeloo and Dekker 1996; MS pers. obs.). The maleo has been fully protected under Indonesian law since at least 1970 but the laws are rarely enforced; although generally not needed for subsistence, maleo eggs remain a coveted high-status item and are offered openly in local markets and through the internet, generally selling for Rp 25,000–50,000 (c. USD \$2–4) (Froese and Mustari 2019; MS pers. obs.).

The maleo is also experiencing loss of its rainforest habitat. This century alone, across the species' range 14.3% of forest cover has been lost, and what remains is increasingly fragmented (Global Forest Watch 2021). With the disappearance and fragmentation of the native Sulawesi forests upon which maleos depend, not only the quantity and quality of their available habitat is decreasing, but remaining maleo subpopulations are also ever more isolated from one another, compromising their overall genetic diversity and long-term resilience (see Stephens and Sutherland 2008).

Once so numerous that Wallace (1869) described nesting beaches as 'black with maleos', the species has declined rapidly, being repeatedly uplisted from Threatened in 1988 to Vulnerable in 1994, Endangered in 2002, and Critically Endangered in 2021 (BirdLife International 2021). Rangewide, at least 48 nesting grounds were abandoned between 1960 and 2005 (MacKinnon 1981; Dekker 1990; Argeloo 1994; Butchart and Baker 2000; Gorog et al. 2005). Most authors, without analysis, have attributed the decline to egg-collecting, habitat loss, human hunting of adult birds, and predation by monitor lizards, pigs, dogs, and cats (MacKinnon 1981; Dekker 1990; Argeloo 1994; Baker and Butchart 2000; Collar et al. 2001). Only three studies have investigated the causes of decline, and none of these were comprehensive. O'Brien & Kinnaird (1996) and Tasirin et al. (2021) attributed local declines to egg-taking, while Gorog et al. (2005) ignored egg-taking and blamed loss of connectivity between nesting ground and forest. Until now, a lack of scientific completeness and consensus has hampered broad-scale efforts to combat the maleo's long-term decline. However, a definitive understanding of the causes and remedies for the maleo's decline could transform its restoration from a distant wish into a realistic prospect, and in so doing, use the recovery of this high-profile species to pave the way for similar recoveries of other species threatened by over-exploitation.

Here we systematically examine egg-taking, habitat loss, and 16 other factors in order to determine their relative importance in driving the decline of the maleo across its range in Sulawesi. We also seek to assess the effectiveness of federally protected areas such as national parks and nature reserves in conserving maleo nesting grounds. We follow the

established approach of using nesting ground status as an indicator of local maleo population size and health (MacKinnon 1981; Dekker 1990; Argeloo 1994; Butchart and Baker 2000; Gorog et al. 2005). However, the standard method for assessing the status of nesting grounds (Dekker 1990) was developed when the variability between them was much greater than it is today. Thirty years on, this method is insufficiently sensitive to gauge subtler but potentially vital variations in nesting ground and habitat connectivity features. We therefore also propose an updated assessment method using the key drivers of nesting ground success and current range-wide maleo conditions.

## Methods

We visited all nesting grounds previously mentioned in the literature (154 sites), except 32 sites abandoned before 2008, hence  $154 - 32 = 122$  (Baker et al. 2000; Collar et al. 2001; Gorog et al. 2005; Gazi 2008; Froese and Mustari 2019). We followed the convention of defining a site as any maleo nesting location at least 1 km distant from another location (Butchart and Baker 2000). Additionally, across Sulawesi (except the south-western arm, where maleos were never reported and which is now deforested: Collar et al. 2001), we interviewed local residents and explored suitable habitat to discover any previously unreported nesting grounds. We thereby identified and assessed 58 ‘new’ sites, 57 of which (by local testimony and physical evidence) had been extant for many years. (The one genuinely new site was artificially created near a long-declining site: see Summers et al. in prep.) We thus assessed a total of 180 sites across Sulawesi and Buton Island. In the process we were told of but did not visit many rumored long-abandoned maleo nesting grounds (in addition to the aforementioned 32 documented as such) and gained the impression that such sites probably number in the hundreds. We conducted our surveys between November 2017 and February 2021, attempting to visit each site during the local peak nesting season, which varies regionally (Collar et al. 2001).

We collected data on 44 different physical, biological, and socio-cultural aspects of all 180 sites. We began with the parameters developed by Dekker (1990), who rated nesting grounds based on ‘Condition’ (of the nesting ground itself), ‘Access’ (for maleos traveling from nearby forest), and ‘Status’ (overall threat level) (see Table 1, Appendix B). However, significant modifications and additions to the Dekker parameters are needed to better match present-day conditions. First, Dekker’s three categories of maleo Access—‘Free’ ( $\geq 50\%$  contiguous with natural forest); ‘Limited’ ( $\leq 50\%$  contiguous with natural forest); and ‘Disrupted’ (requiring travel through secondary vegetation or converted lands)—were never entirely apposite, as even once-healthy beachside sites like Bangkiriang (Central Sulawesi) and Molobog (North Sulawesi) always had  $< 50\%$  contiguity with forest; moreover, some assessment of *degree* of ‘disruption’ is needed now that the majority of sites fall in that category. Second, the four nesting ground ‘Status’ classifications—‘Not Yet Threatened,’ ‘Threatened,’ ‘Severely Threatened,’ and ‘Abandoned’—are obsolete, as none now is Not Yet Threatened and the large majority would be Severely Threatened. Moreover, while a Severely Threatened nesting ground was defined as used by only a few pairs and expected to be abandoned ‘within the near future,’ some nesting grounds used by a few pairs are now known to have persisted for decades (MS pers. obs.). Thus, like Butchart and Baker (2000), who added ‘control of egg-collection,’ to Dekker’s three parameters we added 15 more to test a total of 18 parameters relating to predation, habitat,

