BIODIVERSITAS ISSN: 1412-033X
Volume 26, Number 6, June 2025 E-ISSN: 2085-4722
Pages: 3030-3039 DOI: 10.13057/biodiv/d260645

Characteristics of Maleo (*Macrocephalon maleo*) roosting trees in North Buton Wildlife Reserve, Southeast Sulawesi, Indonesia

KEMAL MUHSANDI[1], JARWADI BUDI HERNOWO[2,♥], YUDI SETIAWAN[2,3]

[1]Tropical Biodiversity Conservation Study Program, Department of Forest Resources Conservation and Ecotourism, Faculty of Forestry and Environment, Institut Pertanian Bogor. Jl. Ulin, Lingkar Akademik Kampus IPB, Dramaga, Bogor 16680, West Java, Indonesia
[2]Department of Forest Resources Conservation and Ecotourism, Faculty of Forestry and Environment, Institut Pertanian Bogor. Jl. Ulin, Lingkar Akademik Kampus IPB, Dramaga, Bogor 16680, West Java, Indonesia. Tel./fax.: +62-251-8621947, ♥email: jblina11@gmail.com
[3]Center for Environmental Research, International Research Institute for Environment and Climate Change (CER-IRIECC), Institut Pertanian Bogor. Jl. Taman Kencana, Babakan, Bogor 16128, West Java, Indonesia

Manuscript received: 13 April 2025. Revision accepted: 11 June 2025.

Abstract. *Muhsandi K, Hernowo JB, Setiawan Y. 2025. Characteristics of Maleo (*Macrocephalon maleo*) roosting trees in North Buton Wildlife Reserve, Southeast Sulawesi, Indonesia. Biodiversitas 26: 3030-3039.* Maleo (*Macrocephalon maleo*) exhibits a high degree of selectivity in choosing roosting trees, a behavior influenced by the availability and specific characteristics that ensure safety and comfort. This study was conducted in the North Buton Wildlife Reserve, Southeast Sulawesi, Indonesia, a conservation area known for its Maleo population, and focused on examining the attributes of roosting trees. A purposive sampling method was employed to identify Maleo roosting trees, and a single-plot method was used for vegetation analysis to determine the composition and structure of surrounding tree species using the Importance Value Index (IVI). The characteristics of roosting trees were analyzed based on several parameters, including total tree height, Diameter at Breast Height (DBH), crown architecture, branching structure, roost height and position, and proximity to food sources and nesting grounds. Wilcoxon rank-sum tests compared tree height and DBH between roosted and non-roosted trees. The results indicated that Maleo roost trees are emergent trees, taller than surrounding vegetation, spatially isolated, and characterized by open crowns with widely spaced, relatively flat branches. Horizontally, Maleos typically roost at the center of the tree crown; vertically, their roosting position is far from the main trunk, reducing disturbance. Roosting trees near food sources and nesting grounds reflect efficient habitat utilization. This efficient spatial utilization of the Maleo bird is a testament to its adaptability and is truly admirable.

Keywords: Characteristics, disturbance, emergent tree, *Macrocephalon maleo*, Maleo, roosting trees

INTRODUCTION

Maleo (*Macrocephalon maleo*) is an endemic bird species of Sulawesi, belonging to the Megapodiidae family, and is distributed across the Sulawesi mainland and surrounding islands (Summers et al. 2023). This bird exhibits unique communal nesting behavior by burying its eggs in geothermally heated soil in forests or on sun-warmed sandy beaches (Maulany et al. 2021). The natural habitat of the Maleo consists of lowland tropical forests that provide essential elements, including nesting grounds, food sources, and roosting trees, which serve as shelters for rest (Santrio et al. 2021).

Research on roosting trees used by Maleos is crucial for understanding the ecological traits and habitat elements essential for the survival of this species. Roosting trees are vital habitat components, offering Maleos safe and comfortable resting places. However, not all trees are utilized for roosting, as selection is influenced by the birds' need for comfort and protection from disturbances and predators (Jones et al. 1995). Despite this importance, most previous studies have only offered general insights into Maleo habitats and have not extensively analyzed roosting tree availability, characteristics, or ecological roles.

The structural characteristics of trees play a central role in attracting birds for roosting. Morphological attributes such as crown size, height, and branch density are often decisive in the selection process, as they support roosting comfort and visibility (Charbonnier et al. 2016). Roosting trees provide strategic vantage points, concealment from predators, and specific structural features that increase their suitability for roosting (Hernowo et al. 2018). These structural features influence predation risk and the birds' sense of safety (Goodenough et al. 2017).

Beyond providing shelter, roosting trees contribute to other ecological functions, including thermoregulation (Ellison et al. 2019) and seasonal adaptation (Fei et al. 2019), helping birds cope with climatic variability. Several hypotheses have been proposed to explain avian roost-site selection, such as the importance of predator avoidance (Jara et al. 2020), the need for thermal comfort, and specific preferences for particular tree species (Mah and Ramji 2020). Additionally, avian sleep behavior is closely tied to effective energy management (Siekiera et al. 2022), highlighting the importance of roosting site quality.

Although prior research has documented Maleo roosting trees (Karim et al. 2022), it has generally been limited to species identification, lacking an in-depth analysis of structural and ecological characteristics that influence selection. Meanwhile, Maleo roosting trees are under growing threat due to deforestation, land-use change, and habitat fragmentation often caused by illegal logging, agricultural expansion, and infrastructure development (Froese and Mustari 2019). These pressures are particularly evident in the North Buton Wildlife Reserve, one of the remaining strongholds of the species (Santrio et al. 2021). As a result of such habitat degradation, the Maleo is currently listed as Critically Endangered by the International Union for Conservation of Nature (IUCN) (Tasirin et al. 2021). The Indonesian Government designated it as a protected species (Aldiansyah et al. 2024).

Scientifically synthesized knowledge of bird tree associations has been widely used to develop habitat indices, assess vegetation quality, and evaluate the effectiveness of habitat management strategies relevant to conservation (Khan 2017). In releasing birds back into their natural habitat, identifying suitable roosting trees is critical to fulfilling ecological and behavioral requirements (Hernowo and Haquesta 2021). This practical approach can directly support the long-term viability of threatened species such as the Maleo.

The North Buton Wildlife Reserve was selected as the study site due to its high ecological value and role as one of the last Maleo habitats in Southeast Sulawesi, Indonesia, particularly on Buton Island. Although Maleo roosting trees have been observed in this region, no scientific publication has comprehensively described their characteristics. This study aimed to identify the features of trees selected by Maleos as roosting trees in the North Buton Wildlife Reserve. The focus was on tree species, structural characteristics such as height, diameter, crown structure, and spatial proximity to nesting and foraging areas. The research also investigated potential disturbances, including human activity and predator presence. This study provides essential insights into Maleo habitat composition by uncovering the factors influencing the roost site selection. It supports evidence-based conservation strategies to maintain the viability of remaining populations.

MATERIALS AND METHODS

Study area

The research was conducted in the North Buton Wildlife Reserve, a conservation area located at 4.643801° S and 122.876870° E, covering an area of 911.41 km² (Figure 1). The reserve features diverse topography, with elevations reaching 1,061 meters above sea level. The average annual temperature ranges from 23.1°C to 32°C, and the area receives approximately 2,700 mm of yearly rainfall. The ecosystem predominantly comprises lowland tropical rainforests in North Buton District and Muna District in Southeast Sulawesi Province, Indonesia. The landscape varies from gently undulating terrain to hilly regions and includes four major forest types: primary forest, secondary forest, shrubland, and savanna grassland. The study was conducted over four months, from January to April 2024, within the North Buton Wildlife Reserve.

