Roosting ecology of endangered plant-roosting bats on Okinawa Island: Implications for bat-friendly forestry practices

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Abstract

Roosting information is crucial to guiding bat conservation and bat-friendly forestry practices. The Ryukyu tube-nosed bat Murina ryukyuana (Endangered) and Yanbaru whiskered bat Myotis yanbarenensis (Critically Endangered) are forest-dwelling bats endemic to the central Ryukyu Archipelago, Japan. Despite their threatened status, little is known about the roosting ecology of these species and the characteristics of natural maternity roosts are unknown. To inform sustainable forestry practices and conservation management, we radio-tracked day roosts of both species in the subtropical forests of Okinawa’s Kunigami Village District. We compared roost and roost site characteristics statistically between Murina ryukyuana nonmaternity roosts (males or nonreproductive females), maternity roosts, and all Myotis yanbarenensis roosts.

Generalized linear models were used to investigate roost site selection by Murina ryukyuana irrespective of sex and age class. Lastly, we compiled data on phenology from this and prior studies. Nonreproductive Murina ryukyuana roosted alone and primarily in understory foliage. Murina ryukyuana maternity roosts were limited to stands >50 years old, and ~60% were in foliage. Myotis yanbarenensis roosted almost entirely in cavities along gulch bottoms and only in stands >70 years old (~1/3 of Kunigami’s total forest area). Murina ryukyuana maternity roosts were higher (4.3 ± 0.6 m) than conspecific nonmaternity roosts (2.3 ± 0.5 m; p < .001) and Myotis yanbarenensis roosts (2.7 ± 0.5 m; not significant). Model results were inconclusive. Both species appear to be obligate plant roosters throughout their life cycle, but the less flexible roosting preferences of Myotis yanbarenensis may explain its striking rarity. To conserve these threatened bats, we recommend the following forestry practices: (a) reduce clearing of understory vegetation, (b) refrain from removing trees along streams, (c) promote greater tree cavity densities by protecting old-growth forests and retaining snags, and (d) refrain from removing trees or understory between April and July, while bats are pupping.

Keywords
Chiroptera, foliage-roosting, forest management, reproduction, roost switching, tree-roosting
Understanding species-specific roosting requirements is critical to effectively conserving bats (Altringham, 2011). Bats are of high conservation concern, with over a third of the world’s >1,200 assessed bat species considered threatened or data deficient (Frick et al., 2019). Bats also serve as bioindicators (De Conno et al., 2018; Jones et al., 2009) and provide key ecosystem services including pollination, seed dispersal, and the regulation of insect populations (Kunz et al., 2011). Protecting roosting habitats, where bats rest and reproduce (Racey & Entwistle, 2000), is essential to restoring and maintaining bat populations and communities. Maternity roosts are of particular interest to conservationists (Naďo & Kaňuch, 2015) because reproductive females are important to population viability and often more sensitive to disturbance (Pryde et al., 2005). Although bats are often associated with underground roosts, many species roost in trees or other plants. Here, we use the term “plant-roosting” to refer to bats that roost in any part of a tree (commonly referred to as “tree-roosting”) or any other plants (ferns, shrubs, bamboo, pitcher plants, etc.). This includes bats that roost in woody cavities (“cavity-roosting”) or foliage (“foliage-roosting”). These plant-roosting bats can be particularly difficult to study as they often roost alone or in relatively small colonies in difficult to find roosts and switch roosts often (Lewis, 1995).

Forestry-driven changes to forest composition and stand age affect bats according to their roosting and foraging ecology (Russo et al., 2016). Cavity-roosting bats usually roost in larger diameter trees and snags (Kalcounis-Rüppell et al., 2005; Naďo & Kaňuch, 2015). If ecological values are not considered, foresters are incentivized to remove such trees for sale, to improve remaining tree regeneration, or to reduce safety hazards associated with falling debris (Guldin et al., 2007). Less is known about foliage-roosting bats, but some may also prefer larger trees in mature forests (Carter & Menzel, 2007). Studies generally recommend preserving old-growth stands or retaining mature trees and snags in mixed-age stands since many tree-roosting bats appear reliant on these habitats (e.g., Burgar et al., 2015; Perry & Thill, 2007; Webala et al., 2010). Thinning trees or clearing understory foliage to promote the growth of remaining trees may benefit open-space and edge-foraging bats while negatively impacting clutter-foraging species (e.g., Patriquin & Barclay, 2003, Carr et al., 2020). For example, species including the open-space foraging *Lasiurus seminolus* prefer roosting in relatively open forests (Perry et al., 2007), while the clutter-foraging *Barbastella barbastellus* prefer roosts in unmanaged forests with dense understory (Russo et al., 2004). Forestry practices can reduce negative impacts to bats, or sometimes even benefit bats, by taking their ecological requirements into account (Hayes & Loeb, 2007). However, forestry managers often lack sufficient information to adopt more bat-friendly practices (Law et al., 2016). Furthermore, though general trends exist, the interactions between various forestry practices and different bat species may differ between regions and forest types.