**Table 1** Parameters used to analyze drivers of nesting ground success or abandonment. Ag Agricultural areas; Def Definition; NG nesting ground

Parameter	What parameter measures/describes	Possible values	How assessed	Definitions/Notes
<b>Predation factors</b>				
Travel time (TravTime)	Accessibility to humans	5–270 min	Measured in field	Travel time defined as minutes to a settlement of $\geq 10$ people, or to a major thoroughfare where $\geq 10$ people pass each day based on road destination and nearby populations. Means of travel (foot, motorbike, boat, etc.), although recorded, was not found to be significant in the analysis. Travel time was log transformed to account for a strong left skew
Egg-taking (EggTake)	On-site management of egg poaching	Unlimited, Limited, Hatchery, In situ Protected	Assessed in field and through interviews with locals	'Unlimited' = no on-site management; 'Limited' = some (part-time) management, or cultural inhibitors to poaching (e.g. maleos nesting in graves); 'Hatchery' = eggs relocated to a hatchery; 'Protected' or 'In situ Protected' = human entry to NG controlled, eggs left in place
<b>Habitat factors</b>				
Corridor length (= Distance to Forest)	Distance between NG and non-breeding forest habitat	0–27,070 m	Desktop using satellite imagery	Def: Distance between NG and nearest large patch of unbroken forest. On current landcover image, we manually fitted a 1 km <sup>2</sup> hexagon to the nearest patch of $\geq 95\%$ natural forest cover, then measured distance in m to nearest edge of NG
Corridor quality (CorrQual)	Ease of travel between NG and non-breeding habitat	Poor, Fair, Good	Estimated in field	Def: Overall quality of the habitat linking NG and nearest unbroken forest. Poor = Significantly ( $\geq 50\%$ ) converted (maleos must cross Ag, may cross roads and/or pass near settlements; natural cover patchy and/or discontinuous). Fair = Some conversion (maleos cross Ag and/or roads but significant natural and connected cover, including roost trees, remains). Good = maleos enter directly from forest

**Table 1** (continued)

Parameter	What parameter measures/describes	Possible values	How assessed	Definitions/Notes
<b>NG characteristics</b>				
Active vs. Inactive (= Abandoned; Numbers Class = Zero)	Defines current or historic-only NG	Active, Inactive	Assessed in field, through interviews, and using published sources	Derived from Numbers Class: Numbers Class > 0 for all Active sites, while all Inactive (Abandoned) sites are Numbers Class = Zero. Some Inactive sites may yet be restorable
Numbers class	Index of NG health or success	Zero, Low, Moderate, High	Estimated in field and through interviews with locals	Maximum number of maleo pairs per day on site at peak nesting season. Zero = Inactive. Very Low: < 1 pr/wk. Low: 1 pr/wk – 2 prs/day. Moderate = 3–10 prs/day. High = 11–30 prs/day. Very High ≥ 30 prs/day. See text for amalgamation of classes in analysis
Protection status	Presence/absence of formal protection for NG and/or its environs	None, Federal, Local	Identified through maps and confirmed through government and local sources	Are NG lands and/or their environs under any government-declared protection (national parks, nature reserves, etc.)? None = no formal protection. Federal = part of the national protected areas system (e.g. <i>Taman Nasional, Cagar Alam, Suaka Margasatwa</i> , etc.). Local = some kind of locally-organized protection effort (e.g. conservation group, NGO, etc.). Sites with both Federal and Local protection were listed as Local.
Landscape type	Descriptor of NG context	4 Types: Beachside; Geothermal; Riparian; Balds & other inland	Assessed in field	Formerly only Coastal and Inland were recognized. Beachside = coastal or lakefront (sandy soil). Geothermal = geothermally heated areas, usually forested and inland, varying soil types. Riparian = sandy areas along riverbanks or oxbows. Balds & other inland = various other locations maleos have been found to nest: balds (small patches of bare ground), borrow pits, etc

Table 1 (continued)

Parameter	What parameter measures/describes	Possible values	How assessed	Definitions/Notes
Elevated risk	Liability to flooding, landslides, or other natural disaster	Yes, No	Assessed in field	Is NG located within a flood- or tide-plain, or landslide area? All eggs are lost during periodic inundations. Affects many riparian and some beachside sites. Likely to increase with climate change
Soil diggability	Ease of burrow-digging for maleos	Soft & Abundant, Limited	Assessed in field	Soft=Nest site soil is soft, easy to dig (e.g. sand), and abundant. Limited=Soil is harder, holds its shape when dug, and maleos tend to re-use burrows multiple times. Refers to intrinsic soil characteristics, not potential closure by vegetation (see 'Condition')
Area of warm soil	Area available for nesting	Small, Medium, Large	Measured or estimated in field	Small = < 500 m <sup>2</sup> . Medium = 500–2000 m <sup>2</sup> . Large = > 2000 m <sup>2</sup> . Refers to NG area potentially available, not what is currently used, which may vary considerably over time. NGs of a given area may also have smaller available space due to vegetation encroachment (assessed in 'Condition')
Access (Dekker)	Ease of travel between NG and non-breeding habitat	Free, Limited, Disrupted	Assessed in field	Free=NG surrounded by rainforest for ≥ 50% of its periphery, giving maleos free access. Limited=NG surrounded by rainforest for ≤ 50% of its periphery, giving birds access from one side only. Disrupted=NG fully separated from rainforest; birds must pass through cultivated lands, secondary vegetation, or anthropogenically disturbed areas
Condition (Dekker)	Condition of NG with respect to its potential	Dekker: Intact, Partially Destroyed, Destroyed. This study: Good, Fair, Poor	Assessed in field	Good=NG largely intact. Fair=NG partially closed by vegetation or human influence (e.g. beach structures). Poor=NG destroyed, closed over with vegetation, or otherwise unavailable for nesting. Some 'poor' NGs may be restorable. Dekker definitions are largely retained here but terms have been changed

and physical features suspected of influencing nesting ground success under contemporary conditions.