Data collection

Roosting tree data collection

Data were collected using purposive sampling. Systematic observations were conducted from early morning until late afternoon (05:00-18:00 Central Indonesian Time), during which Maleos were observed roosting on or descending from their roosting trees. Roosting trees were identified based on the presence of Maleo droppings beneath them, which served as key indicators of both the species and the number of trees utilized as roosting sites. Single vegetation plots measuring 20×20 m^2 were established, each centered on a roosting tree, to analyze vegetation characteristics (Figure 2). These plots were explicitly designed to capture the Importance Value Index (IVI) of vegetation's structural and compositional attributes associated with Maleo roosting preferences.

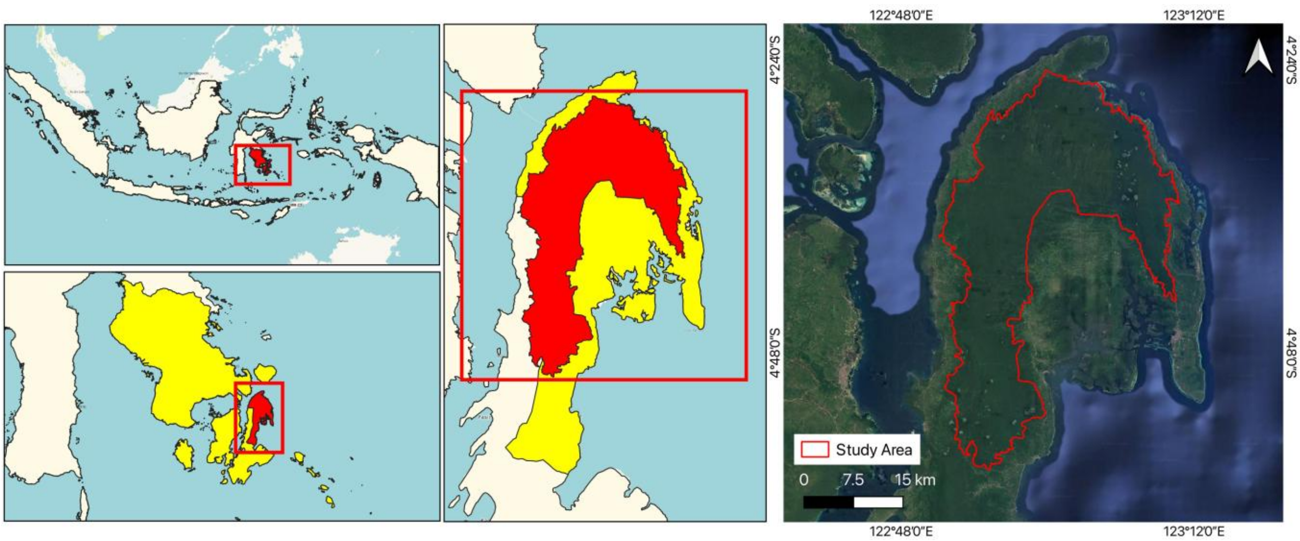

Figure 1. The research site was located in North Buton and Muna Districts, Southeast Sulawesi Province, Indonesia, namely in North Buton Wildlife Reserve

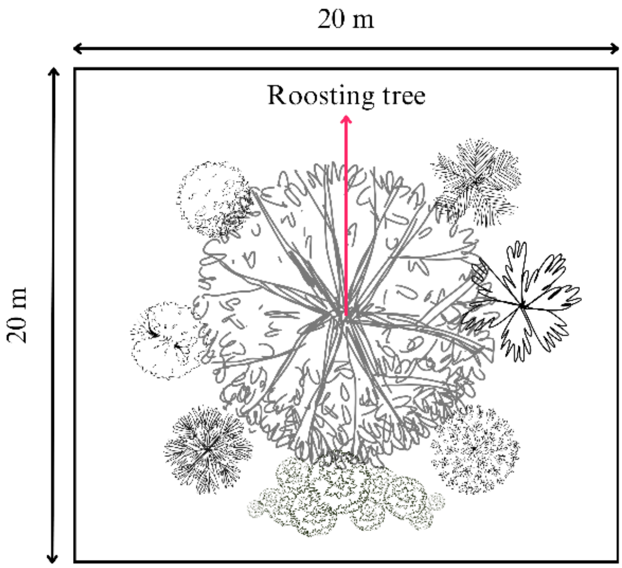

Figure 2. Design of vegetation plots (20x20 m^2)

The plot size followed standard vegetation sampling protocols for tropical forest ecosystems, allowing for adequate representation of tree diversity and structure (Arellano et al. 2016). The number of plots corresponded to the number of confirmed roosting trees within the study area during the observation period. Additional data on the species and locations of roosting trees were obtained from the North Buton Wildlife Reserve management team based on prior patrols and monitoring activities. In instances where direct observation of Maleos was hindered due to their sensitivity to human presence, the center of the plot was determined based on the location of droppings, supplemented by information from the reserve's management team.

In this study, the parameters selected for measuring tree height, Diameter at Breast Height (DBH), and crown architecture were based on ecological considerations relevant to avian roosting behavior. Total tree height was measured using a clinometer, as it correlates with the safety and stability of the roosting site. Taller trees provide better protection from predators and create more favorable microclimatic conditions (McGinn et al. 2023). DBH was measured to indicate tree strength and maturity since trees with larger diameters generally have stronger branches and offer more crown space for roosting (Komlós et al. 2024). The crown architecture was classified following the Hallé et al. (1978) system to identify branching patterns that may influence Maleo preferences, such as crown structures that provide protection or horizontal branches that facilitate roosting access. These three parameters were chosen to represent the structural characteristics of trees selected by Maleos for roosting.

Observation on tree canopy strata

The roosting positions of Maleo were documented based on horizontal and vertical stratification, which describes both the horizontal distribution of the tree canopy and the vertical height of the roost within the canopy (Figure 3) (Pearson 1971; Partasasmita et al. 2017). The height of the roost was measured using a vertical distance meter from the ground surface to the exact position of the roost within the canopy. Observers recorded the precise location of Maleo's within the canopy stratification horizontally and vertically while minimizing disturbance to the birds' activities. Observations were primarily conducted in the afternoon and evening when Maleo rested or slept on their roosting trees.

Distance measurement of the feeding tree and nesting ground

Measuring the distance between feeding trees and nesting grounds is essential for understanding the behavioral ecology of Maleos, particularly their spatial use and resource allocation. At the study site, nine types of feeding trees were identified based on their use by Maleos for fruit and seed consumption. Twelve nesting grounds were also recorded, consistent with previous findings (Santrio et al. 2021), and characterized by open sandy soil, nesting holes, and direct observations of nesting behavior. After identifying and marking the roosting trees, we recorded the precise GPS coordinates of all roosting trees, feeding trees, and nesting grounds. Euclidean (straight-line) distances between these points were calculated using ArcGIS 10.8.