Most of our knowledge concerning plant-roosting bat ecology comes from research on tree-roosting bats in North America, Europe, and Australia (e.g., Lacki et al., 2007; Law et al., 2016), while data from other regions are sparse (Kingston, 2010; Racey, 2015). Threatened but poorly understood species are unfortunately common among the bats of Asia and the Pacific Islands (Wiles & Brooke, 2009, Conenna et al., 2017). The genus *Myotis* is the most represented in tree-roosting bat studies thanks to extensive research on the relatively small proportion of *Myotis* species native to Western countries (Naďo & Kaňuch, 2015), but the majority of *Myotis* in other regions are poorly studied (Moratelli & Burgin, 2019). Similarly, few *Murina* species have been the subject of roosting studies (e.g., Fukui et al., 2012; Schulz & Hannah, 1998), and the proportion grows increasingly small when considering the remarkable rate of recent species discoveries in this genus (Yu et al., 2020). In Japan, ecological research concerning endemic plant-roosting bats has been limited despite most being threatened (Preble et al., 2021).

The Ryukyu tube-nosed bat *Murina ryukyuana* and Yanbaru whiskered bat *Myotis yanbarensis* are rare forest-dwelling bats endemic to three islands in Japan’s central Ryukyu Archipelago: Okinawa, Tokunoshima, and Amami Ōshima (Maeda et al., 2001, 2002; Maeda & Matsumura, 1998). *Murina ryukyuana* and *M. yanbarensis* are considered “Endangered” and “Critically Endangered,” respectively, by the IUCN and Japanese Ministry of the Environment (Fukui & Sano, 2019a, 2019b; Ministry of the Environment, 2014). These assessments consider these species reliant on intact mature forests. However, ecological information is limited, especially concerning *M. yanbarensis* (Funakoshi et al., 2013, 2019), and research has been practically absent on Okinawa. *Murina ryukyuana* have been found roosting mostly in understory foliage, and only seven *M. yanbarensis* roosts have been reported, five in tree cavities and two in culverts (Asari et al., 2021; Funakoshi et al., 2019; Watarai & Funakoshi, 2013). Neither species is likely to hibernate, but winter records are sparse. Notably, no natural maternity day roosts have been reported for either species, although maternity colonies of *M. ryukyuana* have used artificially placed dry leaves as day roosts (Funakoshi et al., 2013), and mothers with prevolant pups were observed night-roosting in canopy foliage on Amami Ōshima (V. Dinets, unpublished). Both species have been identified as high research priorities because they are threatened, endemic, and poorly understood (Preble et al., 2021).

We radio-tracked *M. ryukyuana* and *M. yanbarensis* on Okinawa over two years to clarify the roosting habits of these elusive bats and thereby inform conservation measures and bat-friendly forestry practices. Specifically, we sought to (a) determine what types of roosts and roost sites these bats use to inform conservation of these habitats, (b) determine when and where maternity colonies form so forestry activities can avoid these sensitive roosts, and (c) compare roosting ecology between *M. ryukyuana* and *M. yanbarensis* to determine to what degree management strategies must be species-specific. We were particularly interested in the influence of stand age as existing local biodiversity conservation plans prioritize the preservation of older forests (Okinawa Prefecture Department of Agriculture, Forestry, & Fisheries, 2013). Our primary hypotheses were that both species roost only within forests, that *M. ryukyuana*...
roosts flexibly in both foliage and cavities in stands of various ages, and that M. yanbarenensis roosts only in cavities in old-growth stands.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study was conducted in the forests of the Kunigami Village District (26°45′N, 128°15′E), part of the Yambaru region of Okinawa, Japan. The low human population (~5,000 people) is concentrated around the coasts, and the interior of the roughly 20,000 ha area consists of low mountains (max. ~500 m altitude). Numerous streams weave through subtropical broadleaf forests dominated by Castanopsis sieboldii (Family Fagaceae). Yambaru is one of Japan’s most biodiverse regions (Ito et al., 2000). Yambaru’s forests have also served as a wood resource since the Ryukyu Kingdom period (15th–19th century). Heavy logging of secondary forests occurred during the 1950s postwar reconstruction period (Saito, 2011). Mature trees were targeted from the 1960s to 1990s, and since around 1990, forestry has greatly declined. As a result, Okinawa’s northern forests are mostly of moderate age, with only 3% of total forest area <30 years old and 32% >70 years old (Figure 1). Large mature trees occur in low densities and are limited to old-growth stands remaining in the Kunigami Village District and the US Military’s Northern Training Area. Local forestry is government-subsidized to stimulate the economy, and there is increasing pressure on the government to properly manage forests for biodiversity conservation (Ito et al., 2000; Sugimura, 1988), especially given the recent National Park and UNESCO natural World Heritage site designations.

