Massive declines and local recoveries: First range-wide assessment spotlights ending egg-taking as key to the survival of the *Macrocephalon maleo* (Maleo)

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ABSTRACT

The communally nesting, Critically Endangered *Macrocephalon maleo* (Maleo) is an iconic species endemic to Sulawesi, Indonesia, yet despite decades of legal protection its populations have declined sharply across its range. We performed the first-ever range-wide field survey of Maleo nesting grounds, visiting 122 known and identifying 58 previously unrecorded sites, collecting physical and biological data and interviewing local informants at each. We added information from the literature for another 48 abandoned sites, documenting a total of 228 historic and current nesting grounds. We then constructed a profile of historic and current populations and area of occupancy (AOO) units across Sulawesi. Between 1980 and 2019, 55% of active nesting grounds became inactive, and all but one of the 94 sites that remained active in 2019 had fewer birds. In 2019, 83% of all nesting grounds active in 1980 were either completely abandoned or just barely active, hosting no more than 2 pairs day^{-1} at peak season. However, conservation efforts have also produced significant recoveries and discoveries. Our survey increased the range of described landscape types where Maleo nest from 2 to 4, and documented Maleo nesting in previously unrecorded places, including artificially created sandy areas. As the Maleo's maximum travel distance beyond nesting grounds is unknown, we applied a cost-based approach using possible maximum travel distances of 25, 40, and 50 km to define AOO "Units" that represent a set of separate range-wide subpopulations defined by each maximum travel distance. Between 1980 and 2019, the overall AOO declined by 37%, 26%, and 19% at maximum travel distances of 25, 40, and 50 km, respectively; the number of active nesting grounds in each isolated unit declined by 58%, 78%, and 80%, respectively; and fragmentation (i.e., the total number of units) increased by 5%, 100%, and 125%, respectively. In some areas, Maleo may be changing their behavior in response to egg predation by humans. Ending egg-taking has now clearly been shown to produce Maleo increases in multiple locations and is crucial to range-wide recovery of the species.

Keywords: AOO, connectivity, Critically Endangered, fragmentation, historical, *Macrocephalon maleo*, predation, Sulawesi

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LAY SUMMARY

- In 2019, we surveyed 228 nesting grounds of the Critically Endangered *Macrocephalon maleo* (Maleo), mascot of Sulawesi, Indonesia, throughout its range. We documented the current and historical status of all known and many previously unknown sites.
- We found that since 1980 the number of active sites and the number of Maleo attending them declined sharply, due primarily to egg-taking by humans.
- The Maleo's range across the island has also shrunk and become more fragmented into isolated subpopulations, reducing opportunities for breeding, genetic mixing, and social interactions. We present three possible fragmentation scenarios.
- Maleo are nesting in a broader range of landscapes than previously known, including newly created sites, and may be changing their behavior in response to predation pressure from humans.
- Despite the overall decline of the species, a few sites are now recovering through egg protection; preventing egg-taking at more existing and possible new sites is the key to averting the Maleo's extinction.

Penurunan besar-besaran dan pemulihan lokal: pengkajian berskala lengkap pertama menekankan penghentian pengambilan telur sebagai kunci kebertahanan hidup Maleo

ABSTRAK

Maleo (*Macrocephalon maleo*) yang Terancam Punah Kritis adalah spesies ikonik di Sulawesi, Indonesia, yang bertelur secara komunal. Namun meskipun telah dilindungi oleh hukum selama beberapa dekade, populasinya telah menurun tajam di seluruh wilayah. Kami melakukan survei lapangan komprehensif pertama ke tempat-tempat bertelur Maleo, mengunjungi 122 lokasi yang sebelumnya diketahui dan 58 lokasi yang belum pernah didokumentikasikan sebelumnya, dengan mengumpulkan data dan mewawancarai informan lokal pada setiap lokasi. Terhadap ini, kami menambahkan informasi dari literatur untuk 48 lokasi lain yang sudah terlantar, sehingga secara keseluruhan mendokumentasikan 228 tempat bertelur Maleo historis dan yang masih ada saat ini. Kemudian kami menyusun profil populasi-populasi historis dan yang masih ada saat ini serta unit-unit wilayah hunian (*Area of Occupancy, AOO*) populasi Maleo di seluruh Sulawesi. Antara tahun 1980 dan 2019, 55% tempat bertelur aktif menjadi tidak aktif, dan dari 94 tempat bertelur yang tetap aktif pada tahun 2019, semuanya, kecuali satu, mengalami penurunan jumlah burungnya. Dari keseluruhan tempat bertelur yang aktif pada tahun 1980, 83% sudah terlantar sama sekali, atau menginangi dua atau kurang pasangan/hari pada musim puncak. Meskipun demikian, upaya-upaya konservasi juga telah menghasilkan beberapa pemulihan dan penemuan yang signifikan. Survei kami meningkatkan jumlah tipe lanskap tempat bertelur yang telah dijelaskan dari dua menjadi empat, dan mendokumentasikan Maleo yang bertelur di lokasi-lokasi yang sebelumnya tidak tercatat, termasuk tempat bertelur yang dibuat secara artifisial. Jarak tempuh maksimum (*Maximum Travel Distance, MTD*) Maleo di luar tempat bertelur tidak diketahui, tetapi kami menggunakan pendekatan 'berbasis biaya (*cost-based*)' yang melibatkan kemungkinan *MTDs* sejauh 25, 40, dan 50 km untuk menentukan ‘Unit-Unit’ *AOO* yang mewakili serangkaian subpopulasi-subpopulasi seluruh wilayah terpisah yang ditentukan oleh setiap *MTD*. Melalui penggunaan *MTDs* ini, kami memperkirakan, bahwa antara tahun 1980 dan 2019, jumlah *AOO* Maleo menurun sebesar 37%, 26%, dan 19% pada jarak 25, 40, dan 50 km secara berturut-turut, dan jumlah rata-rata *NGs* dalam satu unit menurun sebesar 58%, 78%, dan 80%. Sementara itu, fragmentasi (jumlah Unit) meningkat sebesar 5%, 100%, dan 125%. Di beberapa lokasi, Maleo mungkin telah mengubah perilakunya sebagai respons terhadap pemangsaan telur. Mengakhiri pengambilan telur oleh manusia telah secara jelas terbukti memfasilitasi peningkatan Maleo di berbagai lokasi, dan ini adalah kunci bagi pemulihan spesiesnya di seluruh wilayah jelajah.

Kata kunci: wilayah hunian, konektivitas, Terancam Punah Kritis, fragmentasi, historis, *Macrocephalon maleo*, pemangsaan, Sulawesi

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INTRODUCTION

Macrocephalon maleo (Maleo) was once so numerous that in 1869 British explorer Alfred Russel Wallace (1869) described beaches in its native range of Sulawesi, Indonesia, as “black with Maleos”. Today, however, this unique black, white, and salmon-pink chicken-sized megapode is Critically Endangered owing to a precipitous decline throughout its range (BirdLife International 2021). Adult Maleo pairs spend most of their time in primary forest, but travel to communal nesting grounds, where they select a spot for laying a single, huge egg. The egg is incubated by solar or geothermal heat, and the chick emerges fully feathered 60–90 days later, immediately flying off into the forest to develop without any parental care (Collar et al. 2001).

The Maleo is culturally important in Sulawesi (including Buton Island), appearing as the official mascot of provinces and municipalities, as well as in brand names and images all over the island (Argeloo and Dekker 1996, Collar et al. 2001, Manado Tribune 2020). Its widespread popularity, however, has not prevented its sharp decline toward extinction, due primarily to the taking of its large eggs by humans (Summers et al. 2023). The Maleo has been protected under Indonesian laws since at least 1970, but the laws are rarely enforced, such that uncontrolled egg-taking—for sale or consumption as a prestigious delicacy—has long been routine and ubiquitous (MacKinnon 1981, Baker and Butchart 2000, Tasirin et al. 2021). Meanwhile, since 2000, Sulawesi has lost 14.4% of its forest habitat, with the rest increasingly fragmented and threatened by mining, oil palm and other agriculture, development, and other human activities (Global Forest Watch 2024). Habitat loss—specifically, degradation of corridors connecting nesting grounds to primary forest—is the second most important driver of Maleo declines (Summers et al. 2023), as healthy corridors are critical for adult pairs to access nesting grounds for laying and for newly hatched chicks to reach interior forest to develop to adulthood.

