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Maleo *Macrocephalon maleo* population recovery at two Sulawesi nesting grounds after community engagement to prevent egg poaching

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ABSTRACT

Sulawesi's endemic maleo bird *Macrocephalon maleo*, a megapode that lays its eggs in communal nesting areas of warm sand or soil, is classified as Endangered on the IUCN Red List, with its decline generally attributed to habitat loss and poaching of its large eggs. Despite decades of protection under Indonesian law and numerous field conservation efforts, no conservation projects have yet documented a recovery in local numbers, and the overall maleo population continues to decline. We aimed to test whether the maleo's decline could be reversed in two community-based conservation programs in the Tompotika region of Central Sulawesi, in which maleo eggs were left undisturbed *in situ* and egg-taking (poaching) by humans ceased by community agreement. Subsequently, maleo numbers have increased four-fold after 14 years and three-fold after 5 years at two different locations. Our results suggest that: a) at these sites, egg poaching by humans is the primary threat to maleos, above habitat loss and natural predation; b) maleo populations can recover if egg poaching is prevented and eggs are left undisturbed; c) interventions such as translocating and/or artificially incubating eggs may be unnecessary if poaching is stopped; d) communities may voluntarily choose to end poaching with appropriate outreach work, which may or may not include economic incentives.

1. Introduction

The maleo *Macrocephalon maleo* is an iconic megapode endemic to Indonesia's island of Sulawesi. Nineteenth-century British explorer Alfred Russel Wallace (1869) first described the maleo's communal nesting habits: the chicken-sized birds do not incubate their own eggs, but travel from their forest habitat to a beach or hot spring area, where a pair excavates a hole in the ground to lay a single large egg and then bury it (Fig. 1A, B). The egg, which is 5–6 times the size of a chicken egg, is incubated by solar or geothermal

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heat for 2–3 months, after which the fully-developed chick hatches out, burrows to the surface, disperses, and matures completely independent of parental care (BirdLife International, 2001). Maleos may not reach sexual maturity until 3–5 years of age, at which point they form strong pair bonds, and captive birds have lived 37 years or more (Wildlife Conservation Society, 2016). Traditionally, the maleo's large egg is a prized human delicacy, and though generally not needed for subsistence, maleo eggs remain a coveted high-status item in areas where the species persists, and on the black market *via* Facebook or other channels, often selling for Rp 20, 000–40,000 (USD $2-3) (S. Mahalaya pers. comm). The species also plays an important role in Sulawesi culture, serving as the official mascot of provinces and parks, businesses and brand-names (Manado Tribune, 2020).

Notwithstanding its popularity, since Wallace's time the maleo has suffered dramatic population declines which have generally been attributed to loss and degradation of its primary forest habitat and uncontrolled egg-collecting (MacKinnon, 1981; Dekker, 1990; Baker and Butchart, 2000). Indonesian laws have provided full protection for the maleo even prior to the wide-ranging Natural Resource Law of 1990 (UU no. 5), but these laws are rarely enforced; egg-poaching is commonplace, and local extinctions have been numerous, with many historic nesting grounds now empty of maleos (Dekker, 1990; Argeloo, 1994; Butchart and Baker, 2000; Gorog et al., 2005). The maleo has been classified as Endangered on the International Union for Conservation of Nature (IUCN) Red List since 2001 (BirdLife International, 2016).

Typically, maleo conservation efforts have utilized hatchery systems, in which eggs are transferred to a structure where they are protected from human poaching and other predators, and incubated either naturally in the soil on-site at a nesting ground or artificially at another location (MacKinnon, 1981; Hafsah et al., 2008). Since the 1970s, at least 19 hatchery projects sponsored by government, NGOs, and corporations have been implemented, some running continuously for decades. Promising recent developments suggest that maleo numbers at some hatchery programs may now be increasing (I. Hunowu, pers. comm.). However, to date even the most well-managed programs have documented, at best, only a stabilization of maleo numbers at the associated nesting grounds (Clements, 2009), and many hatchery programs have been assessed to be in continued decline (Butchart and Baker, 2000). Development of more effective conservation approaches is therefore needed.

We set out to work with self-selected local communities to test whether a low-intervention, habitat-based approach, in which poaching by humans was prevented and eggs were left undisturbed, could result in increased numbers of maleos using the nesting ground. Using this approach, two maleo nesting grounds in Central Sulawesi's Tompotika region were protected from human poaching by community agreement and collaborative monitoring, and eggs were left undisturbed to hatch naturally in place. Here we report a four-fold increase in maleo visitation numbers over 14 years using this approach at one site, and a three-fold increase over five years at the other.