2.2 | Bat capture and radio tracking

We captured bats using a combination of harp traps, mist nets, and acoustic lures across 50 sites between September 2017 and September 2019. Capture devices were usually set perpendicular to flight paths over trails or streams. To increase capture rates, we broadcast synthesized stimuli based on social calls of unrelated species and conspecifics using Sussex Autobat acoustic lures (Hill & Greenaway, 2005). Captured females were categorized as non-reproductive, reproductive (pregnant or lactating), postlactating, or juvenile. Juveniles were identified by their lack of wing joint ossification (Brunet-Rossini & Wilkinson, 2009). We attached VHF radio transmitters (Holohil LB-2X) to 17 M. ryukyuana (eight male and nine female) and ten M. yanbarenensis (seven male and three female; Appendix S1) to identify roosts. We attached transmitters between each bat’s shoulder blades using Pros-Aide Adhesive (ADM Tronics Unlimited, Inc.). Transmitter weight was 3.3%–3.8% and 4.7%–5.4% of tracked M. ryukyuana and M. yanbarenensis bodyweight, respectively.

We tracked bats to day roosts using a handheld radio receiver and Yagi antenna. When we could not visually confirm roosts, we triangulated their location. From May 2018 onwards, we used a thermal imager to improve visual searching (Pulsar Quantum XQ23V, Yukon Advanced Optics Worldwide). For each roost, we recorded roost type (foliage or cavity), roost height (to nearest 0.5 m), and roost plant species. Understory cover at each roost site (5 m radius plot surrounding the roost) was estimated visually to the nearest 5%. We recorded diameter at base height (DBH) for roost trees, tree ferns, and bamboo. When cavity roosts could be reached, we measured the entrance area and internal dimensions to calculate cavity

**FIGURE 1**  Left-most histograms show stand age of unique *Murina ryukyuana* (*n* = 68) and *Myotis yanbarenensis* (*n* = 10) roost sites (5 m radius plots around roosts) for which stand age data were available. Right-most histogram shows total area (ha) by stand age within the Kunigami Village District to illustrate the distribution of stand ages potentially available within the study area. * Kunigami Village stand ages are measured from 2014, as reported in the most recently available local forest register, instead of 2020 because stand ages could not be updated across the whole district as they were for roost sites.
volume following Sedgeley & O’Donnell (1999). Roosts were categorized as maternity roosts if they included multiple bats and juveniles, reproductive females, or postlactating females. We recorded the minimum number of individuals per roost using various methods including visual inspection, emergence counts, and rarely by capturing roosting bats.

