BIODIVERSITAS
Volume 27, Number 4, April 2026
Pages: 11

ISSN: 1412-033X
E-ISSN: 2085-4722
https://doi.org/10.13057/biodiv/d270431

Environmental factors affecting *Macrocephalon maleo* presence in nesting habitats of Lore Lindu National Park, Indonesia

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Manuscript received: 21 July 2025. Revision accepted: 21 April 2026.

Abstract. *Fatkhiyah R, Nurvianto S, Subrata SA. 2026. Environmental factors affecting* Macrocephalon maleo *presence in nesting habitats of Lore Lindu National Park, Indonesia. Biodiversitas 27 (4): d270431. https://doi.org/10.13057/biodiv/d270431. Macrocephalon maleo*, commonly known as the maleo, is a critically endangered bird endemic to Sulawesi, recognized for its distinctive nesting strategy of burying eggs in geothermally or solar-heated soil. This study examined nesting habitat characteristics and environmental factors influencing its presence in Lore Lindu National Park (LLNP), Central Sulawesi, Indonesia. From June 2024 to February 2025, field surveys and camera trap monitoring were conducted at 27 nesting sites. Active nesting grounds were primarily located on gentle slopes from lowland to lower montane forests, which associated with sandy soils near geothermal sources. Soil temperature at nesting sites ranged from 25 to 41°C. Canopy cover ranged from 24-88%, while understory cover ranged from 46-89%. Logistic regression analysis indicated that understory vegetation cover was the only variable significantly associated with maleo presence (p-value: 0.00997), with higher understory cover corresponding to lower occurrence. Other measured environmental variables showed no significant relationship with maleo presence, indicating that soil and thermal conditions across nesting sites met the species' nesting requirements, whereas understory structure directly influenced nesting accessibility and predator detection. These results demonstrate that maleos select nesting habitats with open ground conditions. Conservation management should therefore prioritize the maintenance of open understory structure and the protection of confirmed active nesting grounds. This study was limited to a single-season observational design and did not address interannual variation in nesting activity. The findings provide quantitative ecological evidence to support habitat-based conservation of maleo populations in LLNP and Sulawesi.

Keywords: Environmental factors, Lore Lindu National Park, maleo, nesting habitat, presence

INTRODUCTION

The maleo (*Macrocephalon maleo*) is a Sulawesi endemic bird currently suffering severe population decline. It is listed as Critically Endangered (CR) by the IUCN and is legally protected under the Indonesian Regulation of the Minister of Environment and Forestry No. P.106/MENLHK/SETJEN/KUM.1/12/2018, over two-thirds of its known nesting sites have been abandoned, leaving an estimated 8,000-14,000 mature individuals (BirdLife International 2021). Population declines are driven by habitat degradation, hunting, and natural threats (Summers et al. 2023).

The maleo's unique reproductive strategy of burying eggs in the ground for incubation makes it particularly vulnerable to predators and dependent on specific habitat conditions for successful hatching (Froese and Mustari 2019). Key abiotic factors influencing nesting habitat include elevation, slope, soil temperature, humidity, pH, and light intensity, all of which determine optimal conditions for egg incubation. Biotic factors, particularly vegetation structure, understory density, and canopy cover, contribute to microhabitat stability, predator concealment, and nest site selection. Across Sulawesi, egg poaching remains the leading cause of maleo decline, often exceeding the impacts of habitat loss and predation (Tasirin et al. 2021). Nesting site viability also depends on the integrity of forest-to-nesting-ground habitat corridors, as degradation of these corridors can render sites inactive even within protected areas (Gorog et al. 2005).

In Lore Lindu National Park (LLNP), several studies have examined aspects of maleo ecology. Hafsah et al. (2008) identified optimal incubation conditions of 30-35°C soil temperature and 60-71% humidity, while Hafsah et al. (2009) reported that Saluki nesting sites typically have sandy-loam soils, neutral pH, and low organic matter. Apriadi (2009) found that maleo prefer geothermal areas with gentle slopes and minimal human disturbance, foraging and resting in zones with abundant food plants. Dhafir et al. (2022) documented nesting-related behaviors through direct observations, including active nest excavation, assessment of substrate and surrounding conditions prior to egg laying, and digging of decoy holes near nesting sites. Mallombasang et al. (2023) assessed the Kadidia site's habitat health index at a moderate level (0.55), underscoring the need for improved conservation measures.

However, most research in LLNP has concentrated on well-known sites like Saluki, Kadidia, and Bora, using direct observation. Many active sites remain unmonitored, leading to potential sampling bias. Presence surveys relying solely on direct observation may also be influenced by observer skill (Tirtaningtyas et al. 2024). Furthermore, only a limited number of studies have quantified environmental variables influencing maleo presence, restricting the development of habitat management strategies that replicate optimal natural conditions, such as those applied in semi-natural hatcheries at Saluki and Pakuli Utara (BBTNLL 2022). These limitations point to three key knowledge gaps in LLNP, which are limited spatial coverage of monitored sites, observations have relied mainly on direct visual methods, and the lack of standardized and quantitative measurements of environmental variables.

A stronger understanding of maleo nesting ecology is especially important in LLNP, one of the remaining strongholds for the species in Central Sulawesi. In LLNP, current management is hindered by ecological data that are often outdated or incomplete. Ongoing population decline, habitat alteration, and the need for spatially explicit management plans require updated ecological assessments. Without site-specific information, it is challenging to prioritize active nesting areas, design effective restoration measures, or mitigate threats such as poaching and vegetation overgrowth.

To address these knowledge gaps, this study conducted a comprehensive survey across several nesting areas in LLNP that had previously received little to no ecological monitoring. The survey combined camera trap observations with detailed measurements of abiotic and biotic habitat variables. In total, thirteen environmental variables were measured, and maleo presence at twenty-seven nesting sites was analyzed using logistic regression. This approach provides more standardized ecological data and broadens the spatial coverage of monitored nesting grounds, thereby offering an improved baseline for habitat-based conservation planning in LLNP. The results provide essential baseline information for refining conservation management and enhancing the long-term viability of this critically endangered species.