2. Methods

2.1. Study Area

Tompotika is a c. 2500 km^2 peninsula situated at the far eastern tip of Sulawesi's central arm. The human population of the peninsula is approximately 70,000 distributed in 106 villages located primarily along the coast (Kabupaten Banggai, 2020). Deforestation for mining, oil palm, and other agriculture is causing ongoing forest fragmentation. However, the interior of the peninsula is mountainous and remains largely covered by primary native forest, where maleo are found year-round (AL, PK, MS, pers. obs.).

Fig. 1. A, B A) Maleo pair (photo: Noval Suling). B) Libuun maleo nesting ground in 2018 (Photo: Adrianus Bawotong).

Throughout the year, but in higher numbers during the driest months (generally September—March), maleos travel on foot from their forest habitat in the interior to communal nesting grounds located primarily on sunny coastal beaches. Our study focuses on the Libuun nesting ground located 5 km from the village of Taima, Bualemo District, and the Kaumosongi nesting ground 1.8 km from Teku and Toweer villages, Balantak Utara District. Taima (population c. 580) and Teku/Toweer (population c. 1050) are located about 18 km apart on the north and east coasts of the peninsula, respectively (Fig. 2), and c.70–90 km, or a 3–5 h motorbike ride, from the regency capital, Luwuk.

2.2. Developing the conservation approach

Maleo conservation efforts began at the Libuun nesting ground in August 2006. Prior to that time, residents of the nearby village of Taima had little awareness of the maleo's protected status, and a long-standing, well-organized system for taking eggs: each day two villagers, on a rotating basis, had the "right" to dig for eggs, which they consumed or sold. However, under this system virtually all eggs were taken and villagers reported steadily declining numbers of maleos using the nesting ground, such that by 2006 individual egg-diggers got few or no eggs for their efforts. When a visiting conservation biologist (MS) made village leaders aware that similar situations elsewhere had led to local maleo extinctions, they asked for her help to prevent the same from occurring in Taima. This led to a series of meetings over the following 20 months in which all interested villagers, especially poachers, were encouraged to participate. During this period, additional local, national, and international conservationists known to the parties were invited to join the discussions, and eventually the conservation group formalized into a new NGO focused on this and related local conservation issues (hereinafter, "the NGO").

At the Kaumosongi site, maleo protection efforts began considerably later, in 2014. The Kaumosongi nesting ground had formerly hosted dozens of maleos daily, but by 2014 maleos had become almost completely extirpated there. Nearby villagers from Teku and Toweer villages, having observed the successes at the Libuun nesting ground, requested their own partnership with the NGO to develop a conservation program, and, as at Taima, a series of open meetings over a period of six months was held to design a program to fit that community and location. At each site, the goal of the villager-NGO partnership was to facilitate an increase in maleo numbers at the nesting ground, while also ensuring that villagers had the opportunity to participate in and benefit from the conservation efforts.

The approaches taken at each of the two sites shared the same basic structure and participatory community-based conservation style (Waylen et al., 2010; Dyer et al., 2014; Davis and Goldman, 2019), while following the differing values and preferences of the respective villages. After a series of meetings with village leaders and community members in which the wonder, uniqueness, and imperiled status of the maleo, along with local villagers' long history alongside it, was emphasized, each village made a formal agreement to collaborate with the NGO to end poaching and protect their respective maleo nesting grounds and adjacent forest. Formal Memoranda of Understanding (MOUs) were established with Balai Konservasi Sumber Daya Alam (BKSDA), the provincial wildlife authority, to authorize the NGO's conservation management of the two sites. In each village, specific sanction procedures based on Indonesian law and customs were put in place to deal with possible violations, although these have been very rare.

To help encourage broad participation in and benefits from the project, villagers themselves, on a village-determined rotating basis,

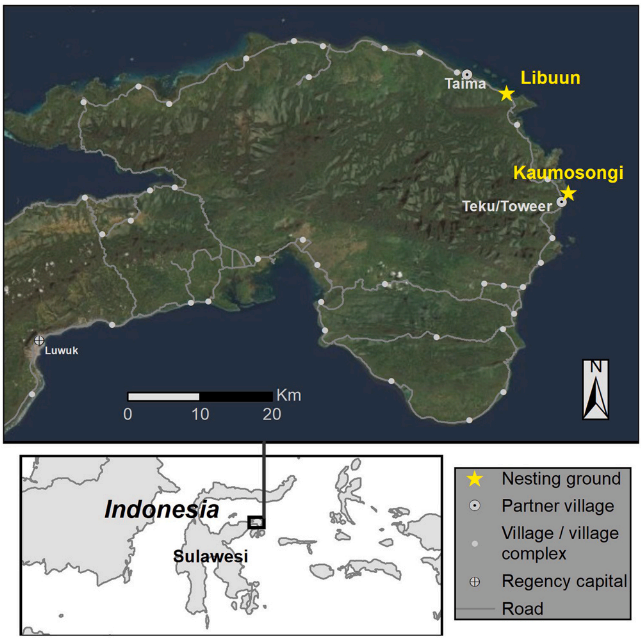


Fig. 2. Map of the Tompotika peninsula showing the maleo nesting grounds at Libuun and Kaumosongi and their partner villages. Unnamed villages show locations of outreach activities.