Maleo populations use the same communal nesting grounds for decades or even centuries (Collar et al. 2001), and the locations of these sites tend to be well-known to local people. Historically, some nesting grounds spanned up to a kilometer or more of beach, with 200 or more Maleo pairs in attendance daily at peak season. The ease of harvesting their undefended eggs gave rise to complex systems for harvest privileges, lease of nesting grounds, and sale of eggs, playing a major role in local social systems and economies (Wallace 1869, Uno 1949, Argeloo and Dekker 1996, this study). All known Maleo nesting grounds show evidence of human exploitation (this study). Conservation efforts focused on protecting eggs have been in existence since the 1980s, but until recently few have shown signs of success. To date, most such efforts have used on-site hatcheries, where eggs are dug up and placed in enclosures for protection until hatching. Previously, none of these programs had shown increased Maleo numbers (MacKinnon 1981), but this has recently changed: the hatchery program at Tambun in Bogani Nani National Park (Figure 1, #20), which saw no increase in the number of Maleo visiting from 2001 to 2009 (Clements 2009), now reports a 150% increase from 2002 to 2020, citing improved supervision since 2012 to protect eggs and prevent human disturbance. (Bashari et al. 2022). Meanwhile, in the Tompotika region a different strategy, leaving eggs in situ while guarding them against poaching, has resulted in 4- to 7-fold increases in Maleo numbers at 3 nesting grounds since 2006 (Tasirin et al. 2021, Anonymous 2024).

Several field surveys of Maleo nesting grounds took place in the 1990s and early 2000s (Dekker 1990, Argeloo 1994, Butchart and Baker 2000, Baker et al. 2000, Gorog et al. 2005, Gazi 2008). Ever since, estimates of the overall range-wide population abundance of the species, in combination with estimates of the number of eggs laid per female per year, have been based on these surveys (BirdLife International 2025). However, not all surveys used the same methods, and each assessed only a portion of the species’ range, which has since undergone widespread development and conversion to human

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activities. A fully range-wide nesting ground survey, using consistent methods, has never been attempted and is thus long overdue. We undertook the first such survey, beginning with sites mentioned in the literature in English and Bahasa Indonesia, and interviewing local people in every part of the island (except the southwest peninsula, where the species has never been reported and which is now deforested: Collar et al. 2001) to discover any additional sites not previously recorded. In a separate study, we analyzed data collected at all these sites to identify the primary drivers of nesting ground decline or recovery across the species' range, and examined how attitudes and behaviors of local residents affected nearby Maleo nesting grounds and numbers. We found that degree of egg-taking was the most important predictor of nesting ground status, followed by the quality (not the length) of travel corridors (Summers et al. 2023). To inform future conservation efforts, here we seek to establish the former and current status of Maleo nesting grounds across the species' entire range; to assess the possible effects of the recent decline on the distribution and connectivity of populations; and to identify the full range of landscape types used for nesting, while assessing changes over time in the use of nesting areas.

METHODS

Historic and Current Nesting Ground Locations and Status

We visited all 122 Maleo nesting grounds throughout Sulawesi described in the literature as being active or recently abandoned (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 nesting ground as any Maleo nesting location at least 1 km distant from another (Butchart and Baker 2000). We conducted our surveys over a total of 148 days between November 2017 and April 2021, with most visits occurring in 2018–2019; there may have been further changes since our visits. We aimed to visit each site during the local peak nesting season, which varies regionally (see Supplementary Material S1, Table A).

Traveling by car, boat, and foot throughout all 51 *kabupatens* (regencies) outside of Sulawesi's southwestern peninsula, we stopped in hundreds of villages and sought out informants with experience of the Maleo, who were generally well-known to fellow villagers. Many of the 209 informants that we interviewed were current or former egg-diggers, as well as village heads, hunters and woodsmen, community leaders, and elders. We explored widely in areas where Maleo were known or rumored to occur historically or currently, and inquired in areas where Maleo had not been reported. In this way, we identified and assessed an additional 58 previously undocumented sites. We thus visited a total of 180 sites (see Supplementary Material S2, Table B).

Across Sulawesi, we likely missed some sites where Maleo occasionally or regularly nest. Of the 180 sites we visited, some quite remote, all had evidence of some human exploitation and thus were known to local people, but there may be nesting grounds in extremely remote areas that have escaped human notice. Nevertheless, given (1) the number and geographical breadth of our field explorations and interviews with local people, (2) the thoroughness with which local people are familiar with Maleo in their areas, and (3) the drastic decline in overall Maleo numbers, both the number and size of active sites not included here are likely to be low (none hosting >2 pairs per day). On the other hand, given the species' long-term decline, some abandoned sites probably disappeared before they could be recorded.

At each of the 180 surveyed nesting grounds, we collected data on 44 different physical, biological, and socio-cultural parameters (see Supplementary Material S2, Table C), including an

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estimate of the maximum number of Maleo attending per day at peak season, degree of control of egg-taking, length and quality of the vegetation corridor connecting the nesting ground to adjacent forest, formal protection status, and an assessment of the nesting ground's landscape context or type.

At each site, we also conducted semi-structured interviews, in Bahasa Indonesia or a local language, with a total of 209 local residents who had current and/or historical knowledge of that nesting ground, inquiring about current and past human interactions with Maleo at the nesting ground, including how many individuals it hosted currently and formerly, how humans have exploited it, and what management, restrictions or local traditions might have been applied to it. Statements from local informants were not incorporated verbatim but were evaluated in combination with other evidence. Details on interviews with local residents are in Supplementary Material S2, D, and discussed more completely in Summers et al. (2023).

In addition to the 180 sites we visited in our field survey, we included information on 48 additional nesting grounds recorded in the literature as abandoned prior to our survey (Supplementary Material S2, Table B). Eighteen of these sites were abandoned prior to 1980 (Uno 1949, Wind 1984, MacKinnon 1978, MacKinnon 1981, Watling 1983, Baltzer 1990, Dekker 1990, Andrew and Holmes 1990, Indrawan 1992, Argeloo 1994, Prawiradilaga 1997, Baker et al. 2000, Butchart and Baker 2000, Gorog et al. 2005, Gazi 2008, Froese and Mustari 2019). The total number of known historic and current sites for this analysis was thus 228 (180 visited + 48 long abandoned). Figure 1 and Supplementary Materials S1, Table A display and list these sites, with associated details.

We chose 1980 as the historic benchmark to compare against current (for simplicity we use 2019) Maleo status for 3 reasons. First, this date represents approximately 3 generations of Maleo prior to the current survey, as one Maleo generation (defined as the average age of a parent bird) is estimated to be 13 years (BirdLife International 2025) and IUCN considers three generations the interval to assess species (IUCN Standards and Petitions Committee 2024). Second, 1980 marked the beginning of a period of increased Maleo research and hence information in the resulting literature. Third, many local people whom we interviewed remembered 1980 as the start of a decade and were able to give details from that date.

Precise numbers of Maleo attending nesting grounds were available for 9 sites. We used these to calibrate physical signs (e.g., Maleo seen or heard, tracks, feathers, or eggshells; number and age of nest-pits; area and characteristics of sand or soil; vegetation growth) and to identify ranges or "Numbers Classes" of Maleo pairs visiting nesting grounds in 2019 (see below, and Supplementary Material S2, Table E). At each nesting ground visited, we assessed the physical evidence and combined it with information from the literature and interviews with local residents to assign the site to a current Numbers Class, based on the estimated maximum number of Maleo pairs attending per day at peak season. We then used these same Numbers Classes to categorize Maleo numbers at each nesting ground in 1980. For the 1980 estimates, most evidence came from the literature or interviews, and we took a conservative approach: Numbers Classes given for 1980 are applied to *minimum* estimates of Maleo visiting and true numbers at many sites may well have been much higher (if so, this would simply increase the magnitude of the decline we report in this analysis). We classified each nesting ground into 1 of 7 Numbers Classes in 1980 and 2019, as follows.

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Changes in Area of Occupancy and Connectivity across Sulawesi

Area of occupancy (AOO) represents the area within the full extent of the species range that is actually occupied by the species at a given time (IUCN Standards and Petitions Committee 2024). Maleo travel primarily on foot (Collar et al. 2001), but the maximum distance they typically travel from natal or adopted nesting grounds is unknown. We use subpopulation here to refer to a fraction of the overall Maleo population that shares one continuous geographic area but does not mix physically or genetically with other subpopulations. Therefore, to estimate Maleo AOO and to identify possible isolated subpopulations across Sulawesi, we chose a range of plausible maximum distances that an individual could travel from a given nesting ground. These distances represent the maximum radial area within which a Maleo may range and encounter conspecifics (for instance, for breeding), and also the maximum distance between any two nesting grounds used by a single Maleo, should this occur.