MATERIALS AND METHODS

Study area

This study was conducted in Lore Lindu National Park, located in Central Sulawesi, Indonesia, between 119°58'-120°16'E and 1°8'-1°3'S. LLNP covers approximately 214,984 hectares and encompasses parts of Sigi and Poso Regencies. The park comprises a wide range of elevations from 300 to 2,350 meters above sea level and serves as a critical conservation area for endemic species. The park's climate is classified as tropical, with annual rainfall exceeding 2,500 mm and high relative humidity ranging between 77-85%. Temperatures vary by elevation, with minimum temperatures as low as 12°C and maximums reaching 35°C. The ecosystem types range from lowland forest to submontane and montane forests. Most monitored nesting sites were situated in lowland forest ecosystems below 1,000 meters above sea level (Figure 1).

Field surveys were conducted from June 2024 to February 2025, which corresponds to the dry season in Central Sulawesi and represents the breeding season of the maleo. Maleos visit nesting grounds year-round, but their numbers are higher during the dry season (Tasirin et al. 2021). As the survey covered only one breeding season, potential temporal bias may exist, since environmental conditions and nesting activity can vary seasonally. Surveys were carried out across nine locations distributed under five park management resorts (Table 1), all of which are located within UTM Zone 51S.

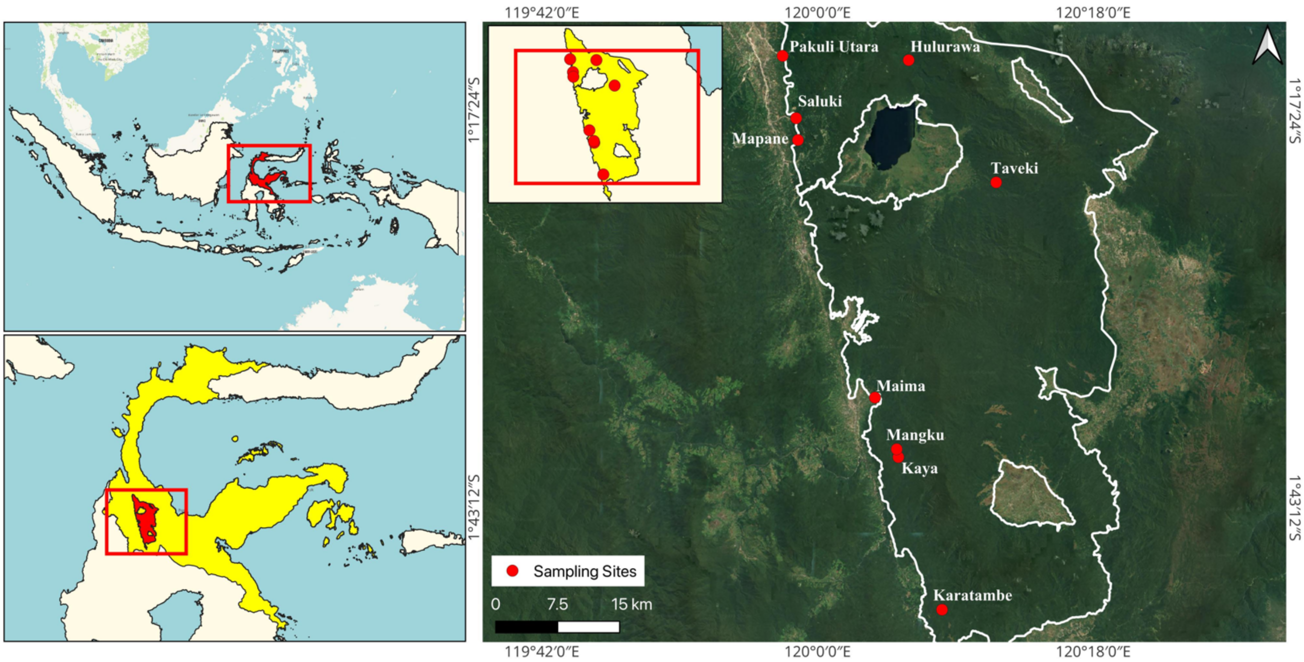

Figure 1. Map showing the distribution of nine study locations in the Lore Lindu National Park, Central Sulawesi, Indonesia

Table 1. Locations of maleo nesting sites in Lore Lindu National Park, Central Sulawesi, Indonesia

Location name	Ecosystem type	Elevation range (m asl)	Remarks
Karatambe	Lowland forest	0-1000	Newly discovered during patrol (BBTNLL 2022); Suspected ongoing maleo activity
Mangku	Lowland forest	0-1000	Exact status unknown; Highly threatened (Butchart and Baker 2000); Suspected ongoing maleo activity
Kaya	Lowland forest	0-1000	Exact status unknown; Highly threatened (Butchart and Baker 2000); Suspected ongoing maleo activity; egg collection suspected; nesting area threatened by landslides
Maima	Lowland forest	0-1000	Possibly still active; Not reported in Butchart and Baker (2000); High potential disturbance due to proximity to farmland and a hot spring tourism site
Pakuli	Lowland forest	0-1000	Access is difficult due to a large river crossing; Hatchery exists but is poorly managed; no well-managed population data/monitoring, high natural predator threats (BBTNLL 2022)
Saluki	Lowland forest	0-1000	Easily accessible but close to farmland; Hatchery present well-managed data; High natural predator threats and egg collection due to use as a public forest trail (BBTNLL 2022)
Mapane	Lowland forest	0-1000	Status unknown; Threatened (Butchart and Baker 2000); Threatened by egg collection
Hulurawa	Lowland forest	0-1000	Active; Not threatened (Butchart and Baker 2000); Remote from settlements, but occasional egg collection reported
Taveki	Lower montane forest	1000-1500	Status unknown; Threatened (Butchart and Baker 2000); Remote from settlements, but occasional egg collection reported

All nesting locations were selected using purposive sampling, based on previous monitoring records, ranger observations, and habitat management reports compiled by BBTNLL (2022), which identified active and recently used maleo nesting grounds. This approach was chosen because maleo nesting activity is spatially restricted and not evenly distributed across the landscape. Although previously unrecorded nesting sites may have been overlooked, focusing on known nesting areas ensured coverage of sites with high ecological relevance for the species. Consequently, inference from this study is limited to nesting environments and does not represent habitat conditions across the entirety of LLNP.