made up part of the teams that monitor each nesting ground. Former poachers could now participate in guarding and recording data at the nesting grounds, and were paid the government-determined local minimum wage to do so (in 2020, Rp 70,000/day, or c. USD $5.5). At the start of the project, the number of visiting maleos had dwindled so low at each site that the wage was more than poachers would have earned by selling their eggs.

At the same time, the NGO team worked with each village to identify local needs and devise a system of community benefits to accompany the conservation efforts. These were framed as an expression of thanks from the international conservation community (as represented by the NGO) to villagers for their support of the conservation efforts. In Taima, this eventually took the form of a monthly cash payment of Rp 2,000,000 (c. USD $155) to the village treasury, through which the NGO formally leased the Libuun nesting ground as a conservation area. At Teku/Toweer, villagers chose instead to work together to identify a set of non-monetary benefits that would improve all villagers' quality of life. These included equipment and practices to improve trash management, and a public statue of the maleo in a central location.

2.3. Guarding and monitoring the nesting grounds

At each site, teams of one or two NGO staff plus one or two villagers, in one-week shifts, monitor the nesting grounds all day, every day of the year. The guard teams comprise both villagers and NGO staff (who are local to the Tompotika area but from other villages) in the expectation that this ensures both strong villager participation and accountability to the wider conservation community. Villagers go home at night, while NGO staff stay on-site at a guard hut day and night. During daylight hours, monitoring teams prevent poaching by humans and record numbers of maleos present and their activities each hour, as well as details such as weather and any disturbances. Overnight, while adult maleos roost in nearby trees, the teams prevent intruders and check the nesting ground for maleo chicks, which typically hatch, emerge from the sand, and disperse at night. All these processes are allowed to proceed without intervention. The obvious presence of the guard teams deters any poaching or disturbances by humans, and although visitors occasionally come to observe maleos, virtually no attempts have been made to take eggs. However, natural predators such as monitor lizards (*Varanus* spp.) are commonly present, and are not interfered with, although they do occasionally predate eggs.

The guard teams also make regular patrols of the forested corridor of natural vegetation linking each nesting ground to primary interior forest. These patrols prevent clearing of trees or other vegetation, remove snares which are occasionally set for junglefowl or adult maleos, and prevent other disturbances. In both locations, as part of the project villagers agreed to support the protection of these forested corridors, which largely are owned by the government and classified as *Hutan Lindung*, or "Protection Forest," but which would likely be subject to gradual degradation and/or conversion without preventive attention. At the Libuun site, this corridor (c. 1200 m × 500 m) was later formally declared a protected area through the national Kawasan Ekosistem Esensial ("Essential Ecosystem") program (KBB, 2013). Overall, and within the region's natural weather and seasonal cycles, the physical condition of the natural habitat surrounding the two nesting grounds has remained more or less unchanged.

Although the overall population of maleos around each site and in the region is unknown, the number of maleos (usually, but not always, in pairs) visiting each nesting ground and laying eggs is easily observed. At each site the maleo count varies throughout the day and is recorded every hour. The maximum number of birds seen simultaneously on a given day ("Daily Max") is the base value utilized in our analyses. This number prevents any double-counting and represents a minimum number of confirmed individuals in the local population at that moment.

The Libuun maleo nesting ground is a c. 50 × 25 m patch of coastal sand surrounded by natural vegetation (Fig. 1B). At the Libuun site, virtually all poaching has been prevented for over 14 years, with two interruptions. Data are recorded from 1 August of one year to 31 July of the next. In 2008–10, guarding ceased for periods of up to several months due to personnel issues; thus data from these years were collected inconsistently and were omitted from the analysis below. In 2013–14, expiration of the then-current village-NGO agreement (agreements were made for periods of 3–5 years) led to resumed egg poaching for nearly five months until a new agreement was reached. Notably, during the five months of no agreement, only 13 individual egg-diggers chose to resume poaching, while prior to the beginning of the conservation partnership in 2006, over 200 people regularly dug eggs. In other years, while guarding and data-collection at the nesting ground continued uninterrupted, major disturbances in the corridor area, such as road-widening (2011–12), illegal forest clearing (2012–13), and forest fires (2015–16), may have affected maleos moving to and from the nesting ground and hence the numbers recorded there.