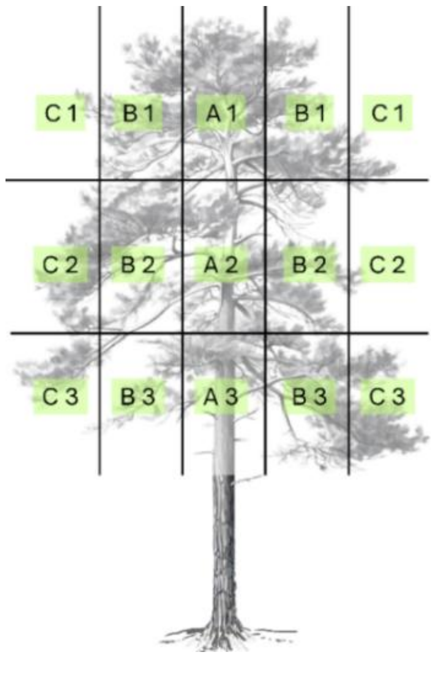

Figure 3. Stratification of canopy layers in Maleo-roosting trees. Note: The X-axis delineates the stratification of the canopy by height, with layer 1 representing the upper canopy, layer 2 denoting the middle canopy, and layer 3 indicating the lower canopy. The Y-axis illustrates the horizontal Position A within the canopy, where Position A is centrally located, Position B is situated at the canopy edge, and Position C is positioned at the canopy tip

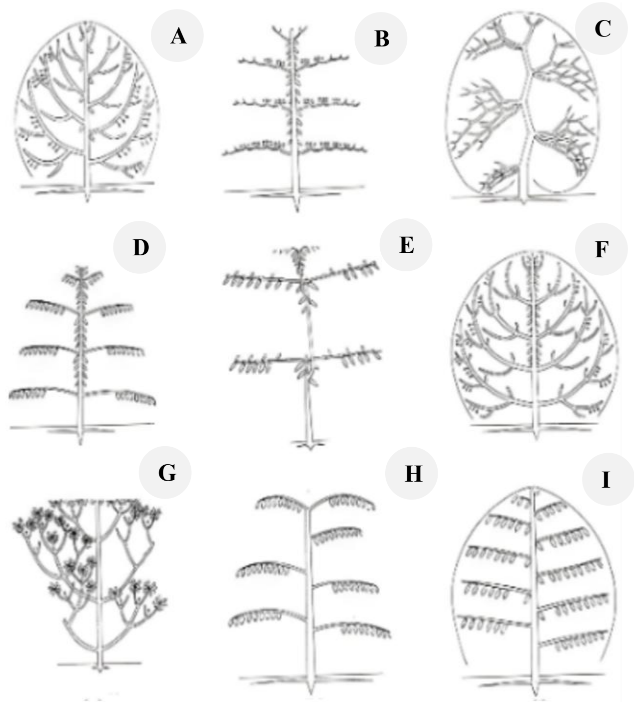

Figure 4. Tree architecture models: A. Attims, B. Aubréville, C. Koriba, D. Massart, E. Prévost, F. Rauh, G. Scarrone, H. Troll, I. Roux

Data analysis

The collected data were subjected to both qualitative and quantitative analyses. The qualitative analysis aimed to characterize the features and disturbances affecting Maleo roosting trees. These features included crown architecture models, the position of the roosting space based on horizontal (A, B, and C) and vertical stratification (1, 2, and 3) (Figure 4, and roosting height). The quantitative analysis involved comparing roosting and non-roosting trees, focusing on tree height and DBH. This comparison was conducted using the Wilcoxon rank-sum test in R version 4.3.1, with a significance level of α: 0.05 (Qomariah et al. 2023). Trees with a high IVI tend to have larger populations, occur more frequently, and dominate the ecosystem (Shirima et al. 2015). We hypothesized that Maleos more frequently roost in trees with a high IVI and that are dominant in the habitat. The vegetation parameters were used to determine the structure and composition of each male roosting tree species. IVI values were calculated by determining the dominance of each tree species based on density, frequency, and dominance metrics (Mueller and Ellenberg 1974) using the following formula:

$$IVI = RD + RF + RDo$$

$$\text{Relative density (RD)} = \frac{\textit{Number of individuals of species}}{\textit{Total number of individuals}} \times 100\%$$

$$\text{Relative frequency (RF)} = \frac{\textit{Frequency of species}}{\textit{Sum frequency of all species}} \times 100\%$$

$$\text{Relative dominance (RDo)} = \frac{\textit{Dominance of species}}{\textit{Dominance of all species}} \times 100\%$$

RESULTS AND DISCUSSION

Roosting tree species

The study of tree vegetation in Maleo habitats, particularly around roosting sites, documented 168 individual trees representing 44 different species (Table 1). These trees were distributed across 15 observation plots. Field observations revealed that Maleos utilized only five tree species as roosting (sleeping) trees, accounting for 11.36% of the recorded species. The species used for roosting included *Anthocephalus macrophyllus*, *Artocarpus elasticus*, *Guazuma tomentosa*, *Nauclea orientalis*, and *Terminalia* sp.. Each of these species was used by only one or two individuals Maleos, indicating that Maleos selectively chose specific tree species for roosting. In contrast, most available tree species were not used for this purpose.

Characteristics of a roosting tree

The roosting trees used by Maleos exhibited distinct structural characteristics that differentiated them from non-roosting trees. The mean height of roosting trees ($\bar{x}$: 13.83±1.17-15.12±2.16 m, n: 21) was significantly greater than that of non-roosting trees ($\bar{x}$: 9.96±1.06 m, n: 286), as indicated by the Wilcoxon rank-sum test (W: 336.00, p<0.001). Similarly, the mean DBH of roosting trees ($\bar{x}$: 27.48±2.20 cm, n: 21) was significantly larger than that of non-roosting trees ($\bar{x}$: 21.87±2.93 cm, n: 168) (W: 6.17, p<0.001). Regarding species dominance, *A. macrophyllus* exhibited the highest IVI at 21.40%, indicating its predominance in Maleo roosting habitats. In contrast, *G. tomentosa* recorded the lowest IVI at 1.97%, suggesting a relatively limited role as a roosting tree.

The classification of roosting tree species based on crown architecture revealed several models associated with Maleo roosting trees (Table 2). *Anthocephalus macrophyllus* and *N. orientalis* exhibit the Prévost crown architecture model, characterized by a continuous vertical axis with rhythmic, horizontal branching. This formation creates a rounded, layered crown, offering stable and expansive roosting platforms for Maleos. *Artocarpus elasticus* follows the Roux model, which features monopodial branching with a dominant vertical trunk and regularly spaced lateral branches. This structure results in a clear, stratified crown that supports roosting at various vertical levels. *Guazuma tomentosa* aligns with the Troll model, which is also marked by monopodial growth but with spiral arrangements of leaves and branches. This produces a relatively open, upward-reaching crown, potentially aiding vertical access. *Terminalia* sp. corresponds to the Aubréville model, which involves sympodial branching that ceases after a particular growth phase and is replaced by lateral branches. This pattern forms a layered and horizontally expansive crown, offering a broad and accessible canopy suitable for roosting activity.