Data collection

Habitat characteristics (abiotic and biotic) and maleo presence were documented during the field survey. Abiotic variables including altitude (m asl) was measured at each nesting site using a calibrated GPS by recording geographic coordinates and elevation. Slope (°) was measured using a clinometer positioned along an approximately 10 m transect parallel to the slope surface. Light intensity (lux) was measured using a lux meter placed horizontally in an open area adjacent to the nesting site with the sensor directed toward the primary light source. Nest depth (cm) was measured using a roll meter from the soil surface to the bottom of the nest chamber. Distances (m) to hot springs were measured directly in the field using a roll meter when accessible. Distances to roads, plantations, and settlements were calculated using ArcGIS based on georeferenced nesting site coordinates. Soil temperature (°C), soil moisture (%), and soil pH were measured using a calibrated multifunction digital soil tester with LCD display (temperature range -9 to 50°C; moisture range 0-100%; pH range 3.5-9.0). Measurements were conducted between 07:00 and 08:00 WITA to minimize diurnal variation. At each nesting site, a minimum of 10 nest holes were sampled, or all nests were measured when fewer than 10 were present. For each nest, the probe was inserted to a minimum depth of 10 cm after partial excavation (15-20 cm), ensuring no damage to eggs. One standardized reading per parameter was recorded per nest. For each nesting site, measurements were summarized as mean values across sampled nests, except for soil temperature and pH, which are presented as minimum-maximum ranges. Moreover, biotic factors were assessed through vegetation surveys. Vegetation data were collected using square plots of 10×10 m for poles and 20×20 m for trees. Within each plot, plant species were identified (local and scientific names), and their diameter and height were recorded to calculate frequency, density, dominance, and importance value index (IVI) following Odum (1998). Canopy and understory cover were measured using ocular tubes following the sampling protocol of Noon (1981). Five sampling plots were established per nesting site and placed within the active nesting ground.

The selection of these environmental variables was guided by previous studies (Hafsah et al. 2009) that identified their ecological relevance to maleo nesting ecology. Soil temperature and moisture are known to influence embryo development and hatching success (Hafsah et al. 2008), while nest depth contributes to thermal stability and protection from predators. Elevation and slope were included due to their effect on geothermal heat distribution and drainage capacity (Rosalia et al. 2025). Soil pH, light intensity, and proximity to anthropogenic features are also known to influence nesting site selection. Biotic variables such as vegetation composition, canopy cover, and understory density were selected for their ecological functions as natural protection against predators and disturbance. Vegetation cover also helps stabilize the microclimate surrounding the nest, as reported by Nafiu et al. (2015) and Moghuri et al. (2021). The inclusion of these biotic factors, in addition to commonly studied abiotic ones, aimed to provide a more holistic picture of the habitat requirements of maleo. Although direct measures of predator presence or human activity (e.g., frequency of intrusions) were not recorded, several selected variables, including vegetation cover and distance to settlements, serve as proxy indicators for those pressures.

Maleo presence was documented using both direct and indirect methods. Direct observations were conducted between 06:00 and 10:00 WITA from concealed blinds near or within nesting areas. Observers recorded sightings, vocalizations, or nest activity. Sampling effort was standardized across all study sites. Each site was surveyed for three consecutive days using the same observation protocols and measurement procedures to ensure comparability among sites. Indirect observations were conducted using camera traps positioned approximately 30 cm above ground and deployed for at least 30 days. or this study, "presence" was defined as the confirmation of at least one of the following indicators recorded during the survey period: (i) direct observation of individuals (visual sightings or vocalizations), (ii) active nesting pits, identified by fresh soil disturbance and thermal measurements consistent with incubation conditions, or (iii) indirect signs, such as fresh footprints or eggshell fragments, that were unambiguously attributable to maleos. All presence records were validated in the field by trained observers, and indirect signs were only accepted as evidence only when verified by at least two independent observers based on predefined morphological characteristics (e.g., footprint size and shape consistent with maleo tracks). Ambiguous signs that could not be confidently distinguished from those of other ground-dwelling birds were excluded from analysis. Local reports were not used as sole evidence but were followed up with direct verification at the site.

Data analysis

Maleo presence in the camera data was processed using the camtrapR package in RStudio 2025.05.1 version. Metadata from images and videos was extracted using ExifTool. The output included a summary of independent detection events (IEs, with a $\geq$30-minute threshold between events) and species encounter tables. Detection rates (detections/100 trap-nights) were calculated following (O'Brien et al. 2003), using the formula:

$$\text{Detection rate} = \frac{\text{Number of independent events}}{\text{Number of trap} - \text{nights}}\ x\ 100\%$$

Independent events were defined as detections of the same species separated by at least 30 minutes at the exact camera location to avoid repeated counting of the same individual (O’Brien et al. 2003; Ash et al. 2021). Statistical analysis was performed to identify environmental predictors influencing maleo presence. Logistic regression analysis was conducted in R Studio using the GLM function (binomial family), with maleo presence (1: present, 0: absent) as the dependent variable. The initial model included all measured abiotic and biotic predictors. Multicollinearity was tested using the Variance Inflation Factor (VIF), with variables exceeding a VIF of 10 excluded. Backward elimination was applied to select significant variables ($p<0.05$). Variables removed during the selection process were excluded due to high multicollinearity or lack of statistical significance. Model fit was assessed using the Hosmer and Lemeshow goodness-of-fit (GOF) test, which evaluates discrepancies between observed and expected values based on model predictions (Hosmer and Lemeshow 1980; Surjanovic et al. 2024). Model performance was further evaluated using the AUC value and confusion Matrix function. Odds Ratios (OR) were used to interpret the strength and direction of each predictor's effect. Given the relatively limited sample size, model complexity was deliberately constrained by restricting the number of predictors in the final model. This parsimonious modeling approach helps reduce the risk of overfitting and improves interpretability while maintaining statistical robustness.