We used 25 km as the smallest possible maximum range value or maximum travel distance (MTD). In our survey, the four most distant nesting grounds were 23–27 km from the nearest patches of intact forest, demonstrating that some birds are already traveling at least that distance. Also, Argeloo (1994) reported a tagged female that was seen at a nesting ground ~25 km from her natal nesting ground. To date, evidence of Maleo traveling farther than 27 km is thin, but the possibility that they do so is clear. Thus, we chose 40 km and 50 km as 2 additional maximum travel thresholds that we consider plausible, in order to explore the possible effects of decline on the connectivity of populations and the implications for conservation.

For each MTD, and for historic and current nesting grounds, we used geographic information systems (GIS) in a cost-based distance approach (deSmith et al. 2018) to define a series of “buffers” around each active nesting ground. Using raster cell sizes of 30 × 30 m and the forest landcover map from Vancutsem et al. (2021), we assigned all land the same low-cost value (1) except for the shoreline and inland lakes, which were set to high values (1,000) to act as barriers. We ran the distance allocation tool within ArcGIS Pro Version 3.1.0 (ESRI 2023) at distances of 25, 40, and 50 km around all active nesting grounds in 1980 and 2019. Each distance allocation run was then converted from a raster to a polygon shapefile to create buffers. Where these buffers overlapped, they were combined into a single geographical subpopulation unit, (hereafter, “Unit”), where multiple nesting grounds shared the same area and genetic mixing could be assumed to occur. Total area, area of forest, and numbers of nesting grounds were calculated within each Unit. We examine forest habitat and other features of these Units in a separate analysis (Summers et al. personal communication)

Classification and Changing Use of Landscapes for Maleo Nesting

During our survey, we recorded physical features, such as landscape context, heat source and nesting substrate, of each nesting ground (see Supplementary Material S2, Table C) and developed a new classification of nesting ground landscape types, encompassing all sites and based on the similarity of these features. We also noted any further evidence, such as the placement of eggs within the nesting ground, shell fragments indicative of egg predation, and soil temperatures, that could indicate specific responses to local conditions.

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RESULTS

Historic and Current Nesting Ground Locations and Status

Figure 1 shows the locations of the 180 Maleo nesting grounds we visited during our survey, including the 58 previously undocumented nesting grounds, plus the 48 additional long-abandoned nesting grounds from the literature (total 228 sites). Details for each of these sites are given in Supplementary Material S1, Table A.

Figure 2 shows the massive decline in Maleo numbers at these 228 sites between 1980 and 2019. Between 1980 and 2019, Maleo numbers declined in all regions and in all landscape types across Sulawesi (Figures 2, 3, and 6). Both the *number of active nesting grounds*, and the *number of Maleo attending each active nesting ground* declined sharply during this period. Overall, active nesting grounds declined from 210 to 94 in 1980–2019, an extinction of 116 sites (55%) in 39 years (a rate of ~3 yr^{-1}). At least 18 additional sites were known to have already been abandoned before 1980. Nesting grounds with both healthy and ailing Numbers Classes became inactive: of 82 sites hosting Moderate, High, Very High, or Highest numbers in 1980, 58 (71%) became Abandoned by 2019, while 38 of 50 (76%) Low or Very Low sites did the same. Most nesting grounds lost many, not few birds: 138 (66%) of sites in 1980 declined by two Numbers Classes or more. Moreover, while two-thirds of active nesting grounds (138 or 66%) in 1980 hosted Moderate or greater numbers, with only one-third (38) with Low or Very Low, in 2019 those proportions were reversed: of the 94 nesting grounds still active in 2019, 59 (63%) hosted Low or Very Low numbers, while only 35 (37%) hosted more than two pairs/day. In 1980, 8 nesting grounds hosted >50 pairs day^{-1}, and 13 nesting grounds hosted 31–50; none of these 21 "mega-nesting grounds" still hosted such numbers in 2019. In 1980, the most common nesting ground class was Moderate; in 2019, it was Very Low. Only one of 14 Very Low nesting grounds in 1980 was still active in 2019, and no nesting grounds inactive in 1980 returned to activity in 2019. Only a single nesting ground active in 1980 (#162, Libuun) hosted increased numbers in 2019 (see Discussion). In sum, 193 (85%) of all 228 known nesting grounds, and 175 (83%) of the 210 Maleo nesting grounds that were known to be active in 1980, are now either inactive or host no more than 2 pairs day^{-1}.

Changes in Area of Occupancy and Connectivity across Sulawesi

Between 1980 and 2019, under all MTD scenarios, the area of Sulawesi occupied by Maleo both shrank in size and became more fragmented, with the extent of shrinkage and degree of fragmentation varying with MTD (Figures 4 and 5). AOO is determined by MTDs around active nesting grounds; losing 116 active nesting grounds between 1980 and 2019 resulted in a 37% reduction in total AOO at 25-km MTD; 26% at 40 km, and 19% at 50 km (Figure 5A). Meanwhile, the number of separate Maleo subpopulation Units increased from 19 in 1980 to 20 in 2019 at an MTD of 25 km; from 7 to 14 for 40 km; and from 4 to 9 for 50 km (Figure 5C). Thus, the effects of decreasing AOO and increasing fragmentation between 1980 and 2019 work in opposite directions: as MTD increases between 25, 40, and 50 km, the change in total AOO becomes proportionately smaller (−37%, −26%, and −19% respectively), while the change in total fragmentation is proportionately larger (+5%, +100%, and +125% respectively) (Figure 5A, C).

The chances of an individual Maleo within any Unit encountering conspecifics—and therefore the possibility of genetic and social mixing—are determined by the size and number of other nesting grounds within its Unit, both of which decreased sharply between 1980 and 2019. Fragmentation decreased the size of subpopulations but increased their number (Figure 5B, C), and as the total number of active nesting grounds declined (Figure 3), the average number of active nesting grounds within a Unit also decreased—by 58%, 78%, and 80%, respectively, at MTDs of 25, 40, and 50 km (Figure 5D).

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Classification and Changing Use of Landscapes for Maleo Nesting

[LEVEL HEADING 3] *Classification of landscape types*

Where previous studies have distinguished only between "coastal" and "inland" sites (Dekker 1990, Argeloo 1994, Gorog et al. 2005), our more comprehensive survey found that Maleos can nest in a somewhat broader range of landscapes than previously described. In most cases, these are not novel changes, but are long-used nesting grounds known to local people but not yet documented by the scientific community. Our results suggested 4 general landscape types of Maleo nesting grounds—Beachside, Geothermal, Riparian, and Balds and Other Inland. Table 2 and Figure 6 give details about these new nesting ground landscape types, and numbers of each type in 1980 and 2019.

Beachside nesting grounds, the most common type (e.g., Panua #65, Tikke #122, and Bangkiriang #172), provide both numerous locations and large nesting areas of sun-warmed sand on the coast or lakeshore. But with 66% of these nesting grounds having become inactive since 1980, Beachside sites have also been lost more than other landscape types. Geothermal nesting grounds, which include all sites offering ground-source heat for incubation, have declined by 55%, and include some of today's most well-known sites, such as Tambun (#20), Muara Pusian (#18), and Saluki (#105). Geothermal sites offer the clear advantage of a consistent and concentrated heat source. Riparian or riverside sites, which were not previously considered a distinct landscape type, often comprise multiple small nesting "spots" strung out along several kilometers of sandy riverbanks (e.g., #139–146 and #222–224), providing Maleo with numerous nesting options and making egg-taking by humans more difficult and less efficient; these have declined by 31% and make up 29% of current nesting grounds. Balds and Other Inland sites include open, sunny, rocky, vegetation-free patches ("balds") (e.g., Mempaho #212, Balita #167, and Labuanunuk #81), which offer average daytime soil temperatures up to 4°C warmer than Beachside sites but in an often very hard substrate; this category also includes various other landscapes, but comprises only 9% of currently active nesting grounds.