Table 1. Tree species in Maleo roosting site, in North Buton Wildlife Reserve, Southeast Sulawesi, Indonesia

Family	Tree species	Description	Number of individuals per tree
Acanthaceae	*Dictyoneura acuminata*	Not used	-
Anacardiaceae	*Dracontomelon dao*	Not used	-
Annonaceae	*Cananga odorata*	Not used	-
Apocynaceae	*Alstonia macrophylla*	Not used	-
Apocynaceae	*Cerbera manghas*	Not used	-
Burseraceae	*Canarium asperum*	Not used	-
Calophyllaceae	*Calophyllum inophyllum*	Not used	-
Calophyllaceae	*Calophyllum soulattri*	Not used	-
Clusiaceae	*Garcinia dulcis*	Not used	-
Combretaceae	*Terminalia* sp.	Used	1
Dilleniaceae	*Dillenia serrata*	Not used	-
Ebenaceae	*Diopyros pilosanthera*	Not used	-
Ebenaceae	*Diospyros celebica*	Not used	-
Euphorbiaceae	*Aleurites moluccana*	Not used	-
Euphorbiaceae	*Macaranga gigantea*	Not used	-
Euphorbiaceae	*Mallotus oblongifolius*	Not used	-
Fabaceae	*Erythrina subumbrans*	Not used	-
Fabaceae	*Leucaena leucocephala*	Not used	-
Lamiaceae	*Vitex cofassus*	Not used	-
Lecythidaceae	*Barringtonia racemosa*	Not used	-
Magnoliaceae	*Elmerrillia ovalis*	Not used	-
Malvaceae	*Colona celebica*	Not used	-
Malvaceae	*Guazuma tomentosa*	Used	2
Malvaceae	*Hibiscus tiliaceus*	Not used	-
Meliaceae	*Aglaia odoratissima*	Not used	-
Meliaceae	*Chisocheton ceramicus*	Not used	-
Moraceae	*Antiaris toxicaria*	Not used	-
Moraceae	*Artocarpus elasticus*	Used	2
Moraceae	*Ficus altissima*	Not used	-
Moraceae	*Ficus microcarpa*	Not used	-
Moraceae	*Ficus septica*	Not used	-
Myrtaceae	*Decaspermum fruticosum*	Not used	-
Myrtaceae	*Rhodamnia mulleri*	Not used	-
Myrtaceae	*Syzygium lineatum*	Not used	-
Oleaceae	*Chionanthus nitens*	Not used	-
Phyllanthaceae	*Breynia cernua*	Not used	-
Phyllanthaceae	*Cleistanthus myrianthus*	Not used	-
Putranjivaceae	*Drypetes longifolia*	Not used	-
Rubiaceae	*Anthocephalus chinensis*	Not used	-
Rubiaceae	*Anthocephalus macrophyllus*	Used	2
Rubiaceae	*Morinda citrifolia*	Not used	-
Rubiaceae	*Nauclea orientalis*	Used	1
Sapindaceae	*Mischocarpus sundaicus*	Not used	-
Stemonuraceae	*Gomphandra mappioides*	Not used	-

According to the classification of tree crown space in horizontal and vertical dimensions, Maleo occupies horizontal crown spaces B and 2 (Table 2). Specifically, Maleo selects roosting trees characterized by canopy strata B2 (Figure 3), which have horizontal branches oriented at approximately 90°. These roosting trees are typically free from lianas and insect nests, such as ant nests, and their canopies do not make contact with adjacent trees. The position of the Maleo within the crown is strategically located away from the main trunk and centrally situated within the branching structure, allowing for increased flexibility and mobility in response to potential threats.

In contrast, trees not used as roosting sites tend to have lower heights and smaller trunk diameters. These non-roosting trees fall under several crown architecture models Attims, Koriba, Rauh, and Scarrone (Figure 5). The Attims model features a vertically growing main trunk with limited lateral branching, resulting in a narrow and dense crown that offers insufficient horizontal space for roosting. The Koriba model is characterized by a minimally growing main trunk replaced by large, spreading branches, often creating an unstable or asymmetrical crown. The Rauh model displays a predominantly vertical trunk with symmetrical horizontal branches; however, the crown it forms is typically too tall and narrow to support roosting adequately. Meanwhile, the Scarrone model results in an asymmetrical and laterally spreading crown with irregular branching, presenting challenges for Maleo 's stability and accessibility. These non-roosting trees usually have dense or irregular crowns that do not align with Maleo 's preference for relatively open, horizontal, and easily accessible crown spaces. Additionally, their crowns often intermingle with neighboring trees, and their trunks are frequently overgrown with lianas, further diminishing their suitability for roosting.

Distance between roosting trees, feeding trees, and nesting grounds

The findings of this study revealed that the distances between Maleo roosting trees, feeding trees, and nesting grounds varied notably among the roosting tree species (Table 3). In general, roosting trees were closer to feeding trees than nesting grounds, indicating a spatial preference that may reflect the birds' foraging needs and energy conservation strategies. Feeding trees identified as key sources of fruits and seeds included *Dracontomelon dao*, *Aleurites moluccana*, *Lantana camara*, *Muntingia calabura*, *Macaranga gigantea*, *Myristica fatua*, *Ficus* spp., *Pangium edule*, and *Palaquium obtusifolium*. The average distances from roosting trees to feeding trees ranged from 24.47±26.35 meters to 68.5±41.72 meters, with *G. tomentosa* being the closest and *A. elasticus* the farthest in proximity to feeding resources. In contrast, distances to nesting grounds exhibited greater variability, ranging from 145.50±68.77 meters to 194.50±93.75 meters. Among the roosting tree species, *A. macrophyllus* was closest to the nesting grounds, while *Terminalia* sp. was the farthest. These spatial patterns suggest that while proximity to food sources appears to be a stronger determinant in roosting tree selection, the nesting sites, though essential, are generally tolerated at greater distances. This spatial configuration likely reflects the Maleo's behavioral trade-offs between safety, foraging efficiency, and reproductive activities.

Discussion

Selection of roosting trees

Functional tree characteristics such as height, crown architecture, and branching patterns are crucial in their selection as bird roosting sites (Buba and Jaafar 2021). Trees that provide structural stability and spatial openness, particularly those with tall crowns and horizontal branches, are often more favorable as roosting substrates (Zhao 2024). This study identified five tree species as Maleo roosting trees: *A. macrophyllus*, *N. orientalis*, *A. elasticus*, *G. tomentosa*, and *Terminalia* sp.. Detailed architectural measurements indicated that these trees were generally taller and exhibited larger stem diameters than those within the study area. Their crowns tended to be open, with expansive, flat horizontal branches supporting roosting. Additionally, their vertical growth forms typically did not intersect with the surrounding canopy, and they were often free of obstructive vine features that likely facilitated access and ensured secure roosting opportunities.

Structurally, the roosting trees displayed crown architectural models such as Prévost, Roux, Troll, and Aubréville. These models are characterized by layered, stable branching structures that enhance stability and visibility traits associated with preferred roosting conditions. In contrast, non-roosting trees typically exhibited different architectural characteristics, including shorter stature, smaller stem diameter, and crown models like Attims, Koriba, Rauh, and Scarrone, which are associated with more asymmetrical crowns and higher crown overlap.