The Kaumosongi maleo nesting ground measures c. 30 × 8 m in two adjoining patches of coastal sand, surrounded by vegetation. At Kaumosongi, the nesting ground is remote and difficult to reach by land; inclement weather and landslides have also hampered access. Hence, monitoring teams have not been present every day. Prior to the project, poachers typically arrived by boat when passing to and from fishing grounds; since the project began, they generally pass by and do not stop. Overall, Kaumosongi guard-days steadily increased, from 113 in 2015 to 306 in 2019, and were distributed throughout all months in all years. At Kaumosongi, the year is recorded from January to December, and December 2014 was lumped together with 2015 data.

2.4. Outreach and engagement activities

Public education and outreach activities can be an important component of conservation efforts (Williams et al., 2019). Various kinds of outreach activities designed to increase knowledge about, pride in, and love for the maleo began in 2007 and have since been carried out regularly in the host villages and throughout the entire Tompotika peninsula. Outreach efforts focused on schoolchildren, adults, and community leaders (Steinmetz et al., 2014). The NGO staff have visited all 115 Tompotika primary, middle, and high schools at least once, delivering interactive presentations about the maleo to students of all ages. Consequently tens of thousands of schoolchildren have participated in these outreach events, many of them multiple times. Posters, stickers, billboards, and other items have been distributed widely to help reinforce citizen perceptions of the maleo as a unique and treasured part of their natural heritage and cultural identity. A community arts festival including drama, games, music, visual art, and writing on maleo and conservation themes has been held biennially throughout the region since 2014, attracting adult and child participants in the thousands and helping to broaden conservation awareness (Anonymous, 2015; 2017; 2018). In addition, a series of participatory workshops involving local law enforcement personnel was held focused on educating officials about wildlife laws and developing a stronger culture of adherence to them (Anonymous, 2013).

2.5. Data analysis

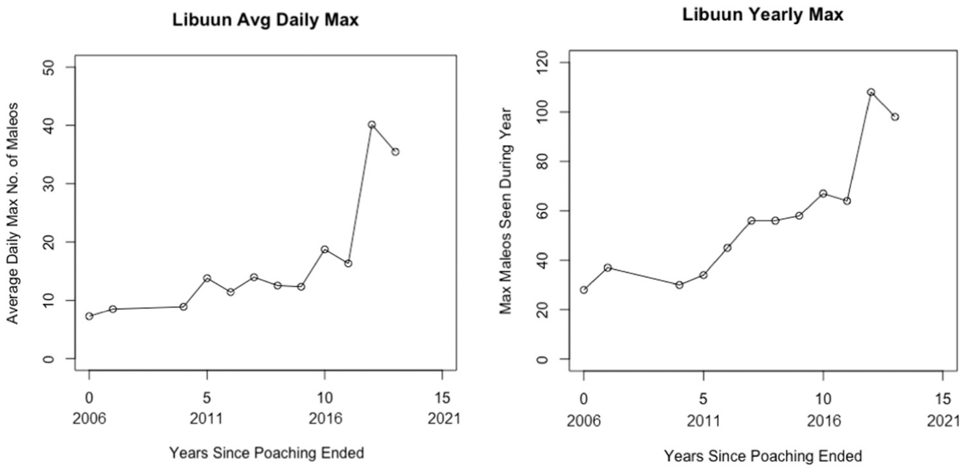
2.5.1. Libuun

At Libuun, the data represent the maximum number of maleos counted on each day (Daily Max) over a period of 14 years. Years were recorded from August 1 of one year to July 31 of the following year. Data from 2008 to 2010 were incomplete, and omitted. Statistical analysis was performed on the entire dataset (3889 daily records).

Maleos visit the nesting ground in order to lay an egg and remain on-site until the process is complete, during which time other birds may arrive. There is also a seasonality in visiting the nesting ground, as birds appear year-round, but in higher numbers during the dry season. Thus the data are effectively a time series of records, with the number of birds present on any one day not being independent of those of previous days (serial dependency). This means that daily counts cannot be assumed to be normally distributed. In order to assess whether there was a trend for counts of birds to increase we therefore had to account for seasonality and serial correlation in bird counts. We used time series generalized linear models with a serial correlation component and harmonic predictor variables (*cos*(2 * *pi**time of year/365), *sin*(2 * *pi**time of year/365) as independent predictors (Al-Banaa et al., 2020). Since the degree of serial dependency can vary, we used autoregressive variables of 1–6 days previously (*beta*_1 – *beta*_6). Models were compared by assessing the extent to which regression coefficients differed from zero, and through comparing AIC (Akaike Information Criterion, a measure of how well a model fits the data it was generated from) for the models with different autoregressive components (1–6 days). We determined that the Poisson error model was appropriate for the residuals using qqplots (a plot of the residuals *versus* the standardized residuals for the model). We then plotted fitted values from the model and observed counts against the time since poaching ended to illustrate goodness of fit.