RESULTS AND DISCUSSION

Maleo presence

A total of 27 nesting ground locations were surveyed across LLNP. Maleo presence was confirmed at 14 sites (51.9%) based on a combination of camera trap records and direct or indirect field indicators (Table 2), suggesting that approximately half of the surveyed nesting grounds were active during the survey period, although this estimate should be interpreted with caution due to potential detection limitations. However, this interpretation should be treated with caution, as non-functional or lost camera traps at several sites may have reduced detection probability. Table 2 also shows that camera traps provided the most decisive evidence of presence, with detections recorded in nearly all active sites, while indirect indicators such as eggshell fragments and ground scratches generally served as supporting signals. Direct encounters were extremely rare, further emphasizing that effective detection of this cryptic species relies heavily on ground signs and camera-based monitoring. At the site level, maleo presence (1) was assigned when at least one confirmed indicator (camera trap record, direct observation, eggshell fragments, or scratches) was detected during the survey period. Sites with no validated indicators were classified as absence (0); however, this classification may include false absences in cases where camera data were unavailable due to malfunction or loss.

From the 27 camera trap stations installed, only 16 stations yielded valid and analyzable data due to technical failures, camera loss, and recordings triggered solely by vegetation movement. From these 16 stations, a total of 228 independent maleo detection events were recorded (Table 3). Four stations (Saluki 2, Karatambe 2, Saluki 7, and Saluki 3) recorded detection rates exceeding 50 detections per 100 trap nights, whereas two stations (Taveki 1 and Taveki 2) recorded no detections. The Saluki complex collectively accounted for the highest number of independent events among all monitored areas.

Table 2. Summary of maleo presence in Lore Lindu National Park as evidenced by camera trap, eggshell, scratches, and direct encounter

Site	Presence (1: Yes, 0: No)	Camera trap recording	Eggshell fragments (1: Yes, 0: No)	Scratches (1: Yes, 0: No)	Direct encounter (1: Yes, 0: No)
Hulurawa 1	1	Maleo captured on camera	1	1	0
Hulurawa 2	1	Maleo captured on camera	0	0	0
Hulurawa 3	0	No image recorded	0	0	0
Karatambe 1	1	Maleo captured on camera	1	1	0
Karatambe 2	1	Maleo captured on camera	0	1	0
Kaya	1	Maleo captured on camera	0	0	0
Maima	1	Maleo captured on camera	1	0	0
Mangku 1	0	no camera, inactive site	0	0	0
Mangku 2	1	Maleo captured on camera	1	0	0
Mapane 1	0	Camera lost, high human activity	0	0	0
Mapane 2	0	No camera, inactive site	0	0	0
Pakuli Utara 1	0	No camera, inactive site	0	0	0
Pakuli Utara 2	0	No camera, inactive site	0	0	0
Pakuli Utara 3	1	Maleo captured on camera	0	1	0
Pakuli Utara 4	0	No image, memory corrupted	0	0	0
Pakuli Utara 5	0	Only moving leaves/insects recorded	0	0	0
Saluki 1	1	Maleo captured on camera	0	1	1 *
Saluki 2	1	Maleo captured on camera	1	1	0
Saluki 3	1	Maleo captured on camera	0	1	1 **
Saluki 4	1	Maleo captured on camera	0	1	0
Saluki 5	0	Camera lost, landslide-prone area	0	0	0
Saluki 6	1	Maleo captured on camera	0	1	0
Saluki 7	1	Maleo captured on camera	0	1	0
Saluki 8	0	Only leaves/insects recorded	0	0	0
Saluki 9	0	Camera error, no image	0	0	0
Taveki 1	0	Camera recorded other fauna only	0	0	0
Taveki 2	0	Camera recorded other fauna only	0	0	0

Note: *) 2 individuals were detected, **) 2 individuals were detected twice

Table 2. Maleo detection rate from 16 valid camera trap stations in Lore Lindu National Park, Indonesia

Station	Setup date	Retrieval date	Trap nights	Independent event maleo	Detection rate (detections/100 trap nights)
Hulurawa 1	26-Jun-24	26-Aug-24	61	12	19.67
Hulurawa 2	26-Jun-24	26-Aug-24	61	5	8.20
Karatambe 1	12-Jul-24	22-Sep-24	72	7	9.72
Karatambe 2	07-Dec-24	17-Feb-25	72	61	84.72
Kaya	21-Jun-24	21-Jul-24	30	1	3.33
Maima	25-Jun-24	04-Aug-24	40	4	10.00
Mangku 2	22-Jun-24	22-Aug-24	61	5	8.20
Pakuli 3	24-Jun-24	01-Sep-24	69	6	8.70
Saluki 1	09-Jan-25	09-Feb-25	31	12	38.71
Saluki 2	09-Jan-25	09-Feb-25	31	41	132.26
Saluki 3	09-Jan-25	09-Feb-25	31	18	58.06
Saluki 4	20-Jun-24	29-Aug-24	70	1	1.43
Saluki 6	20-Jun-24	29-Aug-24	70	15	21.43
Saluki 7	20-Jun-24	29-Aug-24	70	40	57.14
Taveki 1	22-Jun-24	31-Jul-24	39	0	0.00
Taveki 2	22-Jun-24	31-Jul-24	39	0	0.00
				228	

In addition to maleo detections, camera traps recorded several sympatric vertebrate species across the nesting sites (Table 4). The Philippine scrubfowl (*Megapodius cumingii*) was observed using the same geothermal soil burrows as maleos, a pattern that aligns with Idris et al. (2006), who noted the scrubfowl's elusive habits and preference for shared nesting sites. Several opportunistic predators including the Malay civet (*Viverra tangalunga*) and water monitor (*Varanus salvator*), were detected at several nesting locations. The presence of these predators raises important conservation concerns related to the risk of egg predation. However, human egg poaching remains the primary predator-related threat to the maleo and has been identified as the single most primary driver of the species' population decline. Despite existing legal protections and ongoing conservation efforts, egg poaching continues to occur and has contributed to the abandonment of many nesting grounds (Summers et al. 2023).