[LEVEL HEADING 3] *Changing use of nesting landscapes*

We observed at least 15 nesting grounds where Maleo egg-laying behavior reflects the influence of egg-taking by humans. At two sites, Tanjung Kramet (#88) and Deaga (#26), Maleos historically nested widely along beaches adjacent to local cemeteries. According to local people, decades ago Maleo only nested on the beaches, and not in the neighboring cemeteries. Gradually, however, there was a transition towards Maleo laying their eggs in the cemeteries' enclosed sandy gravesites, while beachside sites have continued to remain available but unused. Currently, Maleo lay eggs only directly within the gravesites, where people are more hesitant to dig for them (Summers 2019). Similarly, Maleo historically nested at many locations along the river at the Salubanga site (#119), but although most of these remain available, the birds now lay only in an area reputed as a center of terrorist activity, which local people have avoided for the last 20 or so years.

At some nesting grounds, such as Pakuli (#103) and Batumenangis (#23), Maleo often nest far back under rock overhangs with ≤35 cm of ground clearance, despite soil temperatures being up to 3°C cooler there and the wide availability of areas with warmer substrates. The overhangs, however, prevent human egg-taking, which evidence suggests has been longstanding

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and intense. Similarly, at Pahulongo (#42), Bente (#226) and some other sites, Maleos often place their egg amongst the roots of trees, even when warmer open sites are available. Local informants noted that this may impose a cost for hatching chicks, with rootlets obstructing them from reaching the soil surface. But it also makes eggs significantly harder for humans to locate. Moreover, long-time egg-diggers at a number of greatly reduced sites, such as Pantai Taipa (#204) and Tiwo Complex (#2), reported that Maleo now are much "wilder" than in former times, becoming harder to observe, laying their eggs deeper, and selecting concealed laying spots within the nesting grounds rather than areas of open sand. In these cases, the observed changes in nesting pattern may simply be the result of higher survival of eggs laid in the safer locations. Nevertheless, given that Maleo lay in the company of conspecifics (Tasirin et al. 2021), and pairs explore and carefully select their laying spot within the nesting ground (Collar et al. 2001), this novel behavior could also reflect social learning and local changes in Maleo nesting "culture" in the face of human egg-taking (Whiten 2021).

We also documented Maleo nesting in entirely new—and likely marginal—locations. At two sites, former Beachside nesting grounds near busy villages have been destroyed or abandoned, but small numbers of Maleo were instead nesting in nearby coconut plantations (Salunggaluki #117) and newly planted cornfields (Kayumoloa #118). However, there appear to be no selective advantages in these choices, which may simply reflect displaced Maleo resorting to the nearest seemingly suitable alternative. Whether they will continue to nest there, and whether chicks will successfully hatch and return, needs to be studied, but neither seems likely.

Encouragingly, we also found evidence that Maleo will adopt newly available suitable locations not previously used for nesting. At the Danau Buton Complex (#168), over several years Maleo began nesting in the loose gravel of a newly excavated borrow pit near a series of Beachside nesting spots. We also recorded Maleo laying in an artificially created sandy area, Wosu Atas (#197), in the corridor near a declining Beachside nesting ground. Around 2016, workers noticed Maleo nesting activity in a pile of sand brought in for construction, and an enclosed sandy area was then created in which eggs were laid. In places the sand provided was apparently too shallow: birds dug down ~40–80 cm, where they hit a harder natural substrate, and ceased further activity. Local informants stated that most eggs at this site are currently taken for sale or consumption, but protecting eggs there in future through a hatchery is under discussion (Nur Mallo et al. 2023).

[LEVEL HEADING 3] ***Effects of management interventions***

Most Maleo conservation efforts to date have used semi-natural hatcheries, where eggs are removed from nesting grounds and reburied in a nearby enclosure; our surveys found 12 such current or recent hatchery projects across Sulawesi. Some of these, such as Taba (#135) and Kombot (#32), have failed due to inconsistent or discontinued management. Others, including Saluki (#105) and Tanjung Matop (#80), show evidence of selling eggs or other types of misconduct (this study, Paino 2019). Still others, like Muara Pusian (#18) and Batumenangis (#23), although not showing increasing Maleo numbers, are probably helping to slow their decline.

However, there are sites where Maleo decline has been not only slowed, but reversed. At Tambun (#20) in Bogani Nani Wartabone National Park (BNWNP), an NGO-government conservation partnership using a semi-natural hatchery has resulted in a 150% increase in the number of visiting pairs from 2002 to 2020 (Bashari et al. 2022). The Hungayono site (#44), also in BNWNP and taking a similar approach, also appears to be increasing (this study). In Morowali Nature Reserve, the long-time government ranger

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managing the Busanga nesting ground (#193) reported that, despite having a hatchery, he often leaves eggs in place, guarding them in situ, and in 2019 was seeing as many as 17 pairs day^{-1}, up from 1 pair day^{-1} in 2000 (Butchart and Baker 2000). At 3 nesting grounds on the Tompotika Peninsula, an NGO forming partnerships with local communities and utilizing a so-called “Respect for Nature” approach leaves eggs in place while guarding the nesting ground against human poaching or disturbance, resulting in 7-fold increases in 10–14 years at both Libuun (#162) and Kaumosongi (#166), and a 4-fold increase in five years at Panganian (#163) (Anonymous 2024). Having dwindled to only a few pairs per day in the early 2000s, restored Libuun is currently the sole Maleo nesting ground that hosts >50 pairs day^{-1}, with as many as 199 individuals being counted there at one time in 2022 (Anonymous 2022).

DISCUSSION

Declines in Numbers of Birds and Nesting Grounds

This first-ever range-wide survey and historical reconstruction of all Maleo nesting grounds reveals a catastrophic population decline between 1980 and 2019. In just this period of <40 years, 55% of nesting grounds that were active in 1980 became inactive, and the number of breeding individuals at the remaining active nesting grounds declined sharply. The fact that 85% of all known nesting grounds—including several once hosting hundreds of pairs per day—now host 2 or fewer pairs per day, or none at all, reflects a species in precipitous decline, with numerous remnant populations on the verge of “winking out” across its range.

Furthermore, the steep reduction observed between 1980 and 2019 represents the continuation of a longer-term decline, as the presence of 18 already abandoned nesting grounds in 1980 attests. Even a century ago (in 1907–1930), overexploitation of eggs led to the disappearance of a series of beachside nesting grounds in Gorontalo (Uno 1949). Concurrently, the human population of Sulawesi—and its egg-taking and habitat-destroying pressures—has burgeoned, increasing 5-fold from ~4 million in 1915 to nearly 20 million in 2019 (Biro Pusat Statistik Indonesia 1981; Badan Pusat Statistik Indonesia 2020).

Conservationists must be alert to the fact that current low Maleo numbers could be causing a negative spiral of Allee effects (Stephens and Sutherland 1999, Courchamp et al. 2008). Of active nesting grounds, the most common Numbers Class is now the lowest, hosting fewer than 1 pair per week. Thus, in most extant locations, Maleo pairs are now laying eggs solitarily at greatly depleted nesting grounds, where they encounter few or no conspecifics. Maleo pairs prefer to nest in the company of other Maleo (Tasirin et al. 2021); the fact that so many Maleo now cannot do so will likely affect social interactions and genetic diversity in local populations, and may also compromise the learning, development, and well-being of individual birds in ways that further harm population persistence.

In addition, the decline in numbers at Maleo nesting grounds could possibly be exacerbating the effects of egg predation. If communal nesting evolved as a predator-satiation strategy in this species (MacKinnon 1981, Gorog et al. 2005), the success of this strategy depends on prey (egg) numbers being high enough to satiate the predator. Human predators are hard to satiate: Ruthig and Gramera (2019) found that nesting aggregations among Olive Ridley Turtles (*Lepidochelys olivacea*) actually made them more, not less, vulnerable to predation by humans. But when egg numbers are low, even non-human predators, such as monitor lizards (*Varanus salvator*), may fail to reach satiation, making all eggs more vulnerable than they would

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have been if dispersed (Gascoigne and Lipcius 2004, Zwolak et al. 2022).

Finally, many Very Low nesting grounds where a few pairs still lay may already be functionally extinct, because adult Maleo and chicks may differ in their travel ability. Maleo are long-lived, with some individuals in captivity continuing to breed past the age of 30 years (A. O'Sullivan, personal communication). At some of these sites, corridor quality may have degraded to the point where adult pairs may still be able to reach the nesting ground for egg-laying, but the few chicks that do hatch cannot navigate those same corridor conditions to successfully disperse to inland forest.