2.5.2. Kaumosongi

At Kaumosongi, five years of observations were made as at Libuun. At Kaumosongi, overall maleo numbers were much lower, with many days of zero birds, as well as uneven numbers of data-collection days between years. These factors resulted in non-significant results for a variety of analytical approaches; thus simple summary figures are provided below.



A) B)

Fig. 3. A, B Summary maleo numbers at the Libuun nesting ground since poaching ended, 2006–2020. Growth in maleo numbers is presented in terms of: A) The maximum number of maleos seen at once each day, averaged over the year (Avg Daily Max); and B) the maximum number of maleos seen at once, at any point during the year (Yearly Max).

3. Results

3.1. Libuun

Graphs of summary maleo counts at Libuun from 2006 to 2020 are shown in Fig. 3A and B.

The number of maleos visiting the nesting ground at Libuun after poaching ceased in 2006 increased by a factor of 4.89, from an Average Daily Max of 7.26 birds/day in 2006–07 to 35.46 in 2019–20 (the Avg Daily Max in 2018–19 was larger—40.12, or a 5.53-fold increase over 2006–07). The Yearly Maximum number seen during the same period increased by a factor of 3.5, from 28 in 2006 to 98 birds observed at once in 2019–20 (or, a 3.86-fold increase if using the 2018–19 maximum figure of 108 birds). After steady but smaller increases in the first eleven years after poaching ended, Libuun numbers showed a large jump in 2018–19, twelve years after poaching ended, with 2019–20 numbers slightly lower. A table of yearly summary values is provided in Appendix A.1.

The fitted model and observed data for all daily maleo counts are shown in Fig. 4.

There was a clear and marked increase in the number of birds counted after adjusting for season and lagged counts from preceding days. A qqplot of the residuals was approximately a straight line indicating that the residuals were approximately normally distributed. Using a model with a lag of two days, there was both seasonality and a significant trend with time since the start of the study (Days). AIC for this model was 27,938. When the autoregressive component of the lag in the model was increased, the significance increased up to a lag of 6 days (Supplemental Data Table A.2), but the contribution of the day 6 lag to the variation in birds counted was only c. 8%. (AIC for this model was 26,869.) In all models Days (since poaching ended) was a significant positive predictor of counts. The correlation between the fitted model estimates of counts and those observed was 0.927 (CI 0.9227:0.9315), indicating a good fit between model and observed data. Regression diagnostics for the harmonic autoregressive Poisson time series model are given in the Appendix (Supplemental Data Table A.2).

3.2. Kaumosongi

Fig. 5A & B provide Kaumosongi summaries for A) Birds per data-collection day: the sum of the Daily Maxes for a given year divided by the number of data collection days for that year; and B) Yearly Max: the maximum number of maleos seen at once at any point during the year.

At Kaumosongi, overall numbers of maleos were low, with many days of no birds at all; number of days of data-collection each year also was not constant. Results are thus presented as the number of maleos seen per data-collection day. This figure has increased by a factor of 3.25 from 0.16 birds/day in 2015 to 0.52 birds/day in 2019. A table of yearly summary values is given in Appendix A.3. The Yearly Max at Kaumosongi has tripled over the five-year period. In the first year of the Kaumosongi project (2015), a maximum of two maleos (one pair) was ever seen on the nesting ground; most days had no maleos. In 2018 and 2019, six maleos (three pairs) were seen at once on multiple occasions. However, the observed increases at Kaumosongi are not significant.