Nesting habitat characteristics

The characteristics of the maleo's nesting habitats varied substantially across different sites in the landscape. Altitude, soil temperature, and moisture were abiotic components that were ecologically associated. Maleo nesting habitats in LLNP spanned a wide altitudinal range from 119 to 1,143 m asl (Table 5). However, the majority of active nesting sites were located below 1,000 m asl, corresponding primarily to lowland forest. Sites located above 1,000 m asl, particularly in Taveki, showed no detected maleo activity during the study period. This pattern indicates that maleo nesting activity in LLNP is currently concentrated at lower elevations. This finding aligns with previous studies by BBTNLL (2024), which reported that maleo nesting in LLNP typically occurs within the 200-1,000 m asl range. Soil temperatures recorded in this study ranged from 25°C to 41°C, with the highest readings recorded near geothermal sources such as Karatambe and Saluki. Soil temperature is a critical factor influencing the hatching success of their eggs. Previous studies reported that maleo eggs can successfully hatch at incubator temperatures ranging from 32°C to 36°C, with the highest hatchability observed at 34°C (Rusiyantono et al. 2025). The average temperature at these natural nesting sites is around 32.5°C, with a soil moisture level of approximately 90% (Karim et al. 2022). Soil moisture values in this study were consistently high, often exceeding 80%, particularly at mid- to high-elevation forest sites, suggesting that humid soil conditions support thermal stability during incubation. While not directly comparable due to methodological differences, these findings offer useful contextual support for our results.

Similarly, light intensity across maleo nesting sites also varied widely, ranging from 139.67 lux to 3406.2 lux (Table 5). This variation reflects differences in canopy openness, with active nesting areas tending to occur in partially open habitats rather than extremely shaded or exposed sites. As a diurnal species, maleo is likely influenced by solar radiation in its daily activity patterns and in its nesting ecology. Sunlight intensity affects ground-level microclimatic conditions, particularly soil temperature and humidity. Shaded environments help stabilize temperature fluctuations, while open areas can elevate soil surface temperatures during the day. Therefore, light intensity may play a secondary but ecologically relevant role in defining the thermal suitability of nesting sites (Moghuri et al. 2021).

The soil pH values recorded in this study ranged from 3.8 to 7.6 (Table 5), indicating a broad spectrum of soil chemical conditions. Overall, most nesting sites displayed pH levels within the range of 5 to 7, suggesting that maleo tend to utilize mildly acidic to neutral soils. This finding aligns with previous studies by Muhi et al. (2021), who reported that maleo eggs can successfully incubate in soils with acidic to neutral pH conditions. Kesaulya et al. (2023) further emphasized that when coupled with adequate moisture, acidic soils provide a favorable environment that helps prevent egg decomposition during incubation.

Slope and nest depth data further contextualize site suitability. While slope angles varied from 0% to 45% (Table 5), most active nesting sites occurred on gentle to moderate slopes, which likely provide adequate drainage and stable subsurface thermal conditions. Slope plays a significant role in shaping maleo nesting habitats' thermal and hydrological dynamics. In areas with appropriate inclines, geothermal heat rises more efficiently toward the soil surface, creating ideal incubation conditions for maleo eggs. Additionally, moderate slopes can facilitate groundwater and geothermal energy accumulation and flow, concentrating warmth within specific zones. Gentle to moderate slopes also contribute to adequate surface drainage, which is crucial in preventing nest flooding during periods of heavy rainfall (Rosalia et al. 2025).

Nest depths ranged from 28.6 to 45 cm (Table 5), with shallower nests generally found at sites where geothermal heat is closer to the surface, reducing excavation effort for nesting females. The depth of maleo nests varies depending on the location and environmental conditions. In semi-natural hatcheries, the nests are constructed with an average depth of 32 cm. These hatcheries utilize geothermal heat to replicate natural conditions and support egg hatching (Karim et al. 2022). In the specific case of Lake Towuti, South Sulawesi, the nests have an average depth of 0.6 meters (60 cm) (Karim et al. 2023).

Landscape features, including proximity to geothermal sources, plantations, roads, and settlements, were also considered. Notably, most active nesting grounds were located within 20 meters of geothermal activity (Table 5), reinforcing the species' firm reliance on thermal soil for natural incubation. This pattern aligns with previous reports showing that geothermally heated soils provide maleos with stable incubation temperatures that are less affected by daily or seasonal air-temperature fluctuations. Protecting these sites from human encroachment is crucial. Dekker (1990) emphasized that maleos are fully dependent on volcanically heated soils and that such nesting grounds are increasingly threatened. Additionally, as noted by Dekker (1988) on Hafsah et al (2009), nesting sites closer to geothermal sources tend to have more stable subsurface temperatures, unaffected by surface air fluctuations. In contrast, distance to anthropogenic structures did not show a clear pattern, though such features may still pose indirect threats.

Biotic variables, particularly vegetation structure, were key in shaping microhabitat suitability. Understory cover ranged from 24% to 88% (Table 5) and showed a strong positive association with active nesting sites. Dense understory vegetation contributes to predator avoidance, stabilizes the microclimate, and helps reduce fluctuations in soil temperature, all of which are important for embryo development and hatch success. Canopy cover, by contrast, exhibited more modest variation (ranging from 46% to 89%). Canopy density influences light penetration and indirectly affects ground-level thermal conditions and plant community composition. Sites with partial to moderate canopy cover, including those in Saluki, Mapane, and Mangku, provide balanced exposure to sunlight while maintaining sufficient shading to buffer extreme temperature fluctuations. Moreover, canopy cover may influence predator dynamics by shaping vertical habitat structure and affecting the movement of aerial or arboreal predators. Thus, although not a primary driver of nesting site selection, canopy characteristics contribute to broader habitat conditions that support reproductive success.

The patterns observed in this study emphasize the thermal dependency of maleo nesting, wherein the species exhibits a degree of plasticity in selecting both geothermal and solar-heated sites. Geothermal sites provide consistently warm conditions year-round, whereas solar-heated sites may require behavioral adjustments such as deeper excavation or selection of shaded microhabitats to maintain incubation temperatures. These ecological trade-offs suggest that maleo adaptively balances environmental cues to optimize reproductive outcomes in a landscape with heterogeneous thermal properties. Similar thermal-based nesting strategies are also found in *Megapodius reinwardt*, a mound-building megapode species distributed across eastern Indonesia. According to Yamin et al. (2024), *M. reinwardt* constructs communal nest mounds composed of soil and plant litter in relatively open areas, where solar radiation and decomposing organic material generate sufficient heat for incubation. Nest site selection by *M. reinwardt* was significantly influenced by variables such as light intensity, canopy cover, vegetation density, soil texture, and proximity to water sources. While the nesting strategy differs structurally, the underlying ecological dependency on external heat remains a convergent trait. This comparison highlights a shared thermal adaptation among megapodes, all relying on environmental heat rather than parental incubation.