We also conducted semi-structured interviews to collect information about the history, management, and human activities at each site (see Appendix A). We visited village leaders and elders as a courtesy and to identify community members most knowledgeable about maleos in the area, including current and former egg-takers. By this means we interviewed 157 local people at 125 sites (many long-abandoned sites did not include interviews). Questions were open-ended and phrased neutrally to avoid leading or inhibiting respondents, who might or might not be aware of the maleo's protected status, but interviewees were generally easy to engage in conversation, often expressing fondness for maleos. Responses were not necessarily used *verbatim* as fact—e.g., locally reported numbers of eggs taken were often greater than published numbers for the same site, suggesting a common tendency to exaggerate—but were combined with other sources of evidence to construct a more complete picture of current and historical conditions at nesting grounds.

The 18 predation, habitat, and physical parameters we identified underwent initial screening to determine their suitability in a large-scale range-wide analysis. Six were then excluded from the ensuing modeling exercise, owing to data unsuitability or to overlap with another, stronger parameter (see Appendix B). The 12 parameters included in our models (Table 1) fall into three general categories: *Predation* factors (Travel Time; Egg-Taking), *Habitat* features surrounding the nesting ground (Corridor Length [Distance to Forest]; Corridor Quality), and *Nesting ground* characteristics (Active vs. Inactive; Numbers Class; Protection Status; Landscape Context; Elevated Risk; Soil Diggability; Area; Access [from Dekker]; and Condition [from Dekker]). Table 1 gives the range of possible values for each parameter, details of how it was assessed, and definitions of each parameter.

We used ordinal logistic regression to investigate the relationship between nesting ground success and potential predictors (Table 1). 'Numbers Class'—a defined range of the maximum number of maleo pairs visible per day at peak season—was used as an index of nesting ground health or success, and tested against potential drivers. For statistical analysis, we combined 'Very Low' ( $n=33$ ) and 'Low' ( $n=26$ ) sites into a single 'Low' Numbers Class, and the one 'Very High' site with five 'High' sites into a single 'High' class. These are relative terms by today's standards: the numbers called 'High' today (11–30 pairs) would have been considered fairly low a few decades ago.

We fitted various combinations of 2–6 factors from Table 1 as possible predictors to identify which factors were most important in driving nesting ground success or abandonment. We used an information theoretic approach to compare models and considered the 'best' model to be the one with the lowest AICc score. Where more than one model had  $\Delta AICc < 2$  we chose the most parsimonious. Where two parameters measured correlated factors—e.g., Corridor Quality and Corridor Length—we used both factors in initial tests but retained the weaker driver in later models only if it improved the model. We thus tested the effects of each Table 1 variable in our models, where the most important drivers were retained in the 'best' models, whereas those showing little effect were dropped.

For Corridor Quality and (Dekker) Access, which both describe the area connecting nesting grounds to forest, we performed a simple chi-square test to confirm their similarity while also comparing their respective contributions as predictors in the models. For Protection Status—which was correlated with Corridor Quality—we performed

ordinal logistic regression using only Protection Status as a predictor to test whether this factor alone drives nesting ground success.

## Results

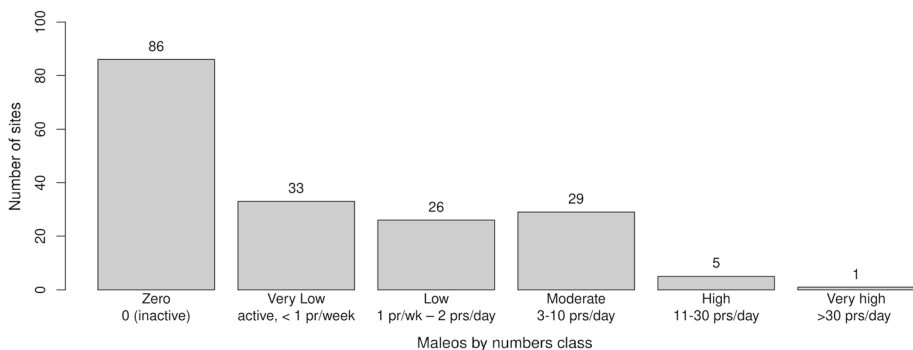
Of the 180 maleo nesting grounds (hereafter often shortened to NGs) we visited, 94 (52%) were Active and 86 (48%) were Inactive (Fig. 1; further details in Summers et al. in prep.). If the 32 Abandoned sites that we did not visit are added (see above), the figures change to 94 (44%) Active and 118 (56%) Inactive sites (total known sites=212). Importantly, 59 (63%) of the 94 Active sites only barely remain active, hosting  $\leq 2$  maleo pairs per day at peak season, with 33 (35%) of them hosting  $< 1$  pair per week. Thirty sites host a Moderate 3–10 maleo pairs/day at peak season and 5 sites host 11–30 prs/day. Only one site hosts more than 30 prs/day.