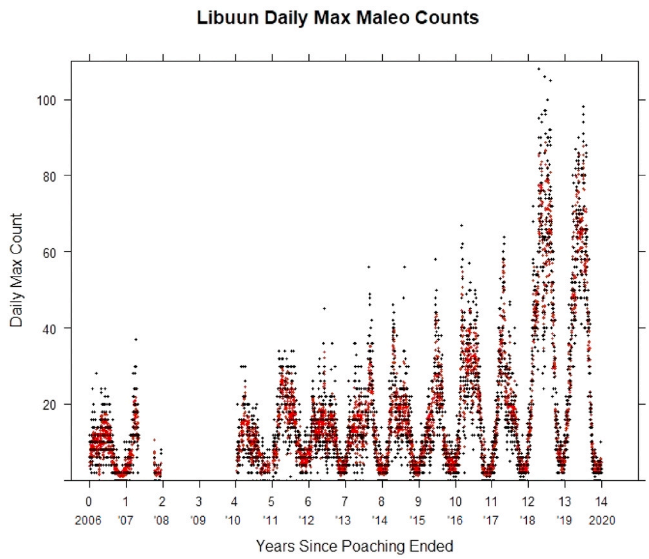


Fig. 4. Fitted (red) and observed (black) values of Daily Max maleo counts at the Libuun nesting ground since poaching ended, August 2006-July 2020. Years were recorded from August 1 of one year to July 31 of the following year. Data from 2008 to 2010 were incomplete, and omitted. Peaks within years reflect seasonality, with highest numbers generally recorded Nov—Jan. N = 3889 daily records. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

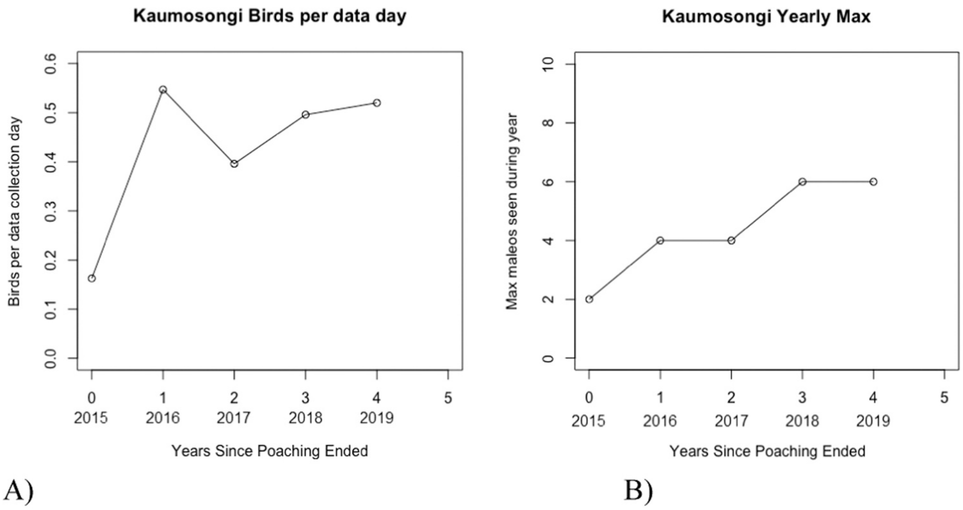


Fig. 5. A, B Maleo numbers at the Kaumosongi nesting ground since poaching ended, 2015–2019. Growth in maleo numbers is presented in terms of: A) number of birds per data-collection day (Birds per data day); and B) the maximum number of maleos seen at once at any point during the year (Yearly Max).

4. Discussion

4.1. Increasing numbers, seasonality, and aggregation among nesting maleos

The observed changes in Libuun maleo visitation numbers show three clear trends: a) a significant temporal trend—that is, increased counts with time; b) significant seasonal variation within years; and c) strong serial dependency between counts over the short term.

The increases in maleo numbers at the two Tompotika nesting grounds after poaching ended are striking. No previous studies have documented sustained increases in maleo numbers in response to conservation efforts. The fact that the Libuun site has demonstrated such significant increases, and solely in response to cessation of egg-taking by humans, is highly noteworthy, and echoes post-poaching recoveries documented among other taxa, such as sea turtles, marine mammals, and seabirds (Lotze et al., 2011), large mammals (Steinmetz et al., 2010), and Yellow-eared Parrots *Ognorhynchus icterotis* (Salaman et al., 2019). The increases noted at Kaumosongi, although not (yet) significant, are ongoing, and generally display a similar trajectory to those at Libuun. As has been seen among other species such as sea turtles, more complete details of population recovery patterns may take years or decades to become clear (Balazs and Chaloupka, 2004).

At both locations, cessation of poaching was followed by increases in numbers of maleos visiting the nesting ground within the first year. At least initially, this could not have been due to reproductive increase in the local maleo population. The age at first reproduction is unknown in the wild, but the youngest zoo-bred maleos have reproduced at five years (females) and three years (males) (WCS 2016). Possibly, simply eliminating the disturbance caused by poachers' presence at the nesting ground may have facilitated increased nesting activity by existing local maleo pairs. It is also possible that the local maleo nesting population may have expanded somewhat through immigration after poaching ended; the strength of maleos' nesting-ground fidelity is unknown (Argeloo 1995), and maleos that previously nested elsewhere may have been attracted to a nesting ground free of human disturbance.