The reliance of maleo on specific thermal niches underscores the importance of habitat protection tailored to the thermal dynamics of nesting grounds. Conservation efforts should prioritize the maintenance of geothermal features, hydrological processes, and vegetation structures that regulate soil temperature and moisture, alongside reducing anthropogenic disturbances near geothermal zones. Protecting a mosaic of geothermal and solar-heated nesting environments will be crucial to ensure reproductive success and long-term population viability under shifting environmental conditions (Yamin et al. 2024).

To better understand the vegetation structure of maleo nesting habitats, the Importance Value Index (IVI) was used as an indicator of species dominance. The IVI is a quantitative measure used to determine the ecological dominance of plant species within a community, calculated from the sum of relative density, relative frequency, and relative dominance. A higher IVI value indicates that a species has a greater role in structuring the vegetation community and influencing habitat characteristics (Odum 1998). As shown in Table 6, several species exhibit high IVI values in both the pole and tree layers, indicating their prominent roles in shaping the structure of maleo nesting habitats. In the pole layer, the dominant species included *Macaranga hispida* and *Pangium edule*, both characteristic of pioneer vegetation that establishes rapidly in open or disturbed areas. These species shape the lower vegetation strata and influence understory openness. In the tree layer, *Pterospermum celebicum*, *Ficus* sp., and *Palaquium* sp. exhibited the highest dominance, indicating the presence of mature forest elements within the nesting environment. The coexistence of pioneer species in the pole layer and climax species in the tree layer highlights the structural and successional diversity of the nesting grounds, which is ecologically important for maleo as it provides microclimate regulation, shade, and food resources.

Environmental drivers of maleo presence

Our regression model showed that the only variable with a statistically significant influence was understory vegetation cover (p-value: 0.00997). The final logistic regression model is logit(P) = 8.021 − 0.1653 × (understory cover). From the parameter estimates, the intercept has a value of 8.021 with a p-value of 0.00649, indicating that when understory cover equals 0, the log-odds of maleo presence is 8.021. In odds ratio terms, this corresponds to a value of 3044.31, meaning the probability of presence is extremely high when there is no understory vegetation cover. Meanwhile, the coefficient for understory vegetation cover is -0.1653 with a p-value of 0.00997, indicating a significant negative relationship with maleo presence.

Table 3. Wildlife species recorded by camera traps across maleo nesting ground sites in Lore Lindu National Park, Indonesia

Species	IUCN redlist	Number of images	Independent Event (IE)	Number of locations
Maleo (*Macrocephalon maleo*)	CR	696	228	14
Common Hill Rat (*Bunomys chrysocomus*)	LC	391	329	11
Common Water Monitor (*Varanus salvator*)	LC	166	137	8
Sulawesi Giant Squirrel (*Rubrisciurus rubriventer*)	LC	68	60	11
Human (*Homo sapiens*)	-	31	17	10
Tonkean Macaque (*Macaca tonkeana*)	VU	18	12	6
Red Junglefowl (*Gallus gallus*)	LC	10	9	2
Snoring Rail (*Aramidopsis plateni*)	VU	5	5	2
Rufous-throated Flycatcher (*Ficedula rufigula*)	NT	4	2	2
Philippine Scrubfowl (*Megapodius cumingii*)	LC	4	3	2
Malay Civet (*Viverra tangalunga*)	LC	2	2	2
Mount Topapu Squirrel (*Prosciurillus topapuensis*)	NT	1	1	1
Common Mabuya (*Eutropis multifasciata*)	LC	1	1	1

Table 4. Summary of nesting habitat characteristics of maleo in Lore Lindu National Park, Indonesia