### Local perceptions of maleo declines

Among 157 local people and authorities interviewed, 146 (93%) reported decline or disappearance of maleos at their site. All of these also acknowledged that some egg-taking by humans took place. Forty-nine (34%) attributed the decline to one or more factors but only two (4% of those offering an explanation) connected it to egg-taking. Cows (3 respondents; 6%) were blamed more often than people. Monitor lizards were cited as the main cause of decline by 13 (27%) of those offering an explanation, and habitat loss or conversion by another 12 (24%). Ten interviewees at abandoned sites insisted that the birds had not died out but rather had ‘moved’ or ‘run’ to another area.

### Nesting ground success driver #1: Degree of Egg-Taking

Considering all the parameters listed in Table 1 as possible drivers of NG success, only three models had delta AICc  $< 2$  and the simplest of these contained only Egg-Taking (EggTake) and Corridor Quality (CorrQual) as predictor variables. This was true whether All sites (i.e. including Inactive/Abandoned/Numbers Class=Zero sites) or only Active sites were being tested (Table 2: Fig. 2). While the combination of EggTake and CorrQual



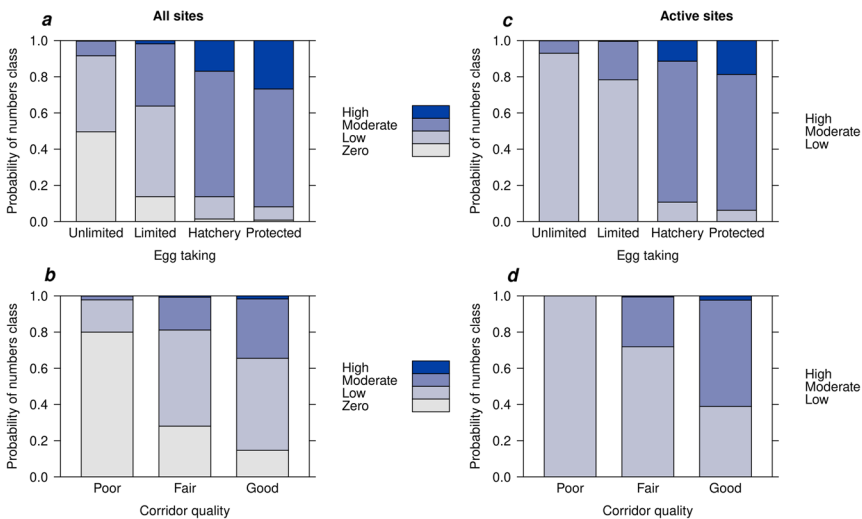
**Fig. 1** Number of nesting grounds in each Numbers Class from our surveys. The number of nesting maleos in each Numbers Class is given in the x-axis. Total number of sites in each class is given above the bar. Total sites surveyed = 180



**Table 2 ‘Best’ model results, drivers of nesting ground success, at All sites and at Active (Numbers Class > Zero) sites only**

Coefficients	All sites		Active sites	
	Beta ( $\beta$ )	SE	Beta ( $\beta$ )	SE
EggTake Limited	1.82	0.66	1.30	0.76
EggTake Hatchery	4.22	0.89	4.71	1.17
EggTake Protected	4.81	1.33	5.29	1.58
CorrQual Fair	2.33	0.48	16.83	0.29
CorrQual Good	3.15	0.52	18.22	0.26
Intercepts				
Zero/Low	1.84	0.40	n/a	n/a
Low/Moderate	4.25	0.49	18.57	0.20
Moderate/High	7.67	0.89	22.74	1.04
AIC	297.90		119.29	

Limited, Hatchery, and Protected degrees of Egg-Taking are shown as compared with Unlimited; and Fair or Good Corridor Quality are shown as compared with Poor. Intercepts denote transitions between Numbers Classes



**Fig. 2 The relationship between maleo numbers class and (a, c) Degrees of Egg-Taking; (b, d) Corridor Quality. A, b: All sites; c, d: Active sites only. Site characteristics are represented along the x-axes while the y-axis represents the probability of each site being found in the Numbers Class indicated by different shades of blue (keys to the right of each figure)**

produced the best model, when each of the two variables was tested alone, only EggTake predicted the most successful sites.

Whether testing All sites or Active sites only, all three managed egg-taking categories (Limited, Hatchery, and Protected) were more likely to be associated with higher Numbers Classes than Unlimited (unmanaged) sites (Table 2, Fig. 2a, c). The highest probability of

being in the highest Numbers Class was associated with sites with active management against egg-taking: EggTake=Protected (0.27) followed by Hatchery (0.17) (Fig. 2a, c).

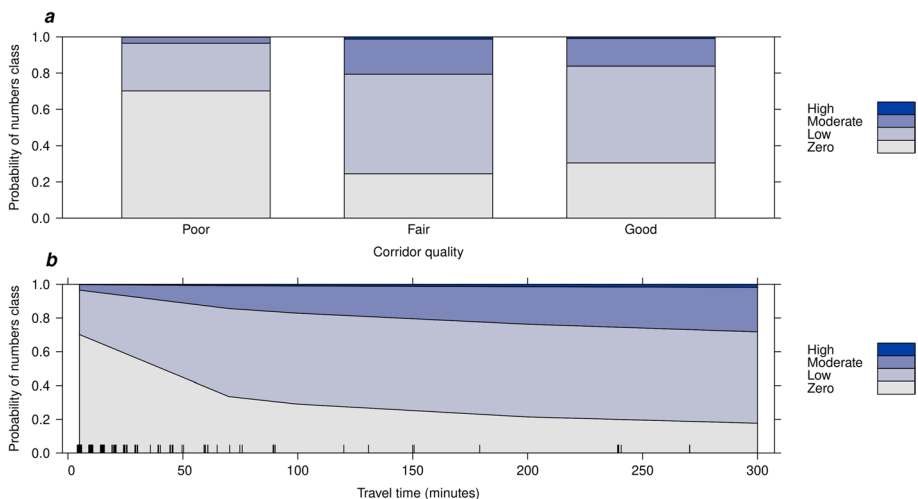
When only Unlimited sites—i.e., sites where egg-taking is not controlled—were considered, Travel Time (a proxy for ease of egg-taking) joined Corridor Quality as the two key drivers of NG success (Figs. 3a, b).