After an initial jump in maleo numbers, both sites show a pattern of slower growth after the first year. As noted above, the increased laying activity observed in the first years could not have been due to increased recruitment. However, the early increases in maleo egg-laying at both sites may have also sparked increased activity by natural predators such as monitor lizards, which in turn could dampen nesting activity and/or slow future recruitment. In all years, food availability, weather, regional agricultural activity, and many other factors may also influence maleo nesting activity in unpredictable ways, and these effects may be more visible when numbers are low, as at Kaumosongi.

However, especially after the initial years at Libuun, it is likely that the observed increases represent growth in the actual local maleo population rather than simply increased nesting activity or redirected nesting from other areas. Their communal nesting habits make maleo egg-laying conspicuous, and the few other possible maleo nesting areas in the region are known to the NGO and village partners and were monitored periodically during this period. Although the normal home range of individual maleos is unknown and may be substantial, these other nesting grounds are many kilometers distant and thus possibly beyond the range of the maleos utilizing the Libuun and Kaumosongi sites. In addition, the overall level of maleo activity at these alternate sites, both before and during the same period of this study, has remained extremely low and ostensibly unchanged.

It is interesting to note that, at Libuun, a steep increase was observed starting in 2018, twelve years after poaching ended. Although this may have been the result of a large new cohort of sexually-mature maleos nesting for the first time, it was unlikely to be the first such. As previously noted, age at first reproduction may be 3–5 years, and is almost certainly earlier than 12 years. Possibly, such a population "bump" might have been observed earlier if not for the five-month period of egg-poaching in 2013–14. The conservation projects at Libuun and Kaumosongi are ongoing, and future data may provide further insights.

As noted in shorter-term studies elsewhere (Dekker, 1990; Argeloo 1995), our results show significant seasonal variation in maleo nesting throughout the year. Although nesting occurs year-round, the dramatically higher numbers observed during the high season (approximately September—March) are thought to be related to generally lower rainfall in that period (BirdLife 2001). Given that coastal-nesting maleos rely on solar heat to incubate their eggs, concentration of nesting when solar heat is strongest—that is, when the sun is least obscured by rainclouds and sand is drier—would be expected. Timing of nesting may also be related to seasonal availability of fruits and other foods.

The auto-correlation in our modeled results also reflected serial dependency in maleo numbers, for up to six days. We suggest that this may be due to two separate factors operating simultaneously: aggregation, or a tendency of maleo pairs to prefer to nest in the company of other maleos rather than separated by time (or space); and variable residence time, or multi-day presence of individual pairs. During the low season, counts of nesting birds sometimes showed a series of zeroes, then a day or two of higher numbers, then zeros again (*e.g.* 0-0-0-8-4-0-0). We suggest that maleo pairs that are more or less ready to lay may linger close-by in the area around the nesting ground until other maleo pairs also appear ready to enter the nesting ground, at which point they all enter together. Such behavior has been observed amongst some populations of olive ridley turtles *Lepidochelys olivacea*, for instance, which aggregate offshore before landing synchronously on a nesting beach in a so-called *arribada* (Bernardo and Plotkin, 2007). With aggregation as one possible source of auto-correlation operating in the background, variation in residence time while on the nesting ground contributes a further source of auto-correlation: color-banded pairs were observed to stay for 1–3 days at the nesting ground. This variation in residence time may reflect differences between pairs in their physical readiness to lay once on the nesting ground. The many and variable pre-nesting behaviors observed, such as shifting between multiple excavation sites, interacting with other maleos, resting, and preening, may play a role in a given female's readiness to lay, and therefore that pair's residence time on the nesting ground.

4.2. Conservation implications

The clear maleo increases observed after cessation of poaching at the Libuun and Kaumosongi nesting grounds suggest several important lessons for maleo conservation. First, the fact that these increases are associated with ending egg-taking by humans, while other major factors—such as availability and quality of habitat, and natural predation—remained more or less unchanged, points to human egg-taking as the primary driver of the previous decline at the two sites, and by extension, possibly the single biggest threat to the maleo's survival. Eliminating or reducing human poaching of eggs alone may therefore be the single most effective step in promoting maleo recovery.