Table 2. Height, DBH, IVI of and utilization of tree crown space by Maleo for roosting in in North Buton Wildlife Reserve, Southeast Sulawesi, Indonesia

Roosting tree species	Number of tree (s)	Average tree height (m)	Average tree DBH (cm)	IVI (%)	Canopy strata used	Crown architecture
Anthocephalus macrophyllus	6	15.17±2.04	27.86±4.19	21.40	B2	Prévost
Artocarpus elasticus	2	16.00±2.83	27.86±2.93	7.09	B2	Roux
Guazuma tomentosa	3	14.33±3.06	26.25±5.47	1.97	B2	Troll
Nauclea orientalis	6	13.83±1.17	25.89±2.44	7.58	B2	Prévost
Terminalia sp.	4	14.25±1.71	27.54±5.99	4.75	B2	Aubréville

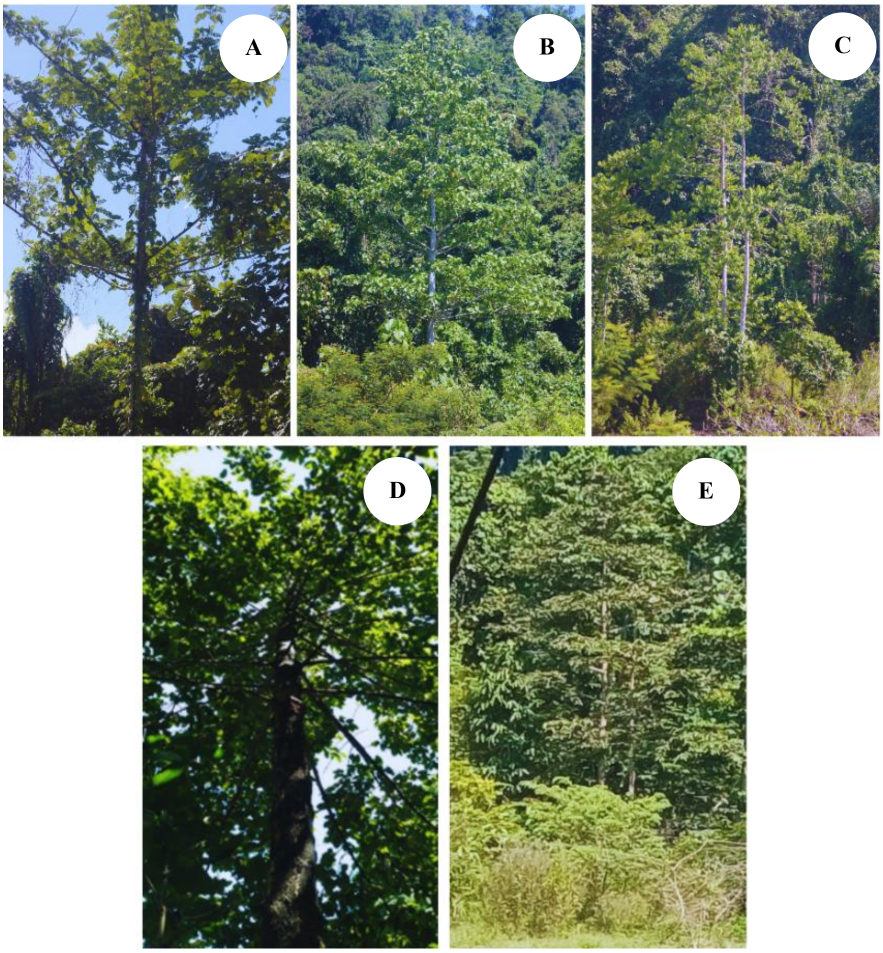

Figure 5. Roosting tree species of Maleo in in North Buton Wildlife Reserve, Southeast Sulawesi, Indonesia. A. *Anthocephalus macrophyllus*, B. *Terminalia* sp., C. *Guazuma tomentosa*, D. *Nauclea orientalis*, E. *Artocarpus elasticus*

Table 3. Distance of roosting trees to feeding trees and nesting ground in in North Buton Wildlife Reserve, Southeast Sulawesi, Indonesia

Roosting tree species	Average distance to feeding trees (m)	Average distance to nesting ground (m)
Anthocephalus macrophyllus	64.17±64.69	145.50±68,77
Artocarpus elasticus	68.5±41.72	151.50±37,48
Guazuma tomentosa	24.47±26.35	153.67±64,61
Nauclea orientalis	45.67±42.16	167.00±83,77
Terminalia sp.	65.25±61.83	194.50±93,75

Among the identified roosting species, *A. macrophyllus* exhibited the highest Importance Value Index (IVI) at 21.40%, indicating its ecological dominance within the Maleo habitat. As noted in previous studies, its physical characteristics, particularly its height and broad, open crown, align closely with architectural traits that favor bird roosting. For example, although taxonomically distinct, *Macadamia hildebrandii* displays similar emergent crown features in Maleo roosting habitats near Lake Towuti (Karim et al. 2022). Similarly, *Pavo muticus muticus* in Baluran National Park has been frequently observed roosting in tall trees with accessible, open canopies (Hernowo 2017), underscoring the broader importance of structural traits in tree selection for roosting across avian species.

Maleos behavior in roosting trees

Maleos typically fly directly to their chosen roosting trees, it often transitioning from adjacent trees or branches to reach sites with specific structural characteristics. These preferred sites are generally emergent trees that rise above the surrounding canopy. Field observations indicated that the average height of roosting trees ranged from 13.83±1.17 m to 15.17±2.04 m. Although these trees were not the tallest across the entire habitat, they consistently stood out as the tallest within their respective plot areas, distinguishing them from surrounding vegetation. This pattern suggests Maleos may favor trees with physical suitability, such as accessible height and strategic advantages, including enhanced visibility and reduced predation risk (Emiliano and Juan 2017). Maleos do not always select the tallest or densest trees available; their selection appears constrained by the species' limited flight capability. Due to their relatively short wings in proportion to body size, Maleos have a restricted flight range, limiting their ability to reach extremely tall trees. Similar flight limitations have been reported in other Megapodiidae species (Shute et al. 2017).

In addition to morphological and ecological factors, social behavior also influences roost tree selection. Maleos roost in pairs, with males and females occupying the same tree (Jones et al. 1995). This behavior suggests that structural attributes do not solely determine roost site selection but are also shaped by pair bonding and social coordination, adding a behavioral dimension to habitat use in this species. As a result, Maleos tend to select trees within an optimal height range, typically between 15-20 meters above ground level, which supports safe and energy-efficient landings (Nafiu et al. 2015). The differences in mean roosting tree height observed in this study compared to previous research are likely due to variations in habitat structure and local ecological conditions. Moreover, tree selection is influenced by height, the availability of suitable branches for roosting, and the possibility of accommodating pair roosting. Trees of moderate height with an appropriate crown structure and strategic location are likely to be preferred.

How Maleo use tree canopies?

Maleos demonstrated clear preferences for specific canopy spaces when selecting roosting sites, both horizontally and vertically. Horizontally, they primarily occupied crown layer B, while vertically, they favored crown layer 2 (Figure 6). Other layers, such as A and C, were generally avoided, likely due to higher exposure to environmental disturbances like wind and rain and increased vulnerability to predators (Eisaguirre et al. 2019). The selected roosting trees corresponded closely with the height preferences observed in particular tree species (Table 2) and featured relatively flat horizontal branches. Similar preferences for such structural attributes have also been documented among other Megapodiidae species (Jones et al. 1995). Maleos tended to be roosting on branches away from the main trunk. This behavior facilitates greater mobility and responsiveness to threats, enhancing safety and reducing the risk of disturbance.