Changes in Area of Occupancy and Connectivity across Sulawesi

In the period 1980–2019, Maleo show a loss of overall AOO at all MTDs. The change is greatest at shorter MTDs (37% at 25 km, vs. 26% at 40 km and 19% at 50 km). As higher AOO is generally related to healthier populations (IUCN Standards and Petitions Committee 2024), any loss of AOO is concerning for a Critically Endangered species. Moreover, particularly for a culturally important species like the Maleo, as its AOO shrinks, there is an associated 'extinction of experience' amongst local human communities as their opportunities to encounter and value wild Maleo are reduced (Soga and Gaston 2016).

Since 1980, Maleo have also suffered the effects of loss of connectivity and reduced numbers of nesting grounds in each subpopulation Unit. The change in the number of separate Units—and thus the change in degree of overall habitat fragmentation the species experiences—increases sharply with increasing MTD: while total Units grow by only 5% (from 19 to 20) at the 25-km MTD, they double from 7 to 14 at 40 km and from 4 to 9 at 50 km. These Units represent isolated subpopulations that are assumed not to mix; increasing fragmentation thus reduces the overall health of the population through reduced genetic fitness and increased vulnerability to local extinctions of one or more subpopulations (Herbener et al. 2012, Lino et al. 2018, Prugh et al. 2008). Similarly, the average number of nesting grounds within each Unit—an indicator of how many total Maleo are in that subpopulation and able to encounter each other—fell by 58% at 25 km MTD, but by 78% and 80% at 40 and 50 km MTDs, respectively. Thus, the *degree* of change experienced by Maleo since 1980 in overall AOO, amount of fragmentation, and number of nesting grounds in a Unit depends on whether MTDs are shorter or longer. However, in all scenarios, the consequences are or are likely to be negative to overall population health, connectivity, genetic fitness and individual well-being. Further research on Maleo home range and travel outside of nesting grounds is needed to better understand these dynamics. Meanwhile, ongoing forest loss and conversion throughout Sulawesi (Vancutsem 2021, Global Forest Watch 2024) make it safe to assume that travel between nesting grounds within a single Unit is more difficult now than it was in 1980. This range-wide decline in overall habitat quality suggests that Maleo today may have to walk farther now than previously, just to access sufficient suitable habitat.

Notably, even in 1980 and at the largest MTD tested (50 km), the entire extent of Maleo occurrence across Sulawesi remained divided into at least 4–5 separate subpopulation Units (here, to mark the distinction, called "biogeographic sections"), and may have been that way even when historical Maleo populations were at their peak (c.f. Figure 4C). This biogeographic pattern echoes the geological history of the island, and is also seen in other taxa, including macaques (*Macaca* spp.) and toads (*Bufo* spp.) (Evans et al. 2003), lizards (*Lamprolepis* spp.) (Linkem et al. 2013), squirrels (*Nannosciurinae*) (Hawkins et al. 2016), and tarsiers (*Tarsius* spp.) (Zakaria et al. 2023). Maleo do not appear ever to have been reported in the zones between

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these biogeographic sections, which include the Poso area in the center of the island, a band across southeast Sulawesi south of the Malili Lakes, the marine gap around Buton Island, and a line bisecting the northern arm near Gorontalo City (see Figure 1). These ancient gaps in AOO suggest that Maleo travel has at times been inhibited by landscape features, but why this might be the case is unclear (south of the Malili Lakes, for instance, much seemingly suitable forest and potential riparian nesting areas are available but show no evidence of ever having been used). Maleo from each of these biogeographic sections may thus represent long-isolated and perhaps genetically distinct subpopulations. To date, molecular studies have only tested Maleo from within the same biogeographic section, and found little variation (Saputra and Yuda 2020); future genetic investigations should examine birds from different sections to provide clues to historical biogeography and current genetic diversity.

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Changing Use and Restoration of Landscape Types for Maleo Nesting

A restored Maleo population of the future would comprise different proportions of nesting ground landscape types than in the past. In previous centuries, most Sulawesi beaches likely hosted Maleo, and Beachside nesting grounds were not only the most common type, but also comprised most former Maleo mega-nesting grounds, which hosted hundreds of birds each day. However, growing human settlements have also concentrated on coastlines, resulting in the disproportionate (66%) destruction of Beachside nesting grounds and corridor areas. Since 1980, all the largest Beachside mega-nesting grounds (e.g., Molobog [#15], Bangkiriang [#172], and Watiwa [#203]) have either been abandoned or reduced to hosting only a few pairs/day. Conversely, however, restoration of even a few Beachside nesting grounds could have a large positive impact on the overall Maleo population, as seen at Libuun (#162).

Some geothermal sites may also have a high potential for restoration, by virtue of being located in national parks which, while not necessarily protecting nesting grounds (Summers et al. 2023), often offer superior-quality surrounding forest habitat (Vancutsem et al. 2021). Riparian sites have suffered smaller declines than Beachside and Geothermal, and their often-remote locations may decrease their vulnerability to future human impacts. Their most obvious drawback is their risk of loss to river flooding, which may increase with climate change. Two of the largest such sites in 1980, Pintu Kubur (#139) and Batukatunda (#191), are now inactive and appear to have suffered this fate. Balds and other inland sites, where Maleos have always nested in relatively low numbers, may represent a high-risk/high-reward landscape type. Their higher temperatures may accelerate incubation times, but the hard substrate causes most nesting burrows, although repeatedly re-used, to be quite shallow, which may put eggs at higher risk from human and non-human predators; in general, these nesting grounds are lower priority for restoration.

Although they depend entirely on environmental heat sources for egg incubation, the fact that Maleo nest in a broader and more plastic range of locations than previously thought expands the possibilities for future conservation and possible re-introduction. Some of the locations we documented, such as coconut plantations and cornfields, may represent opportunistic short-term responses by Maleo that are unable to lay at customary sites and simply make use of the most suitable available substitute. However, the fact that Maleo continued to use a new borrow pit site (Danau Buton Complex, #168) over a period of years suggests that (1) they are capable of establishing new customary laying habits, and (2) simple steps to improve or create nesting ground habitat there and elsewhere could reap rewards in improved nesting success. The birds' use of the artificially created Wosu Atas (#197) site is particularly significant. This opens up the possibility of strategically creating new artificial nesting grounds in critical areas, especially where they help to maintain or enhance connectivity between Units or in other places where it has been lost. It is worth noting, however, that both of these novel nesting sites are near other active nesting grounds. To what extent Maleo would be able to locate and colonize new and more isolated areas, even with suitable nesting sites provided, remains uncertain, but is well worthy of experimentation.

Conclusion: The Way Forward

The success of Maleo recovery efforts will reflect the degree to which egg-taking can be prevented at existing nesting grounds as well as at any newly created sites (Tasirin et al. 2021, Summers et al. 2023). As is underscored by our documentation of Maleo laying eggs in places less accessible to humans, such as cemeteries, rock overhangs, and amongst tree-roots, the taking of eggs by humans is clearly the primary threat which must be eliminated if the decline of the species is to be slowed. However, with 94 sites still active island-wide—let alone new sites that might be created—there are still ample nesting grounds where simply ending the illegal practice of human egg-taking can firmly be predicted to lead to the natural recovery of local Maleo numbers.

The currently favored model for Maleo conservation will not achieve this aim. Separate analysis has revealed that simply being located in a protected area does not prevent the decline or abandonment of nesting grounds; active protection of eggs is required (Summers et al. 2023). Hatcheries, while the most common conservation approach, show mixed success: in general, these projects have proven to be better than no egg protection at all, but less effective than in situ egg protection (Summers et al. 2023). Hatchery procedures could be modified to more closely mimic natural processes, such as by releasing newly hatched chicks at night, which is when they naturally emerge and when they may be less vulnerable to natural predators such as monitor lizards and raptors, rather than in daylight, as at present (M. Summers personal observation). In addition, the practice of holding chicks for weeks or months in so-called 'habituation' cages should be discontinued: Maleo chicks need no help habituating themselves to their environment, and there is no evidence that this aids their survival in any way; in fact, it may be undermining it.