Site	Altitude (m asl)	Range of soil temp (°C)	Soil moisture (%)	Light intensity (lux)	Range of pH	Slope (%)	Nest depth (cm)	Distance to hot springs (km)	Distance to plantations (km)	Distance to road (km)	Distance settlement (km)	Understory cover (%)	Canopy cover (%)
Sites with confirmed maleo presence (coded as 1) were classified as active sites													
Hulurawa1	804.0	30.0-36.0	73.9	360.8	4.5-4.6	30.0	38.7	0.010	3.5	5.0	5.5	38.0	73.0
Hulurawa2	834.0	26.0-39.0	65.4	282.6	4.5-6.3	0.0	38.1	0.010	3.7	5.1	5.7	34.0	76.0
Karatambe1	746.0	31.0-37.0	68.1	246.5	5.3-7.0	5.0	39.0	0.002	8.9	2.1	7.4	33.0	47.0
Karatambe2	751.0	31.0-41.0	72.1	485.8	3.8-6.7	10.0	44.5	0.002	9.0	2.2	7.6	33.0	46.0
Kaya	501.0	28.0-38.0	70.9	1216.6	4.5-7.0	14.0	40.6	0.002	3.2	3.7	4.4	47.0	69.0
Maima	318.0	31.0-37.0	63.7	139.7	5.0-7.0	34.0	43.1	0.004	0.2	1.7	2.5	28.0	61.0
Mangku 2	335.0	27.0-37.0	65.1	209.8	5.2-6.8	18.0	32.9	0.002	3.1	4.0	4.2	61.0	72.0
Pakuli Utara 3	365.0	33.0-36.0	83.0	380.1	5.4-7.0	45.0	32.9	0.002	0.1	1.6	1.6	35.0	72.0
Saluki 1	482.0	32.0-38.0	84.1	867.7	6.2-7.2	30.0	37.3	0.002	0.6	2.4	2.3	26.0	69.0
Saluki 2	167.0	30.0-35.0	84.8	363.1	6.2-7.0	0.0	37.7	0.002	0.5	2.3	2.2	31.0	71.0
Saluki 3	191.0	30.0-38.0	86.4	352.8	6.4-7.0	15.0	35.0	0.001	0.7	2.4	2.3	36.0	77.0
Saluki 4	200.0	28.0-36.0	83.1	411.3	6.4-6.8	0.0	36.3	0.020	1.0	2.7	2.6	33.0	68.0
Saluki 6	119.0	30.0-37.0	90.6	467.9	6.6-6.8	5.0	28.6	0.005	1.0	2.8	2.7	35.0	71.0
Saluki 7	818.0	32.0-34.0	89.5	499.3	6.2-6.6	40.0	40.0	0.002	1.0	3.0	2.9	24.0	67.0
Mean	473.6	29.9-37.1	77.2	448.9	5.4-6.7	17.6	37.5	0.005	2.6	2.9	3.9	35.3	67.1
Median	423.5	30.0-37.0	78.5	371.6	5.6-6.9	14.5	37.9	0.002	1.0	2.5	2.8	33.5	70.0
Sites with no confirmed maleo presence (coded as 0) were classified as inactive sites													
Hulurawa3	731.0	26.0-30.0	67.5	486.7	4.5-6.7	0.0	32.2	0.010	2.8	4.3	4.7	53.0	87.0
Mangku 1	327.0	31.0-34.0	89.0	479.0	6.5-7.0	12.0	45.0	0.010	3.1	3.9	4.1	85.0	67.0
Mapane 1	354.0	31.0-35.0	82.7	2060.5	6.4-7.2	40.0	43.3	0.020	3.2	2.2	2.1	88.0	80.0
Mapane 2	359.0	30.0-37.0	85.6	283.8	6.0-7.0	42.0	41.0	0.005	3.3	2.0	1.9	71.0	70.0
Pakuli Utara 1	343.0	32.0-38.0	83.3	3406.2	6.4-7.2	10.0	33.8	0.001	0.2	1.5	1.5	49.0	68.0
Pakuli Utara 2	356.0	31.0-35.0	81.9	1860.3	5.3-7.3	15.0	35.6	0.010	0.1	1.6	1.5	40.0	58.0
Pakuli Utara 4	383.0	32.0-37.0	85.0	711.6	5.4-6.6	30.0	35.3	0.010	0.02	1.6	1.6	81.0	83.0
Pakuli Utara 5	484.0	31.0-35.0	89.7	1565.3	5.2-6.7	35.0	32.8	0.010	1.4	0.1	0.1	75.0	64.0
Saluki 5	221.0	29.0-37.0	83.9	359.7	6.4-7.0	30.0	40.5	0.200	1.0	2.9	2.8	49.0	80.0
Saluki 8	812.0	32.0-35.0	88.2	433.8	6.7-6.8	30.0	35.6	0.100	1.2	3.1	3.0	68.0	73.0
Saluki 9	787.0	33.0-37.0	91.9	589.3	6.5-7.1	40.0	28.6	0.010	1.2	3.0	2.9	78.0	72.0
Taveki 1	1143.0	25.0-28.0	90.1	280.0	7.0-7.6	15.0	34.6	0.050	3.2	11.5	13.7	74.0	89.0
Taveki 2	1138.0	28.0-30.0	85.1	283.0	6.7-7.6	10.0	32.0	0.070	3.4	11.6	13.5	79.0	66.0
Mean	572.2	30.1-34.5	84.9	984.6	6.1-7.0	23.8	36.2	0.039	1.9	3.8	4.1	68.5	73.6
Median	383.0	31.0-35.0	85.1	486.7	6.4-7.0	30.0	35.3	0.010	1.4	2.9	2.8	74.0	72.0

Table 6. Top five plant species with the highest Importance Value Index (IVI) in pole and tree layers of maleo nesting habitat in Lore Lindu National Park, Lore Lindu National Park, Indonesia

Rank	Local name / Scientific name	Total of individuals	IVI
Poles			
1	Meapo (*Macaranga hispida*)	30	40.448
2	Pangi (*Pangium edule*)	22	32.131
3	Lotu (*Aphanamixis polystachya*)	15	20.647
4	Andolia (*Canangium odoratum*)	11	14.858
5	Lekatu (*Duabanga moluccana*)	10	14.804
Trees			
1	Ntorode/Bayur (*Pterospermum celebicum*)	34	29.773
2	Beringin (*Ficus* sp.)	28	28.33
3	Kume/Nyatoh (*Palaquium* sp.)	38	24.067
4	Tea/Terap (*Artocarpus elasticus*)	28	22.903
5	Rau (*Dracontomelon dao*)	27	16.3

The odds ratio for this variable is 0.848, which means that for every 1-unit increase in understory cover, the probability of presence decreases by approximately 15.2%. Thus, the higher the understory vegetation cover, the lower the probability that a site functions as an active nesting site. This pattern is consistent with the descriptive results (Table 5), which show that active nesting sites generally had lower understory cover compared to inactive sites. From a management perspective, the negative association between understory cover and maleo presence suggests that maintaining relatively open understory conditions may help sustain active nesting sites. Therefore, excessive understory densification may reduce habitat suitability, and habitat management in LLNP should prioritize maintaining structurally open nesting grounds, particularly near geothermal areas.

Further analysis confirmed that understory vegetation cover significantly negatively impacts maleo presence. The Hosmer-Lemeshow test was applied to test the model's goodness of fit. The result showed χ-squared: 3.4207 with a p-value: 0.9053. Since the p-value>0.05, the model fits the data well, indicating no significant difference between the model's predictions and the observed data. The model's performance was then evaluated using a confusion matrix. The model achieved an accuracy of 92.59%, with a sensitivity (ability to detect absence) of 92.31% and specificity (ability to detect presence) of 92.86%. The Kappa value was 0.8516, indicating excellent performance in distinguishing between presence and absence. Further evaluation using the Receiver Operating Characteristic (ROC) curve yielded an Area Under the Curve (AUC) of 0.9725, demonstrating outstanding classification capability. An AUC value above 0.9 indicates that the model can distinguish between present and absent individuals with very high accuracy. Based on these results, it can be concluded that understory vegetation cover significantly affects maleo presence, showing a negative relationship. Nevertheless, given that only one predictor remained in the final model, the results should be interpreted as highlighting a dominant differentiating factor rather than representing the full ecological complexity of maleo nesting habitat.