Maleos' selection and use of roosting trees are further influenced by canopy architectural models, which affect the birds' comfort, security, and access. Different tree species in this study exhibited distinct architectural forms (Figure 4), each offering structural conditions conducive or unsuitable to roosting. *Anthocephalus macrophyllus* and *N. orientalis* exhibit the Prévost crown architecture model, characterized by a continuous vertical axis with rhythmic, horizontal branching. This formation creates a rounded, layered crown, offering stable and expansive roosting platforms for Maleos.

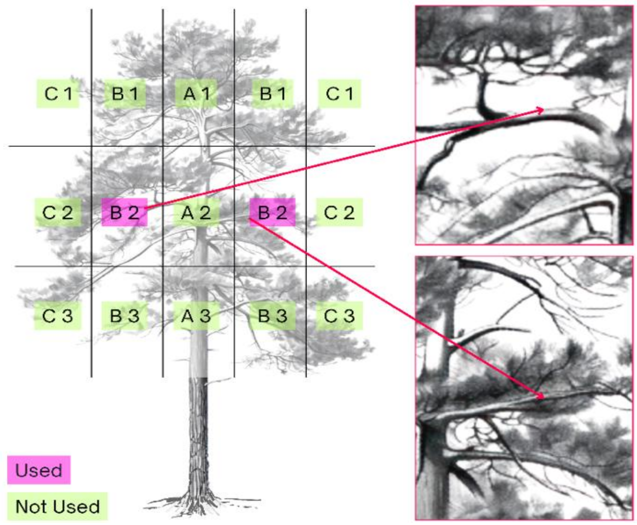

Figure 6. The space and shape of the branches used by Maleo

Artocarpus elasticus follows the Roux model, which features monopodial branching with a dominant vertical trunk and regularly spaced lateral branches. This structure results in a clear, stratified crown that supports roosting at various vertical levels. *Guazuma tomentosa* aligns with the Troll model, which is also marked by monopodial growth but with spiral arrangements of leaves and branches. This produces a relatively open, upward-reaching crown, potentially aiding vertical access. *Terminalia* sp. corresponds to the Aubréville model, which involves sympodial branching that ceases after a particular growth phase and is replaced by lateral branches (Hallé et al. 1978). These structural features likely contribute to the Maleo 's roost site selection, reflecting a combination of ecological suitability, physical accessibility, and behavioral preferences.

Maleos path from trees to nesting ground and feeding tree

Roost tree selection by wildlife often involves balancing resource availability (Suominen et al. 2023). Birds that move longer distances before roosting are more likely to experience nighttime disturbances (Siekiera et al. 2022). This phenomenon is often attributed to increased fatigue, which can negatively impact the quality of rest (Bringmann 2018). In the case of Maleo, similar indications suggest that the distance to primary activity areas influences their spatial utilization patterns. Specifically, the proximity of roosting trees to feeding and nesting sites plays an important role in shaping this species' spatial behavior and distribution.

In degraded habitats, birds are often forced to fly longer distances for food than those inhabiting more heterogeneous environments (Evens et al. 2018). However, our findings indicate that Maleos range over shorter distances between roosting, foraging, and nesting sites due to their presence in diverse, resource-rich landscapes. Roosting trees are situated near food sources and nesting grounds, with spatial patterns influenced by tree species and landscape structure. As terrestrial foragers, Maleos primarily consume seeds and fruits found on the forest floor (Karim et al. 2023a). Therefore, their preference for roosting in trees near their primary activity areas is likely associated with energy conservation and foraging efficiency.

This behavior is consistent with observations of other wildlife species that also choose roosting sites near core activity areas to reduce energy expenditure and minimize predation risk (Saldanha et al. 2019). The consistent presence of food and nesting habitats nearby facilitates seamless transitions between behaviors such as foraging and breeding (Bevanda et al. 2015). In the case of Maleo, the spatial proximity among roosting, feeding, and nesting sites reflects an ecologically strategic space use pattern that optimizes energy conservation and enhances survival. This interconnected landscape configuration likely supports higher reproductive success and is potentially a critical determinant of the persistence of Maleo populations in their natural habitat.

Disturbances to Maleo roosting trees

Maleo roosting trees within the North Buton Wildlife Reserve are in secondary forests ecologically vulnerable to anthropogenic disturbances, including illegal logging, forest encroachment, and land conversion (Karim et al. 2023b). Despite the area's designated conservation status, these activities persist considerably, undermining the protection intended for Maleo populations. This observation aligns with the findings of Roberge et al. (2018), Tremblay et al. (2018), and Tonetti et al. (2024), who emphasized that avian species benefit more from well-managed protected areas with minimal human disturbance. Human presence in habitats containing roosting trees has influenced Maleo activity patterns, particularly in selecting secure and strategically located roosting sites (Nepali et al. 2024).

Chronic disturbances may force Maleos to relocate to suboptimal habitats with limited access to feeding grounds and nesting sites. In addition to habitat degradation, egg exploitation remains a critical threat, contributing to population declines (Santrio et al. 2021). These cumulative anthropogenic pressures highlight the inadequacy of current conservation and management efforts in mitigating ecosystem disruptions. Activities such as illegal logging, land encroachment, and extensive land-use conversion directly reduce the availability of suitable roosting trees (Ocampo-Peñuela and Pimm 2015). These trees are vital to the Maleo 's life cycle, and their loss due to deforestation or land transformation disrupts key behaviors, diminishes habitat quality, and ultimately endangers the species' long-term survival.

This study also documented internal ecological disturbances affecting Maleo roosting trees. Potential predators such as *Malayopython reticulatus* (reticulated python) and *Viverra tangalunga* (Malay civet) were observed near roosting sites. The Malay civet, a primary predator on Buton Island, is nocturnal and arboreal, preying on small mammals (e.g., rodents), birds and their eggs, reptiles, and insects (Jennings et al. 2006). Although our sample size was insufficient to estimate predation rates with statistical confidence (Nyffeler and Birkhofer 2017), these findings support the hypothesis that anti-predator strategies, such as selecting tall, open-crowned trees, play a significant role in male roosting behavior.

While tree characteristics are important, we acknowledge that they represent only one component of the broader ecological context influencing Maleo roosting behavior. A holistic approach incorporating climatic variables in future studies could offer a more comprehensive understanding of roost-site selection factors. Such integration would enhance our insight into how environmental and biological elements interact to influence roosting dynamics. Moreover, this study did not address the potential role of interspecific competition in roosting tree selection. Long-term ecological observations are therefore necessary to examine these potential biotic interactions in greater detail.

Land-use change substantially threatens wildlife, including Maleos, by altering habitat structure and availability. Our findings underscore the urgent need for further research into how Maleos respond and adapt to such landscape-level changes. Incorporating assessments of anthropogenic impacts into future research frameworks could significantly improve our understanding of Maleo's resilience and adaptability across varying environmental gradients. This study was conducted in the North Buton Wildlife Reserve; therefore, the results reflect local ecological conditions. However, these findings can serve as a foundational reference for further research in other regions of Sulawesi, offering opportunities for validation and cross-habitat comparisons to understand broader patterns of roosting tree use better.