At sites where egg-taking was unmanaged, shorter Travel Times (TravTime) were more often associated with NGs of Zero or Low numbers, whereas longer TravTime rendered NGs more likely to be healthier (Low and Moderate) (Fig. 3b). The sole unmanaged site with High numbers can be accessed only by a long boat journey, effectively curtailing egg-taking.

### Nesting ground success driver #2: Corridor Quality

Corridor Quality was the second most powerful driver in all analyses (considering All sites, Active sites only, and Unlimited sites only). For all sites, CorrQual scores of Fair ( $\beta=2.33$ ,  $SE=0.48$ ) and Good ( $\beta=3.15$ ,  $SE=0.52$ ) were more likely to be associated with higher Numbers Classes than sites with a CorrQual score of Poor (Figs. 2b, d and 3a). When CorrQual was Poor, all the associated NGs had either Zero (Inactive) or Low numbers (Figs. 2 and 3).

All the most successful—i.e. Moderate or High—NGs were associated with corridors of Fair or Good quality. The majority of these healthier NGs had Good quality corridors, with one exception: the most successful by far of all NGs (Libuun, > 50 prs/day, vs. the next best at 11–30 prs/day) had a CorrQual of only Fair. Comparing between classes of CorrQual, Good and Fair corridors performed very similarly but were both very different from Poor.



**Fig. 3** The relationship between maleo Numbers Class and: (a) Corridor Quality; and (b) Travel Time (back-transformed to a linear scale), for sites with no control of egg-taking. Site characteristics are represented along the x-axis while the y-axis represents the probability of each site being found in the Numbers Class indicated by different shades of blue (keys to the right of each figure). Tick marks indicate Travel Time for individual sites

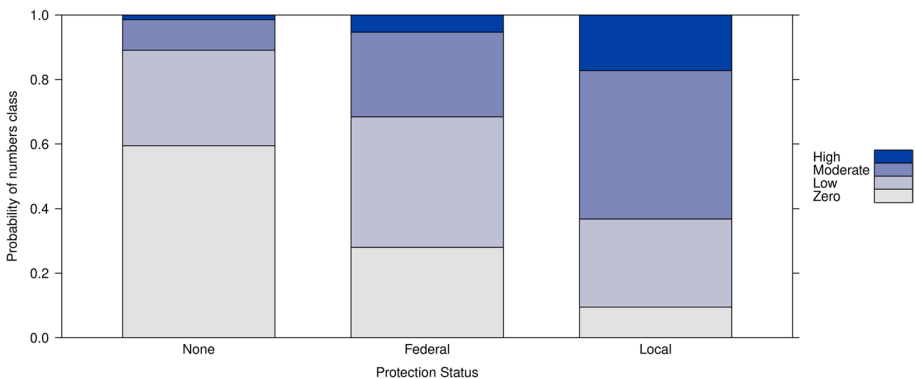
## The role of Protection Status

Protection Status was correlated with both Corridor Quality and Egg-Taking, and thus was positively correlated with nesting ground success, but it was inferior to each of these as a predictor. Using only Protection Status as a predictor, both Federally ( $\beta = 1.33$ , S.E. = 0.32) and Locally ( $\beta = 2.64$ , S.E. = 0.67) protected sites were more likely to be in higher numbers categories than those with no protection. However, being inside a Federally protected area did not reliably protect a nesting ground from becoming abandoned. The probability of an NG becoming abandoned (Inactive) was 0.59 with no protection, 0.28 with Federal protection and 0.09 with Local protection. Conversely, the probability of an NG hosting Moderate or High numbers increased from 0.11 with no protection to 0.32 with Federal protection and 0.63 with Local protection. Thus, although any kind of protection was better than none, Local protection performed markedly better than Federal at both preventing NG abandonment and at promoting higher maleo numbers (Fig. 4). This was true even though Locally protected sites were much less likely ( $p = 0.13$ ) than Federal sites ( $p = 0.78$ ) to have the best (Good) CorrQual. Tellingly, Local sites were much more likely ( $p = 0.63$ ) than Federal sites ( $p = 0.15$ ) to actively control EggTake (Protected or Hatchery).

## Effects of other nesting ground characteristics

We found a small effect of Elevated Risk on NG success. Although this parameter was not included in the 'best' models, it appeared in 33% of the models that had AICc < 2, suggesting that it was an important factor at some sites.

We found no meaningful effect of Area on NG success. Although Area appeared in the 'best' models for some Active analyses, it did not improve the model because all values were similar across all categories. We also found no meaningful effect of Soil Digability (hardness or softness of nesting substrate) on NG success. Although within a given site, maleos prefer to nest in areas with softer soil (MS pers. obs.), this factor was not a predictor between sites. Finally, we found no significant effect of Landscape Type on NG success, suggesting that although an NG's geophysical features may vary widely between



**Fig. 4** The relationship between maleo Numbers Class and Protection Status. *None* = no formal protection. *Federal* = the site is part of the national protected area system, such as national parks, nature reserves, and nature tourism areas. *Local* = a local entity (NGO or other) is engaged in protecting the site. Protection Status is represented along the x-axis while the y-axis represents the probability of each site being found in the Numbers Class indicated by different shades of blue (key to the right of the figure)

Beachside, Geothermal, Riparian, and Bald/Other Inland, levels of egg-taking and corridor quality remain the primary determinants of its success.