Furthermore, the increases in maleo numbers observed in our *in situ* approach to protecting maleo eggs from poaching while leaving them in place have not been shown in the more common hatchery-based approaches (MacKinnon, 1981; BirdLife International, 2001; Clements, 2009; Rusiyantono et al., 2011). Thousands of maleo chicks have been released from hatchery programs to date, and some of these projects are clearly helping to slow or stop the maleo's decline locally (Clements, 2009). However, the fact that overall numbers have not increased in these projects, despite the hatchery's presumed success at preventing egg-taking by humans or natural predators, suggests that hatchery-associated maleos may be exposed to other factors that compromise their survivorship and/or fecundity. For sea turtles, hatcheries may potentially even have a "net negative" impact on populations and consequently are recommended only when *in situ* protection is impossible (Mortimer, 1999). Less intervention, not more, is often more effective in recovering natural systems and processes (Ricklefs et al., 1984; Chazdon et al., 2017). Our results suggest that, apart from preventing human poaching and disturbance, intervention in the maleo's natural hatching process, such as by relocating and/or artificially incubating eggs, is not required, and may even be counterproductive. Thus, a low-intervention approach where nesting ground habitat is protected from human poachers but eggs are left to hatch in place may be a more effective strategy for future maleo conservation efforts, and existing hatchery staff might consider redirecting their efforts toward guarding nesting grounds against human intruders while discontinuing the relocation of eggs.

Second, early and ongoing outreach to and engagement with citizens of partner villages and the wider region were essential. The maleo's protected status under Indonesian law was also necessary, but not sufficient for the project's outcomes. Although the maleo's legal backing was a critical part of discussions, the fact that its official protected status had been ignored locally for decades prior to the start of this project shows that laws alone are ineffective in preventing poaching without steps to improve community awareness, acceptance, and enforcement of those laws. At our sites, the cessation of poaching was achieved largely through patient, wide-ranging consultation and ongoing outreach to villagers and law enforcers at the grassroots community level. The fact that at Libuun in 2013–14, during the five months while there was no signed agreement between the village and the NGO, only 13 out of >200 pre-2006 poachers (<7%) actually returned to poaching, suggests that even without formal agreements or guards, community members' inclination to poach had markedly diminished. As has been found in conservation efforts with other taxa, long-term community support for the projects was sustained and strengthened by education, arts and other activities aimed at raising awareness and enthusiasm for the maleo's importance for local nature and culture (Byers, 2003; Lin et al., 2008; Steinmetz et al., 2014; Barman et al., 2020). Since these activities began, villager support for continuing the conservation partnerships has been strong; the Taima agreement has been renewed four times. Villagers have also cited the partnership aspect of the project as lending strength to the element of accountability: because through the NGO partnership they were collaborating with conservationists from other villages and even the international community, many reported a deeper sense of responsibility and significance in the project because of it.

Third, at both sites villagers welcomed the benefits that they gained from participating in these conservation projects. These included economic benefits such as jobs for guards (both sites) and income from the conservation lease (Taima only). But in discussions villagers at both sites also frequently cited many intangible benefits that nevertheless greatly enhanced their quality of life, such as the joy and pride in being involved in the comeback of one of Sulawesi's most important cultural icons. In addition, often mentioned was villagers' enjoyment of the relationships built through the partnerships, and the experience of direct involvement in a group effort of significance. In Teku/Toweer, villagers never made mention of economic benefits, and the community "benefits" they requested through the partnership were aimed at making further environmental progress (better trash management) and their overall community pride in the maleo (a maleo statue). As found by (Barman et al., 2020), who emphasized similar non-monetary community benefits in their work recovering the Greater Adjutant Stork *Leptoptilos dubius* in India, this suggests that, even amongst poorer communities in a developing country, not only economic development, but love of and pride in a people's natural heritage can be a powerful motivator for conservation.

Finally, our study suggests that building and harnessing community support to control poaching while leaving eggs *in situ* could potentially lead to a major recovery of the endangered maleo across Sulawesi, and perhaps serve as a model for other species threatened by poaching as well. The fact that our conservation efforts were conducted, not at carefully pre-screened and selected sites, but at two locations simply self-nominated by local communities implies that the results may not be highly dependent on particular site features or details, and thus that the approach may be applicable at a variety of other sites in locations where maleos still persist across Sulawesi.

5. Conclusion

This study presents the results of a new and uniquely successful low-intervention approach to maleo conservation in which the nesting ground habitat is protected from human poaching but eggs are left undisturbed to hatch naturally in place. Using this approach, made possible by engagement of nearby local communities to voluntarily end poaching, maleo populations at two Central Sulawesi nesting grounds have increased four-fold over 14 years, and three-fold over 5 years, respectively—results never before achieved for maleo conservation. Our results suggest not only that poaching by humans was the primary driver of the maleo's decline at the two sites—above habitat loss or natural predation—but also that it can be ended with appropriate outreach work. Future maleo conservation efforts may therefore benefit from redirecting their activities away from intervening in the natural hatching process and toward a greater focus on working with nearby human communities on ways to discourage or end poaching. To that end, not only economic incentives, but love, pride, and other intangible factors can serve as powerful motivators. When viewed through this lens—as a problem that might partially solve itself with appropriate outreach to and engagement with human communities—recovery of the endangered maleo across its range seems possible and within reach.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01699.

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