This study concluded that Maleo roosting trees have specific characteristics. These trees generally have special and distinctive characteristics, including species identity, spatial proximity to food trees and open areas, and structural features that provide comfort and security. The height of roosting trees usually exceeds the surrounding vegetation, ranging from 13 to 15 meters. These trees are usually located near food sources and open spaces, which can facilitate access to foraging and nesting grounds. Roosting trees have relatively open crowns, meaning that they have a high proportion of their branches and leaves in the upper part of the tree, and crown architectural models such as Prévost, Roux, Troll, and Aubréville. Roosting positions are usually located in the middle of the canopy layer (horizontal in layer B and vertical in layer 2), especially on relatively flat branches in the inner part of the canopy. These structural characteristics can provide better protection from disturbance and increase comfort when roosting.

ACKNOWLEDGEMENTS

The authors express their sincere gratitude to the Natural Resources Conservation Agency (BKSDA) of Southeast Sulawesi, Indonesia, for granting permission to conduct research in the North Buton Wildlife Reserve. Appreciation is also extended to the Resort Maligano team in North Buton Wildlife Reserve, for their invaluable assistance in data collection. Furthermore, the authors acknowledge their colleagues from Institut Pertanian Bogor, Indonesia, for their valuable discussions and insights during data analysis. Finally, they express gratitude to the Editor-in-Chief and reviewers for their constructive suggestions, insightful perspectives, and thoughtful comments, which have significantly contributed to the improvement of this manuscript.

REFERENCES

Aldiansyah S, Risna, Saputra RA. 2024. Assessing potential distributions of bird endemic species: Case studies of *Macrocephalon maleo* and *Rhyticeros cassidix* and their threats. Geol Environ Eng 18 (3): 45-61. DOI: 10.7494/geom.2024.18.3.45.

Arellano G, Cala V, Fuentes A, Cayola L, Jørgensen PM, Macía MJ. 2016. A standard protocol for woody plant inventories and soil characterisation using temporary 0.1-ha plots in tropical forests. J Trop For Sci 28 (4): 508-516.

Bevanda M, Fronhofer EA, Heurich M, Muller J, Reineking B, Sponseller R. 2015. Landscape configuration is a major determinant of home range size variation. Ecosphere 6 (10): 1-12. DOI: 10.1890/ES15-00154.1.

Bringmann H. 2018. Sleep-active neurons: Conserved motors of sleep. Genetics 208: 1279-1289. DOI: 10.1534/genetics.117.300521.

Buba T, Jaafar RM. 2021. Impacts of trees species and functional traits on bird's visitation in a Nigerian montane forest: Implications for conservation: Trees functional traits and bird's visitation. Sci Afr 12: e00783. DOI: 10.1016/j.sciaf.2021.e00783.

Charbonnier YM, Barbaro L, Barnagaud JY, Ampoorter E, Nezan J, Verheyen K, Jactel H. 2016. Bat and bird diversity along independent gradients of latitude and tree composition in European forests. Oecologia 182 (2): 529-537. DOI: 10.1007/s00442-016-3671-9.

Eisaguirre JM, Auger-Méthé M, Barger CP, Lewis SB, Booms TL, Breed GA. 2019. Dynamic-parameter movement models reveal drivers of migratory pace in a soaring bird. Front Ecol Evol 7: 317. DOI: 10.3389/fevo.2019.00317.

Ellison G, Wolfenden A, Kahana L, Kisingo A, Jamieson J, Jones M, Bettridge CM. 2019. Sleeping site selection in the nocturnal Northern lesser galago (*Galago senegalensis*) supports antipredator and thermoregulatory hypotheses. Intl J Primatol 40: 276-296. DOI: 10.1007/s10764-019-00085-y.

Emiliano AD, Juan IA. 2017. Ecological segregation and vocal interactions in two sympatric *Laterallus crakes*. J Ornithol 158 (2): 431e441. DOI: 10.1007/s10336-016-1397-4.

Evens RN, Beenaerts T, Neyens N, Witters K, Smeets, Artois T. 2018. Proximity of breeding and foraging areas affects foraging effort of a crepuscular, insectivorous bird. Sci Rep 8: 3008. DOI: 10.1038/s41598-018-21321-0.

Fei HL, Thompson C, Fan PF. 2019. Effects of cold weather on the sleeping behavior of skywalker hoolock gibbons (*Hoolock tianxing*) in seasonal montane forest. Am J Primatol 81: 1-10. DOI: 10.1002/ajp.23049.

Froese GZL, Mustari AH. 2019. Assessments of maleo *Macrocephalon maleo* nesting grounds in South-east Sulawesi reveal severely threatened populations. Bird Conserv Intl 2: 497-502. DOI: 10.1017/S0959270918000333.

Goodenough AE, Little N, Carpenter WS, Hart AG. 2017. Birds of a feather flock together: Insights into starling murmuration be-haviour revealed using citizen science. Plos One 12: e0179277. DOI: 10.1371/journal.pone.0179277.

Hallé F, Oldeman RAA, Tomlinson PB. 1978. Tropical Trees and Forests: An Architectural Analysis. Springer-Verlag, New York. DOI: 10.1007/978-3-642-81190-6.

Hernowo JB, Haquesta S. 2021. Evaluation on Bali mynah (*Leucopsar rothschildi* Stresemann, 1912) population, result of release process 1998-2015 in Bali Barat National Park, Indonesia. Biodiversitas 22 (7): 2699-2710. DOI: 10.13057/biodiv/d220719.

Hernowo JB, Kusmana C, Alikodra HS, Mardiastuti A. 2018. Analysis of the javan green peafowl (*Pavo muticus muticus* linnaeus 1758) habitat in Baluran and Alas Purwo National Park, East Java. Hayati 25 (3): 101-114. DOI: 10.4308/hjb.25.3.101.

Hernowo JB. 2017. Determinant factors of the javan green peafowl (*Pavo muticus muticus* Linnaeus, 1758) habitat in Baluran and Alas Purwo National Parks, East Java, Indonesia. Trop Dryl 1 (1): 50-56. DOI: 10.13057/tropdrylands/t010108.

Jara RF, Crego RD, Samuel MD, Rozzi R, Jiménez JE. 2020. Nest-site selection and breeding success of passerines in the world's southernmost forests. PeerJ 8: e9892. DOI: 10.7717/peerj.9892.

Jennings AP, Seymour AS, Dunstone N. 2006. Ranging behaviour, spatial organization and activity of the malay civet (*Viverra tangalunga*) on Buton Island, Sulawesi. J Zool 268: 63-71. DOI: 10.1111/j.1469-7998.2005.00023.x.

Jones DN, Dekker RWRJ, Roselaar CS. 1995. Bird Families of the World: The Megapodes. Oxford University Press Inc., New York.

Karim FR, Masy'ud B, Hernowo JB. 2023a. Welfare assessment of maleo chicks in Hungayono Sanctuary, Bogani Nani Wartabone National Park, Gorontalo. Trop Anim Sci J 46 (1): 20-26. DOI: 10.5398/tasj.2023.46.1.20.

Karim HA, Najib NN, Ayu SM, Fidel. 2023b. Characteristics of maleo bird spawning nests (*Macrocephalon maleo*) in Lake Towuti, South Sulawesi, Indonesia. Biodiversitas 24 (2): 690-696. DOI: 10.13057/biodiv/d240203.

Karim HA, Najib NN, Sofyan N. 2022. Vegetation characteristics of the maleo bird (*Macrochepalon maleo*) habitat at Natural Tourism Park of Towuti Lake, South Sulawesi. J Wasian 9: 63-73. DOI: 10.62142/bpc0tb21.