### Effects of Dekker parameters

As noted above and in Appendix B, Dekker's 'Status' parameter was eliminated owing to its mismatch with current conditions. His Access and Condition parameters had some correlation with NG success, but their inclusion did not improve the models. Dekker Access was significantly correlated with CorrQual (Pearson's chi-squared test:  $X^2=143.4$ ,  $df=6$ ,  $p < 2.2e^{-16}$ ). Dekker 'Free', 'Limited', and 'Disrupted' were similar to CorrQual of 'Good', 'Fair', and 'Poor' respectively, but CorrQual consistently outperformed Access in the models. Dekker Condition was included in the 'best' models for some analyses, but its usefulness was largely that all 'Destroyed' sites had a Numbers Class of Zero; Conditions of 'Partially Intact' and 'Intact' did not correlate well with other Numbers Classes.

### Discussion

Our analysis shows clearly that the degree of egg-taking by humans is the most important determinant of the success or failure of maleo nesting grounds today, followed by the quality—not the length—of the corridor linking the nesting ground to non-breeding forest habitat. Inclusion in the national protected areas system is correlated with nesting ground success, but does not prevent nesting ground abandonment.

#### Driver #1: egg-taking by humans

Several lines of evidence reveal the defining role of egg-taking as the most important driver of nesting ground success. First, the only NGs where maleos reached 'High' numbers (> 10 pairs a day) were those where egg-taking was absent or very limited, through 'In Situ Protected' or 'Hatchery' management (5 sites), or at one site by the long access journey by boat. In situ protection—guarding the NG while leaving eggs in place—was more likely to produce High maleo numbers than removing eggs to a hatchery ( $p=0.26$  vs. 0.17). Second, the few (7) sites showing a Trend of 'Stable or Increasing' were all Protected or Hatchery sites; Trends of sites with Unlimited or Limited EggTake were invariably 'Decreasing' or 'Unknown'. Third, at sites where EggTake was Unlimited, ease of human access, as approximated by TravTime, was a defining factor in its success. Shorter TravTime increased the probability of an NG being Inactive, and vice versa (Fig. 3b). At managed sites, where human access is controlled, TravTime was not significant.

Three examples illustrate these findings. First, at Libuun in eastern Central Sulawesi, protecting eggs in situ through an NGO-community agreement, with no significant change in habitat or natural predation, produced a four-fold increase in maleo numbers over 14 years (Tasirin et al. 2021). This was true even though CorrQual at this site was only Fair. Second, maleos once nested throughout the Tanjung Kramet peninsula in western Central Sulawesi, but now do so only inside the sandy graves of a cemetery there, where people hesitate to dig (Summers 2019). Third, egg-taking is controlled (through hatcheries) at four out of nine NGs in northern Sulawesi's Bogani Nani Wartabone National Park (BNWNP), but at only one out of 14 in Central Sulawesi's Cagar Alam Morowali. Both reserves have high-quality forest habitat and Fair to Good Corridor Quality. Evidently in consequence,

the number of sites hosting Zero or Low maleos is only four out of nine (44%) in BNWNP but 12 out of 14 (86%) in Morowali, which in the 1990s enjoyed NGO management and maleo numbers above 10 pairs/day at multiple locations. (Butchart and Baker 2000).

### Egg-taking in human context

Our interviewees, like those of Froese and Mustari (2019) and Maulany et al. (2021), rarely acknowledged the role of human egg-taking in the maleo's decline, instead blaming predation by monitor lizards, habitat loss, or other factors. When discussing their own egg-taking, interviewees frequently added qualifiers such as, 'we only took them to eat, not to sell,' 'If I don't take it, a monitor lizard will,' or 'we only dug eggs when we were passing by [to do something else]'. Moreover, many interviewees complained about other people (immigrants, people from other villages, souvenir buyers) taking eggs, while implying that their own egg-taking was rightful. Yet, whether the persistent taking of eggs despite the long-standing laws protecting them is due to lack of awareness or a studied unwillingness to acknowledge egg-taking's effects, people frequently expressed surprise and dismay at its final consequences. As the village head put it at one site where the maleo had disappeared, 'People didn't think that one day it wouldn't be there.' Or, in another, 'I would have protected them. But now it's too late.'

The maleo's popularity—as Sulawesi's mascot, its name or image is ubiquitous—stems partly from a genuine love for and pride in the species (Manado Tribune 2020), and partly from centuries-old traditions around harvest and use of its eggs (Argeloo and Dekker 1996). There is no evidence, however, that these traditions were ever 'sustainable'. *Adat* controls likely helped, but it may also simply be that in earlier eras maleo numbers were much higher and human populations much lower, so that the impact of harvest, whether controlled or uncontrolled, would not have been as apparent as it is today, when maleos are few and humans many. Now, at least, the evidence is unequivocal and undeniable: site by site, egg-taking is driving the maleo to extinction and simply must be controlled at all remaining nesting grounds if this fate is to be avoided.

### Driver #2: habitat—corridor quality

It is the *quality* rather than the *length* of travel corridors—the habitat (corridor) linking a given NG to the nearest large patch of primary forest habitat—that constitutes the second important driver of NG success. In general, corridor quality—its provision of cover, roost trees, and perhaps foraging opportunities—decreases with increasing length: the longer the distance between NG and forest, the more opportunity there is for anthropogenic influences to reduce corridor quality, but *CorrQual* was always chosen above *Corridor Length* in the models. This suggests that a maleo NG might retain or recover its health even if distant from primary forest, as long as a high-quality corridor is maintained or restored. In our survey, at least 12 NGs remained active despite being > 5 km distant from intact forest; one site remained active, albeit only barely, although separated from forest by > 24 km (Summers et al. in prep.).