Even so, better-managed hatchery projects such as Hungayono (#44) and Tambun (#20), and, most importantly, protection of eggs in situ, as in Tompotika (#162, #163, and #166) and Busanga (#193), clearly have the potential to restore Maleo numbers and bring back healthy populations. The fact that Libuun enjoys Maleo numbers more than triple those of the next highest site, despite having mediocre corridor habitat, indicates that even second-quality nesting ground habitat can be sufficient for significant Maleo recovery, when egg-taking is controlled (Summers et al. 2023).

Thus, as grim as the Maleo's decline and current status may appear, there is considerable reason for hope. Although sorely depleted, Maleo remain extant at dozens of locations spread widely across Sulawesi. Maleo pairs lay eggs in a broad range of landscapes, use new and artificially created locations for nesting, and may have some capacity to change their behavior in response to threats and changing conditions. Clear methods for preventing egg-taking have been proven to restore their populations. Advocates keen to conserve them still have many choices of where to focus new conservation efforts, while popular support for the Maleo remains very strong in Sulawesi and worldwide (Manado Tribune 2020, Admin Lore Lindu 2023, Tarigan and Alangkara 2023). Extinction of Sulawesi's Critically Endangered mascot is clearly avoidable: channeling that popular support into awareness, pride, and disciplined programs to prevent egg-

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taking, especially if combined with vigorous protection of forests, could facilitate an island-wide Maleo recovery.

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Ethics statement

Our survey was carried out with all appropriate permits from Indonesian government authorities. It did not involve any direct handling of animals.

Conflicts of interest statement

The authors have no conflicts of interest to declare.

Author contributions

NJC, PJKM, JST, PR, and MS conceived the project. MS, ND, PAK, AL, SMS, AB, WA, VTO, AN, and MI performed the survey. MS, MG, and LJS analyzed the data. MG, LJS, and MS created the visualizations. MS wrote the manuscript. NJC, PJKM, PR, and MG edited the paper.

Data availability

Essential data for this study is provided in the manuscript and Supplementary Materials. Additional details include sensitive information and are available by request from the corresponding author.

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TABLE 1. Maleo Numbers Classes at nesting grounds (additional details in Supplementary Materials S2, Table E).

Numbers Class	**Number of Maleo pairs**
Abandoned (inactive)	0
Very low	<1 pair week^{-1}
Low	1 pair week^{-1} to 2 pairs day^{-1}
Moderate	3–10 pairs day^{-1}
High	11–30 pairs day^{-1}
Very high	31–50 pairs day^{-1}
Highest	>50 pairs day^{-1}

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TABLE 2. Maleo use of nesting grounds (NGs) by landscape type, with changes 1980–2019 and comparisons of their possible value to the species.

Landscape type	**Number of active sites 1980**	**Number of active sites 2019**	**% Decline**	**Number of all active NGs, 2019**	**Advantages**	**Disadvantages**	**Notes**
Beachside	119	40	66	43	• Many locations • Large areas • Easy digging • Burrows not re-used, making predation more difficult • Often multiple NGs nearby	• Often easy access (for egg-taking) for humans • Variable solar heat • Too deep = too cold • Possible flood risk • Often increasing corridor degradation • Accessible from only one direction • Coastal areas are areas of highest human population density and growth	• Historically, many very large NGs with hundreds of birds
Geothermal	42	19	55	20	• Access (for egg-taking) often harder for humans • Consistent high heat; chicks may hatch quicker and thus less opportunity for predation • Often embedded in forest—no corridor required	• Limited locations • Limited areas • Generally harder substrate • Reuse of burrows may enable easier predation • Too deep = too hot • Heat patterns may shift	• Most sites located in inland forest • Several high-profile govt-protected National Park sites are geothermal
Riparian	39	27	31	29	• Easy digging • Often multiple NGs nearby • Access (for egg-taking) may be harder for humans • Far inland sites may have more intact forest nearby	• Limited locations • Limited areas • Variable solar heat • Flood risk • Too deep = too cold	Historically, Morowali hosted a number of large riparian sites
Balds and other inland	10	8	20	9	• Often high solar temperatures; chicks may hatch quicker	• Digging usually hard • Eggs usually close to surface • Higher predation risk?	Includes: balds, gravel pits, cemeteries, corn fields, coconut plantations, other

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FIGURE 1. All known historic and current range-wide nesting grounds of *Macrocephalon maleo* (Maleo), *n* = 228 sites. Names and details of each site can be found in Supplementary Materials S1, Table A.

FIGURE 2. Decline in *M. maleo* (Maleo) nesting grounds from (**A**) 1980 to (**B**) 2019. Dot size represents numbers class (maximum number of pairs per day at peak season) at active nesting grounds. X denotes inactive nesting ground. Square ("present") indicates the nesting ground was active but numbers unknown.

FIGURE 3. All *M. maleo* (Maleo) nesting grounds by numbers class, 1980 and 2019. Total *n* = 228. Numbers class represents the maximum number of Maleo pairs attending the nesting ground per day at peak season. For the 22 sites listed as "present" in 1980, the site was known to be active but no precise numbers could be obtained.

FIGURE 4. Change in area of occupancy (AOO) and *M. maleo* (Maleo) subpopulation units, 1980 to 2019 (Mapped). (**A**) 25 km Maximum Travel Distance (MTD). (**B**) 40 km MTD. (**C**) 50 km MTD. NG = nesting ground. Maximum travel distance represents the maximum distance an individual Maleo may range beyond its nesting ground. Colored regions denote AOO in 1980, while stippled regions denote the analogous AOO in 2019. Green dots denote NGs active in both 1980 and 2019, whereas X's denote NGs active in 1980 but inactive in 2019.

FIGURE 5. Change in area of occupancy (AOO) and subpopulation units, 1980–2019 (Graphed). Blue, pink, and orange colors give values for maximum travel distances (MTDs) of 25, 40, and 50 km, respectively. MTDs represent the maximum distance an individual *M. maleo* (Maleo) may range beyond its nesting ground. AOO is a measure of the overall area of habitat occupied by the species, whereas the number of units is a measure of fragmentation. (**A**) Change in AOO, 1980–2019, shows decrease in Maleo AOO between 1980 and 2019 at MTDs of 25, 40, and 50 km, respectively. (**B**) Change in unit area, 1980–2019, shows the decrease in the average area of a unit at each MTD. (**C**) Change in number of units, 1980–2019, shows the increase in the total number of units (fragmentation) at each MTD. (D) Change in number of NGs in a unit, 1980–2019, shows the decrease in total number of NGs (nesting grounds) in each unit at each MTD. Numbers displayed represent the minimum, maximum, and mean number of NGs in a Unit in 1980 and 2019, for each MTD. The number of NGs in a unit is a partial indicator of how many conspecifics an individual Maleo may encounter over its lifetime.

FIGURE 6. Number of active nesting grounds by landscape type, 1980 (*n* = 210) and 2019 (*n* = 94).