Khan 2017. Effect of forest composition on bird species abundance in tropical dry deciduous forest: A case of Bhimbandh wildlife sanctuary, India. Biodiversitas 18 (1): 78-85. DOI: 10.13057/biodiv/d180112.

Komlós M, Botta-Dukát Z, Bölöni J, Aszalós R, Veres K, Winkler D, Ónodi G. 2024. Tall, large-diameter trees and dense shrub layer as key determinants of the abundance and composition of bird communities in oak-dominated forests. J For Res 35: 62. DOI: 10.1007/s11676-024-01714-w.

Mah ANMAH, Ramji MFS. 2020. The Influence of perch height selection on vocalization of pied triller, *Lalage nigra* (Aves: Campephagidae) in Suburban Landscapes, Sarawak. Bor J Res Sci Technol 10: 179-189. DOI: 10.33736/bjrst.2716.2020.

Maulany RI, Aliem MI, Nasri, Ismail. 2021. A preliminary study of maleo (*Macrocephalon maleo*) nesting in Kambunong Cape, West Sulawesi. IOP Conf Ser Earth Environ Sci 681: 012124. DOI: 10.1088/1755-1315/681/1/012124.

McGinn KA, Peery MZ, Zulla CJ, Berigan WJ, Wilkinson ZA, Barry JM, Keane JJ, Zuckerberg B. 2023. A climate-vulnerable species uses cooler forest microclimates during heat waves. Biol Conserv 283: 110132. DOI: 10.1016/j.biocon.2023.110132.

Mueller-Dumbois D, Ellenberg H. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.

Nafiu LO, Aku AS, Rusdin M, Saili T, Nurhalim. 2015. Karateristik habitat maleo (*Macrocephalon maleo* sal muler 1846) di Taman Nasional Rawa Aopa Watumohai (TNRAW). Jurnal Ilmu Teknologi Peternakan Tropis 2 (1): 3782. DOI: 10.33772/jitro.v2i1.3782. [Indonesian]

Nepali A, Katuwal HB, Kc S, Regmi S, Sharma HP. 2024. Flight initiation distance and bird tolerance to humans in rural and urban habitats. R Soc Open Sci 11: 240332. DOI: 10.1098/rsos.240332.

Nyffeler M, Birkhofer K. 2017. An estimated 400-800 million tons of prey are annually killed by the global spider community. Sci Nat 104: 30. DOI: 10.1007/s00114-017-1440-1.

Ocampo-Peñuela N, Pimm SL. 2015. Elevational ranges of montane birds and deforestation in the Western Andes of Colombia. Plos One 10 (12): e14331. DOI: 10.1371/journal.pone.0143311.

Partasasmita R, Atsaury ZIA, Husodo T. 2017. The use of forest canopy by various bird species in tropical forest montana zone, the Nature Reserve of Mount Tilu, West Java, Indonesia. Biodiversitas 18 (2): 453-457. DOI: 10.13057/biodiv/d180202.

Pearson DL. 1971. Vertical stratification of birds in a tropical dry forest. Condor 73: 46-55. DOI: 10.2307/1366123.

Qomariah IN, Perwitasari-Farajallah D, Iskandar E, Berthier JM. 2023. Characteristics of sleeping sites and sleeping trees selected by Celebes crested macaques *(Macaca nigra*) in Tangkoko, North Sulawesi, Indonesia. Biodiversitas 24 (11): 6200-6208. DOI: 10.13057/biodiv/d241142.

Roberge JM, Öhman K, Lämås T, Felton A, Ranius T, Lundmark T, Nordin A. 2018. Modified forest rotation lengths: Long-term effects on landscape-scale habitat availability for specialized species. J Environ Manag 210: 1-9. DOI: 10.1016/j.jenvman.2017.12.022.

Saldanha S, Taylor PD, Imlay TL, Leonard ML. 2019. Biological and environmental factors related to communal roosting behavior of breeding bank swallow (*Riparia riparia*). Avian Conserv Ecol 14 (2): 21. DOI: 10.5751/ACE-01490-140221.

Santrio A, Mardiastuti A, Farajallah DP. 2021. The characteristics of maleo bird (*Macrocephalon maleo*) eggs in the wildlife conservation area, North Buton, Indonesia. Adv Biol Sci Res 20: 477-482. DOI: 10.2991/absr.k.220309.092.

Shirima DD, Totland O, Munishi PKT, Moe SR. 2015. Does the abundance of dominant trees affect diversity of a widespread tropical woodland ecosystem in Tanzania? J Trop Ecol 31 (4): 345-359. DOI: 10.1017/S0266467415000231.

Shute E, Prideaux GJ, Worthy TH. 2017. Taxonomic review of the late *Cenozoic megapodes* (Galliformes: Megapodiidae) of Australia. R Soc Open Sci 4: 170233. DOI: 10.1098/rsos.170233.

Siekiera J, Jankowiak Ł, Profus P, Sparks TH, Tryjanowski P. 2022. Secrets of the night: Roost sites and sleep disturbance factors during the autumn migration of first-year white stork *Ciconia ciconia*. J Avian Biol 2022: e03024. DOI: 10.1111/jav.03024.

Summers M, Geary M, Djuni N, Kresno PA, Laya A, Sawuwu S, Bawotong A, Abas W, Tan Oga VM, Nur AM. 2023. Degree of egg-taking by humans determines the fate of maleo (*Macrocephalon maleo*) nesting grounds across Sulawesi. Biodivers Conserv 32 (3): 899-919. DOI: 10.1007/s10531-022-02527-1.

Suominen KM, Vesterinen EJ, Kivistö I, Reiman M, Virtanen T, Meierhofer MB, Vasko V, Sironen T, Lilley TM. 2023. Environmental features around roost sites drive species-specific roost preferences for boreal bats. Glob Ecol Conserv 46: e02589. DOI: 10.1016/j.gecco.2023.e02589.

Tasirin JS, Iskandar DT, Laya A, Kresno P, Suling N, Oga VT, Djano R, Bawotong A, Nur A, Isfanddri M. 2021. Maleo *Macrocephalon maleo* population recovery at two Sulawesi nesting grounds after community engagement to prevent egg poaching. Glob Ecol Conserv 28: e01699. DOI: 10.1016/j.gecco.2021.e01699.

Tonetti V, Bocalini F, Schunck F, Vancine MH, Butti M, Ribeiro M, Pizo M. 2024. The protected areas network may be insufficient to protect bird diversity in a fragmented tropical hotspot under different climate scenarios. Perspect Ecol Conserv 22 (1): 63-71. DOI: 10.1016/j.pecon.2023.12.002.

Tremblay JA, Boulanger Y, Cyr D, Taylor AR, Price DT, St-Laurent MH. 2018. Harvesting interacts with climate change to affect future habitat quality of a focal species in eastern Canada's boreal forest. Plos One 13 (2): e0191645. DOI: 10.1371/journal.pone.0191645.

Zhao Y, Zhang J, Li Z, Xie Q, Deng X, Zhang C, Wang N. 2024. Use of evergreen and deciduous plants by nocturnal-roosting birds: A case study in Beijing. Avian Res 15: 100177. DOI: 10.1016/j.avrs.2024.100177.