While *CorrQual*, unlike *Egg-Taking*, was a poor predictor of numbers of maleos at a site, it was the best predictor to simply differentiate between Active and Inactive sites: 80% of sites with Poor *CorrQual* but only 43% of sites with Fair or Good *CorrQual* were Inactive (Fig. 2b). Where egg-taking is unmanaged, corridor quality can make the difference between complete abandonment and low-level persistence. Improving *CorrQual*, even just from Poor ( $p=0.22$ ) to Fair ( $p=0.66$ ), triples the probability that the site will remain

active (Fig. 3a). Thus, even where egg-taking is uncontrolled, it may be possible to prolong maleo presence by improving corridor quality through increasing native vegetation cover and preserving roost trees, ‘buying time’ until egg-taking can be addressed.

### The role of protected areas

Our results showed that protection status is not a driver of maleo NG success. Nevertheless, NGs inside protected areas were more likely to have higher numbers than those outside. Two factors may explain this: habitat quality and control of egg-taking. NGs inside protected areas generally have better habitat quality than those outside: most protected areas contain large tracts of the native forest that maleos require. While almost half (49%) (57/117) of NGs with no protection had Poor CorrQual, none within protected areas ( $n=63$ ) did so. Moreover, egg-taking control programs, such as hatcheries, are more likely to be initiated within federally protected areas than outside them. Of Sulawesi’s 11 active hatchery programs, all but one (91%) were in or directly abutting federally protected areas. However, location within a federally protected area does not, by itself, assure a site’s safety: some 28% of NGs inside federally protected areas were Inactive. Active control of egg-taking must therefore be undertaken if federally protected NGs are to survive. Notably, Local protection, usually involving NGOs, proved 2–3 times more effective in our analysis than Federal protection, suggesting that bottom-up efforts engaging local people can be more effective in promoting healthy nesting grounds than top-down authority (Fig. 4).

### Potentially important site-specific drivers

Several parameters may affect success at individual nesting grounds. ‘Trend’ is clearly an important descriptor of NG health, but in our survey the very small number of NGs showing anything other than a decreasing trend made analysis of this parameter impossible. Elevated Risk, which was included in some models, is influential at riparian or beachside sites where periodic inundation—probably increasing with climate change—can destroy all eggs. Additionally, although small sample sizes prohibited testing this factor, higher-than-normal levels of hunting and snaring (elevated Other Predation) may well have accelerated the decline of certain sites. (Conversely, at Ngolos in Central Sulawesi local people believe that hunting is cursed, and only take eggs; maleos have persisted there at low levels but have disappeared from nearby sites.) Finally, the total available Area of an NG may once have been an important factor when maleo numbers were larger, but today, with numbers reduced, Area was not limiting.

### Proposed new nesting ground assessment method

The Dekker method for assessing nesting grounds has been an invaluable tool for thirty years, but our results show that other parameters are now more effective for discerning differences between today’s maleo sites. We therefore propose a set of five new parameters to provide a field-friendly, simple, and sufficiently-complete assessment summary, allowing comparisons between NGs and over time. Each NG should be evaluated for (see details in Table 1):

- (1) Egg-taking: Unlimited, Limited, Hatchery, and In Situ Protected.

- (2) Corridor quality: Poor, Fair, Good.
- (3) Travel time: in minutes.
- (4) Maleo numbers: estimated maximum pairs per day.
- (5) Population trend (if known).

These five factors, when combined, can provide a status profile of any nesting ground, as a guide to its own management needs and potential as well as for comparison with other sites. Other factors, e.g. Protection Status, Elevated Risk, and socio-cultural factors, may furnish helpful supplementary information, depending on the aims of the assessment. An estimate of Maleo Numbers (#4) or Numbers Class (Zero, Low, Moderate, High) alone can also serve as a general indicator of NG health.

## Conclusion: saving the maleo

The maleo's ongoing precipitous decline, as reflected by its recent uplisting to Critically Endangered, is due primarily to uncontrolled egg-taking by humans, and secondarily to degradation of the habitat linking nesting grounds to larger patches of Sulawesi forest. Less than half the 212 known maleo nesting grounds remain active, and of those about two-thirds host no more than two pairs per day at peak nesting season. Only six sites host more than 10 maleo pairs per day, thus making virtually all sites, and therefore the entire world-wide maleo population, highly vulnerable as expanding human populations, agricultural pressure, deforestation, mining, climate unpredictability, and other threats increase in scale and speed. Nevertheless, the maleo's survival today can still be secured by human action. Based on the findings and perceptions of this study, we offer five recommendations for maleo conservation, in order of priority.

- (1) *End egg-taking at all remaining active maleo sites.* Simply ending human egg-taking—preferably through in situ protection (Tasirin et al. 2021), less desirably through hatchery programs (Clements 2009)—is *essential* to reversing maleo population declines. This means persuading local communities, both outside and inside protected areas, to acknowledge the damage that egg-taking does to maleo populations, and motivating and engaging them to celebrate the species in other ways. Inside protected areas, resources currently allocated to building and running hatcheries would be better spent on fully guarding nesting grounds; with eggs protected in situ, high habitat quality within protected areas should lead to the fastest possible population recovery.
- (2) *Maintain or restore maleo corridors.* Protection and/or restoration of habitat in degraded maleo corridors could help maintain and boost populations. Maleos are reportedly shy of humans, and travel mostly on foot (this study; Collar et al. 2001), thus large open areas, settlements, and busy roads are major obstructions which, particularly in combination, maleos cannot be expected to negotiate. Preventing such developments and minimizing human disturbance in known maleo corridors is therefore vital. Moreover, replanting open areas to increase cover and promote succession to native forest, including roost trees, could improve essential corridor quality.
- (3) *Maintain large patches of native Sulawesi forest.* Despite significant deforestation to date, our results suggest that the availability of non-breeding forest habitat in Sulawesi is not currently limiting maleo populations and should be sufficient to stabilize and even increase those populations if recommendations 1–2 are followed. Nevertheless, the maleo's long-term survival depends on the persistence of tracts of forest that are