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Figure 1

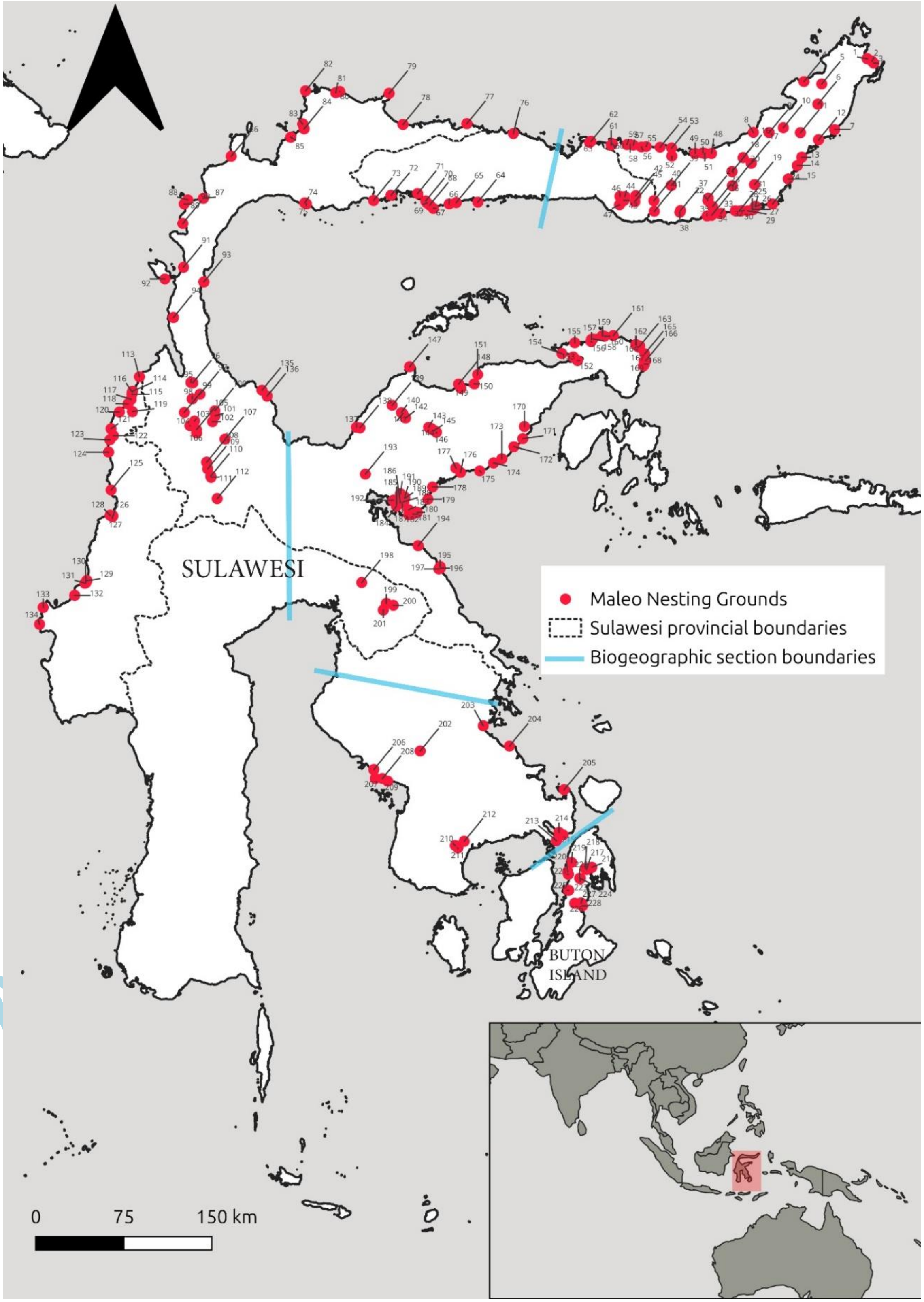

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Figure 2

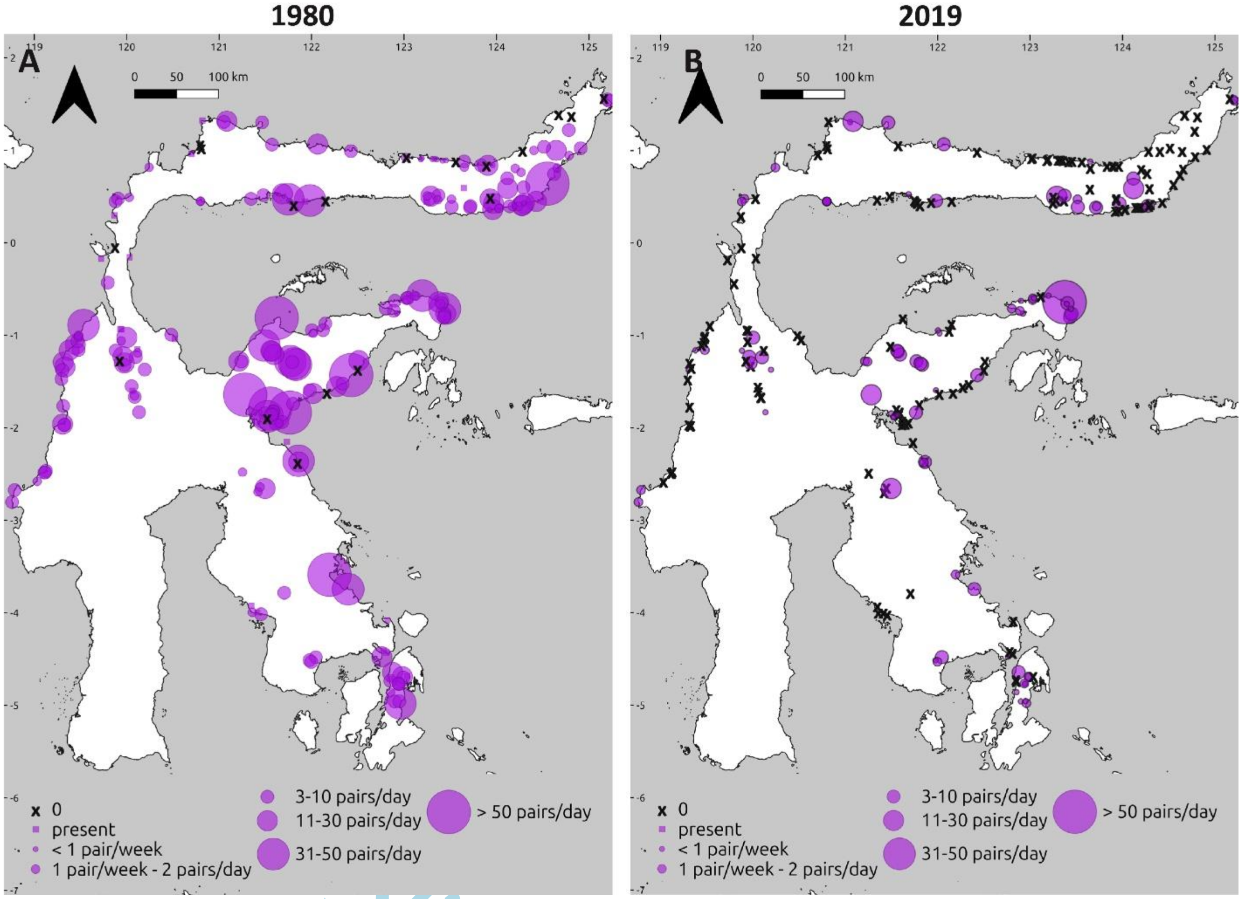

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Figure 3

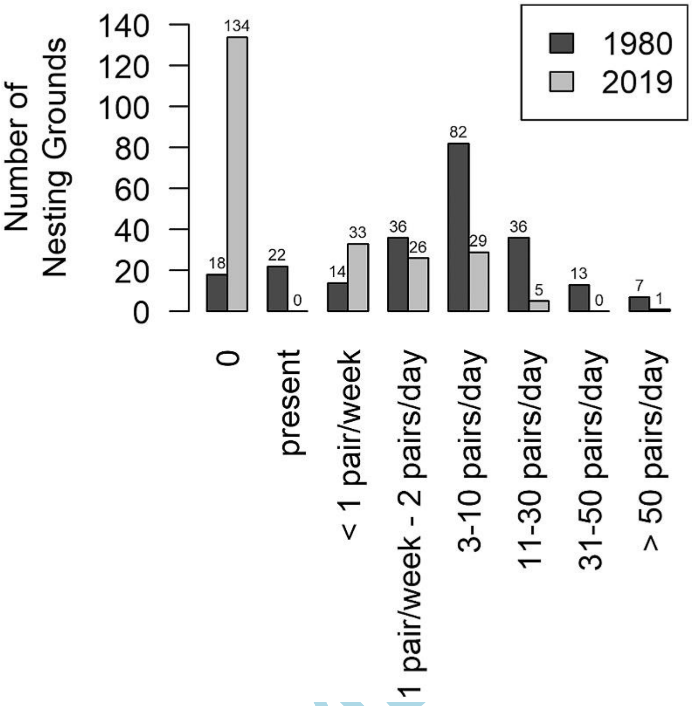