The role of understorey vegetation in shaping maleo presence has rarely been emphasized in previous studies, which have predominantly focused on soil temperature, soil moisture, and canopy cover. However, this study found that maleo presence tended to increase in areas with lower understorey density. This finding indicates that understorey structure functions as a primary microhabitat filter influencing active nesting site use. Sparse ground vegetation may facilitate better accessibility for nesting activities and predator avoidance. This finding is consistent with observations by Karim et al. (2023), who reported that nesting areas around Lake Towuti were dominated by low-growing plants such as grasses (*Imperata cylindrica, Eleusine indica*) and shrubs that provided both concealment and ease of access for the birds during egg-laying activities. Similarly, Jamili et al. (2015) documented that maleo nesting grounds in Rawa Aopa Watumohai were surrounded by selected understorey species that functioned as food sources and shelter, including *Bambusa spinosa* and *Melastoma* sp. In contrast, Karim et al. (2022) noted that dense understory without adequate tree cover was usually avoided, as it restricts visibility and increases disturbance risk. These comparisons suggest that vegetation structure influences nesting suitability through a balance between accessibility and protection, rather than through vegetation presence alone.

Maleo are more frequently found in habitats with lower understory vegetation cover because open ground conditions improve nest excavation efficiency, enhance soil warming, and promote predator visibility. Understorey vegetation, therefore, affects nesting habitat through combined effects on accessibility, thermoregulation, and risk detection. The non-significance of other environmental variables may reflect limited variation among sampled sites or the selective nature of maleo in choosing microhabitats that already meet basic thermal and soil requirements. Where geothermal and soil conditions are generally suitable, fine-scale structural variables may become stronger predictors of presence. Comparisons with other megapodes, including *Megapodius reinwardt*, should be interpreted cautiously. The similarities observed represent functional ecological analogies in nesting strategy rather than direct biological equivalence, and species-specific differences must be acknowledged.

In addition to supporting population growth, habitat management plays a critical role in maleo conservation. For example, the Saluki nesting ground has relatively better conditions than other sites. Current disturbances include predators and dense understory vegetation in some areas. Selective understorey thinning around active nesting clusters is recommended to maintain relatively open ground while retaining peripheral vegetation for structural buffering. Complete clearing should be avoided to prevent excessive exposure. In geothermal nesting areas, maintaining soil heat absorption through controlled vegetation management is particularly important. Identifying active sites with optimal understory structure, favorable soil temperature, and geothermal influence provides ecological benchmarks for refining habitat protection zones within Lore Lindu National Park. Regulating human activity around nesting zones, particularly during the breeding season, is crucial to minimizing disturbance. Seasonal restriction combined with strengthened community-based patrol cycles during peak nesting months may reduce nest abandonment and improve hatching success. The results of this study align closely with Indonesia's Strategi dan Rencana Aksi Konservasi (SRAK) Maleo Senkawor 2020-2030 (SK Menteri LHK No. 76/MENLHK/SETJEN/KSA.2/2022), which prioritizes improving the quality of nesting sites, protecting and restoring habitat, and reducing threats from predators and human disturbance. Integrating these findings into national and park-level strategies will help ensure that conservation actions are both evidence-based and spatially targeted, ultimately enhancing the long-term viability of maleo populations.

Study limitations

Although 13 predictors were initially considered, only one variable remained significant in the final model. This outcome may partly reflect the limited sample size relative to model complexity, which can reduce statistical power and increase the risk of Type II error. Therefore, non-significant variables should not be interpreted as ecologically unimportant, but rather as not detectable within the constraints of the present dataset. To minimize overfitting, model simplification was applied through VIF screening and backward selection, resulting in a parsimonious model focused on the strongest predictor. Given that nesting ecology is inherently multifactorial, the dominance of a single predictor should be interpreted cautiously.

Potential spatial bias may exist, as surveys were limited to accessible nesting sites, while other potentially suitable but less accessible areas may not have been surveyed and could have been overlooked. As a result, the sampled sites may not fully represent the entire range of maleo nesting habitats in LLNP. In addition, the number and placement of camera traps may have constrained the detection of certain predator species, particularly those that are rare or elusive, despite continuous 24-hour operation. Seasonal variation in environmental conditions may also not have been fully captured within the study period. Future research should expand spatial coverage, increase sampling intensity, and incorporate long-term climatic and soil monitoring to better understand temporal habitat dynamics and support adaptive management.

In conclusion, this study highlights that maleo nesting activity in Lore Lindu National Park is primarily influenced by microhabitat structure. Nesting sites were found from lowland to lower montane forests (0-1,500 m asl), typically on flat to gently sloping terrain near geothermal sources, indicating consistent selection of thermally suitable substrates. Soil temperatures ranged from 25-41°C, and maleo presence was strongly associated with lower understory vegetation cover. Among all variables examined, understory vegetation cover emerged as the only significant predictor of maleo presence, indicating a clear habitat preference for open ground conditions that facilitate soil heating and unobstructed nest excavation. These findings emphasize that sustaining suitable nesting habitats requires maintaining geothermal zones and controlling dense understory vegetation through selective management. The ecological relevance of sparse understory highlights the importance of preserving microhabitat conditions that directly support incubation efficiency and predator visibility. Therefore, conservation priorities should focus on (i) delineating and safeguarding geothermal nesting areas, (ii) applying selective understory thinning around active nesting clusters, and (iii) regulating human activities during peak breeding periods. However, implementation should consider practical constraints within the park, including limited resources, staffing capacity, and long-term monitoring capability. Gradual vegetation management and strengthened community-based patrols may provide more feasible and sustainable approaches than intensive intervention. Future research should focus on long-term monitoring of nesting habitats and involve local communities in managing and safeguarding active nesting areas to enhance adaptive management and long-term population persistence.

ACKNOWLEDGEMENTS

The authors express gratitude to the Indonesia Endowment Fund for Education (LPDP), Ministry of Finance of the Republic of Indonesia, for supporting the study. Special thanks are also extended to the Forest Program III Sulawesi for supporting the research and to all friends and colleagues at Lore Lindu National Park, Central Sulawesi, Indonesia, for their invaluable assistance and cooperation.

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