large enough to sustain sub-populations in the absence of gene-flow with other sub-populations. Just how much non-breeding forest habitat maleos require is currently unknown; the precautionary principle thus requires that the current already-diminished area of Sulawesi's native forest should be maintained, with no further loss.

- (4) *Build and enhance a culture of respect for wildlife laws.* The maleo enjoys strong protection under Indonesian law, and in those places where the law is observed (i.e. egg-taking is controlled) the species survives better. Active programs of engagement with communities and authorities to promote greater awareness of and compliance with laws relating to the maleo are vital to building broad public support for maleo conservation and specifically the renunciation of egg-taking.
- (5) *Support and encourage local and island-wide pride in and care for maleos.* The most effective maleo conservation efforts at present are locally-driven; more are needed. Community activities celebrating the uniqueness and preciousness of the maleo, such as those held on 'World Maleo Day' (November 21), build enthusiasm among Sulawesi citizens for the species and lay the groundwork for its conservation (Chairunnisa 2020; Bano 2021).

The above actions are achievable; they are fully within the range of realistic, affordable, and feasible activities given today's conditions and resources, and have already been accomplished at some sites (Tasirin et al. 2021). It remains now to scale them up to other parts of Sulawesi and redirect some existing hatchery efforts. The restoration of the maleo, Sulawesi's treasured mascot, is within reach.

## Appendix A

### Interview questions for local informants at nesting grounds (NGs)

1. How often do you visit this NG, how do you get here, and how long does it take?
2. Do you come specifically to visit this NG, or do you stop here on the way to somewhere else? (If the latter, please describe)
3. When did you last see maleos at this NG?
4. How many maleos did you see?
5. What is the maximum number of pairs you might see/eggs that you and others might get on one day at peak season, nowadays?
6. Have you spent time observing maleos here, and if so, what have you seen them do?
7. When did you first start coming to this NG?
8. If you think back on that time [or another memorable time marker], would you say the number of maleos today is the same, more, or fewer than in the past? By how much?
9. If there has been a change, what do you think caused it?
10. Are there any regulations, now or in the past, about who can dig eggs, or how? If so, please describe. How, if at all, are the regulations enforced?
11. What are eggs used for, now and in the past, by you and by others? (consumption, sale, local traditions, etc.)
12. Do you or others do any hunting or snaring of adult maleos around this site, now or in the past?
13. Are there any local names for maleos, or traditions associated with maleos?



## Appendix B

Parameters eliminated from the modeling exercise

Parameter	What parameter measures/describes	Possible values	How assessed	Definitions/Notes	Reason for elimination
<b>Predation factors</b>					
Means of travel	Accessibility to humans	Foot, Motorbike, Boat, Special	Assessed in field	'Motorbike,' and 'Boat' may also include Foot. 'Special' indicates special accessibility circumstances at this site, e.g. must use zipline to cross river. In general, apart from time, listing order reflects decreasing ease of access	Travel time is more informative and consistent across sites. May be important at selected sites
Other predation	Natural predators, hunting or snaring of adult maleos	Normal, elevated, reduced	Assessed in field and through interviews with locals	All sites are assumed to be 'normal,' with natural predation present and some hunting/snaring of adult maleos, unless there is evidence to suggest unusually high or low levels	Unable to analyze as sample sizes other than 'normal' too small. May be important at selected sites
<b>NG characteristics</b>					
Trend	Index of NG success	Unknown, Declining, Stable or Increasing	Estimated in field, through interviews, and using published sources	Unknown for some sites. Declining= numbers on a generally-declining trend, regardless of absolute values. Stable or Increasing= numbers generally stable or increasing, regardless of absolute values	Unable to analyze as sample sizes other than 'declining' too small. May be important at selected sites

## undefined(continued)

Parameter	What parameter measures/describes	Possible values	How assessed	Definitions/Notes	Reason for elimination
Single site vs. Complex	Descriptor of NG context	Single Site, Complex	Assessed in field	Single site = maleos nest in one contiguous spot. Complex = maleos may nest in multiple spots within a larger landscape, e.g. along a riverbank or beach. Sites separated by $\geq 1$ km between spots are defined as separate sites	Captured in 'Area of Warm Soil.' Marks a distinction without a difference
Elevation	Descriptor of NG context	0–1175 m	Measured in field	Used GPS to measure elevation	Beachside sites are Elevation = 0, others are variable. Captured in 'Landscape Type,' which is more informative
<b>Dekker ratings</b>					
Status (Dekker)	Index of NG success	Abandoned, Severely Threatened (ST), Threatened (T), Not Yet Threatened (NYT)	Assessed in field	Abandoned = no eggs are laid at the NG. ST = Only a few pairs make use of the NG and may be expected to abandon it within the near future. T = NG still used for egg laying by a considerable population of maleos, but it is not considered to be safe for the future, either because eggs are massively collected or because of adverse developments in the area, or both. NYT = the NG is still intact and freely accessible, while egg collecting takes place at a low level or not at all	Definitions no longer valid. Captured in Numbers Class, which is more informative

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**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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