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Figure 4

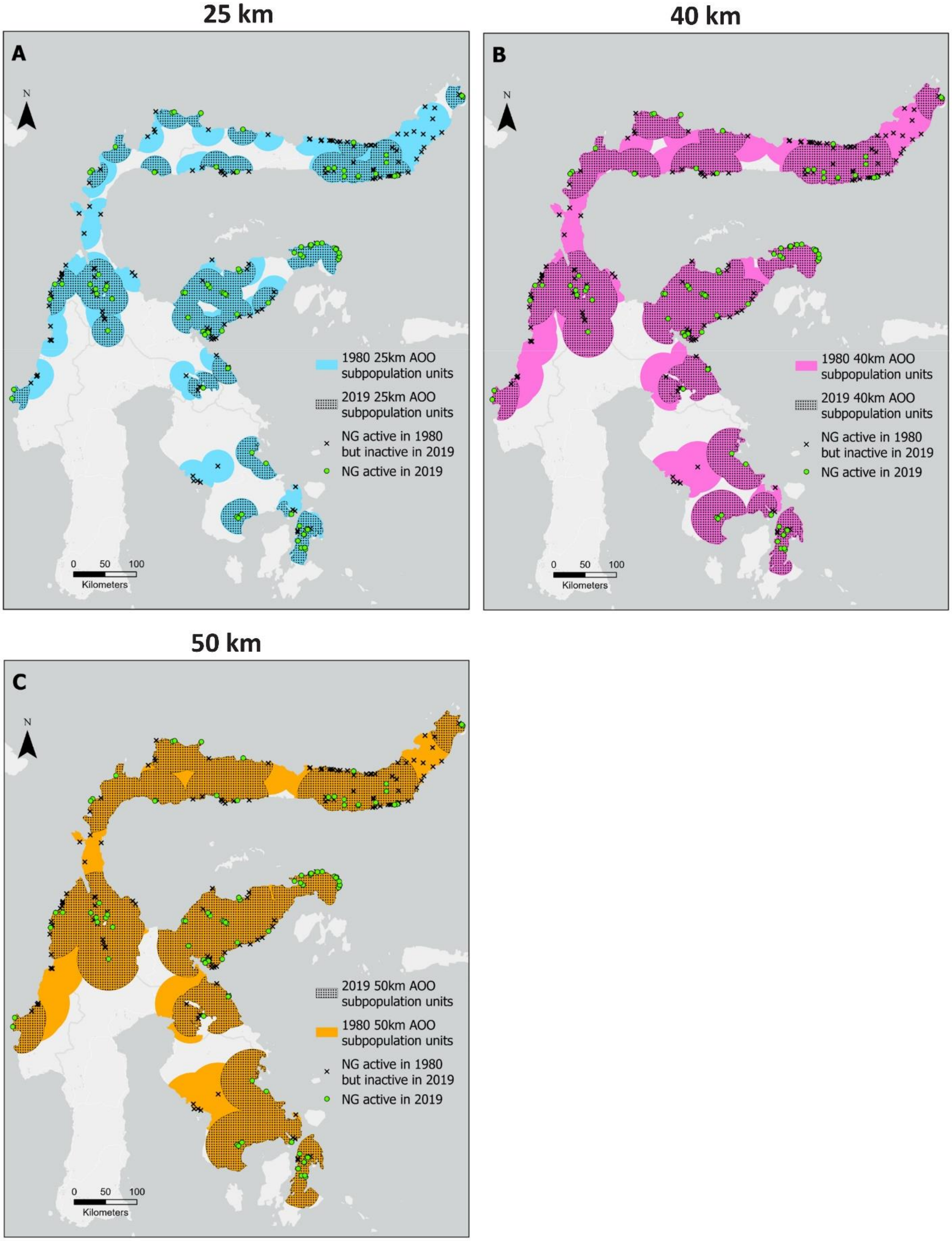

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Figure 5

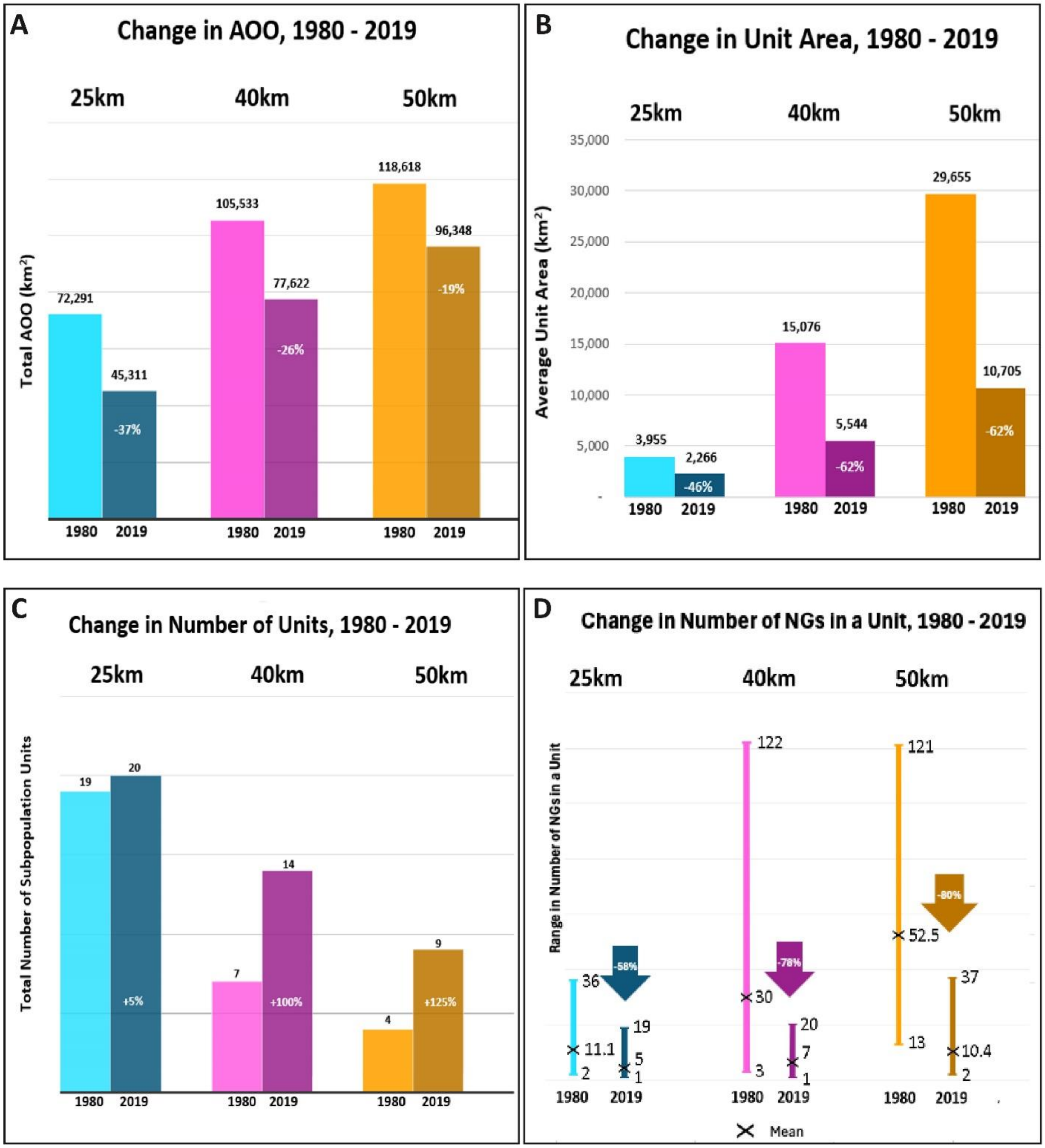

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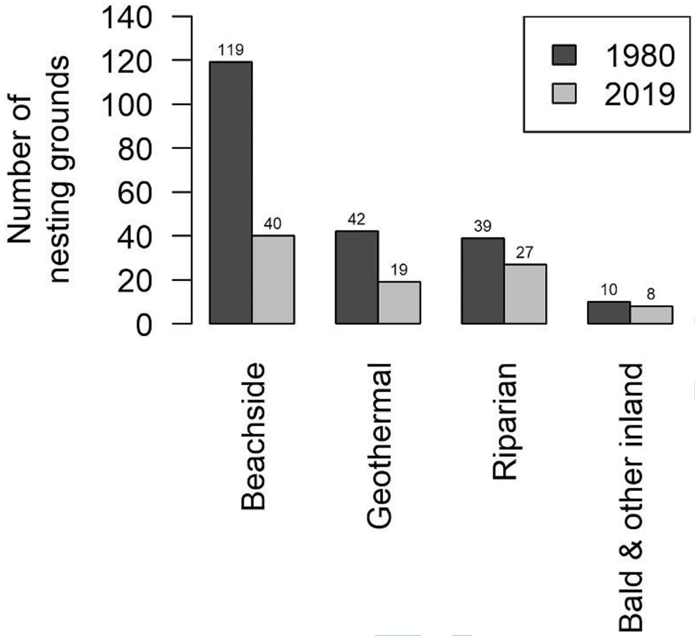
Figure 6



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