2.3 Roost site comparisons

We compared roost type proportions between *M. ryukyuana* non-maternity roosts, maternity roosts, and all *M. yanbarensis* roosts using Fisher’s exact tests with Bonferroni corrections. Sample sizes were too low to assess differences between nonmaternity and maternity *M. yanbarensis* roosts. We used Kruskal–Wallis tests followed by Dunn’s tests with Bonferroni corrections to compare roost height and the following roost site characteristics between the aforementioned groups: understory cover, canopy cover, canopy height, “southwestness” (SWness), slope, topographic position index (TPI), stream distance, and stand age. Stand age was calculated as years since the last clear-cutting or substantial logging measured from 2020. Stand age estimates were based on local forest register data from 2014 and revised if necessary based on historical aerial photography (US Air Force 1944, 1946, 1962; Geospatial Information Authority of Japan 1973, 1977, 1989, 2002; Nakanihon Air Service 2011; NTT Geospace 2013). All other variables were derived from airborne laser scanning LiDAR data (Nakanihon Air Service 2011). LiDAR-derived variables were calculated as the average value of 1 m² cells within a 5 m radius of the site center. Canopy cover was calculated as the proportion of cells within the site where the difference between elevation and vegetation height was >3 m. TPI was calculated using an inner and outer radius of 5 and 15 m, respectively. Stream distance (distance to the nearest stream) was calculated in ArcGIS based on a stream layer created using a minimum flow accumulation of 22,500 m². Aspect was transformed to SWness following Beers et al. (1966), where southwest slopes, most commonly exposed to the sun, were given a value of 2 and northeastern slopes a value of 0. Prior roosting studies have used northness and eastness (e.g., Hammond et al., 2016; Kerth et al., 2001; Law et al., 2016). We assumed higher stand ages to have higher snag densities and average tree diameters. Canopy height was used as a proxy for average tree height and SWness as a proxy for warmer microclimates. For each *M. ryukyuana* roost site, a random site was selected from within a 1 km buffer and similar site variables measured using GIS. The response variable for GLMs was site use (roost site = 1, random site = 0), and the explanatory variables included canopy height, SWness, slope, TPI, stream distance, and stand age. The quadratic term for stand age was also included as histograms suggested *M. ryukyuana* might prefer intermediate values. Canopy cover was not included as inclusion did not affect relative model performance, and only four roost sites and seven random sites had values <100%. We were unable to include understory cover as we did not have random site values. All explanatory variables were sufficiently uncorrelated (Spearman correlation coefficient <0.6). All covariates were centered before modeling. We used Akaike’s information criterion corrected for small sample size (AICc) to assess model fit (Burnham & Anderson, 2002). We considered ΔAICc ≤ 4.0 to be supported by the data and examined well-supported models for uninformative parameters (Arnold, 2010). Data were too scant to repeat this process for *M. yanbarensis*.

2.5 Phenology

To estimate the reproductive phenology of *M. ryukyuana* and *M. yanbarensis*, we compiled all records of reproductive females (pregnant or lactating) captured, maternity roosts, and female nonmaternity roosts from this and prior studies (Funakoshi et al., 2019; Maeda et al., 2001, V. Dinets, unpublished).

3 Results

All 17 tracked *M. ryukyuana* were successfully relocated (Appendix S1), resulting in 141 day roost records (mean ± SE: 6.2 ± 0.6 roosts per individual). We visually confirmed 105 roosts representing 73 unique roosts—56 nonmaternity roosts and 17 maternity roosts. From six *M. yanbarensis* (four male and two female) relocated at least once, we visually confirmed 27 roosts (4.5 ± 1.1 roosts per individual). Ten *M. yanbarensis* roosts were unique, including two maternity roosts. One *M. yanbarensis* roost was used as both a nonmaternity roost and a maternity roost. Roost and roost site characteristics are summarized in Table 2.

2.4 Murina ryukyuana roost site selection

We generated thirteen generalized linear models (GLM) reflecting eleven a priori hypotheses as to what characteristics influence roost site selection by *M. ryukyuana*, as well as a random model and global model (Table 1). Hypotheses included covariates from the literature known to affect roost selection by tree-roosting bats. Higher snag density, tree diameter, tree height, and lower stream distance and canopy cover are generally preferred by tree-roosting bats that use cavities (e.g., Fabianek et al., 2015; Nad'o & Kaňuch et al., 2015). Tree-roosting bats that roost in foliage generally prefer higher canopy cover (e.g., Kalcounis-Rüppell et al., 2005). Tree-roosting bats have also been found to prefer warmer microclimates, such as lower canopies and south-facing slopes (in the northern hemisphere) exposed to greater solar radiation (e.g., Hammond et al., 2016; Kerth et al., 2001; Law et al., 2016). We assumed higher stand ages to have higher snag densities and average tree diameters. Canopy height was used as a proxy for average tree height and SWness as a proxy for warmer microclimates. For each *M. ryukyuana* roost site, a random site was selected from within a 1 km buffer and similar site variables measured using GIS. The response variable for GLMs was site use (roost site = 1, random site = 0), and the explanatory variables included canopy height, SWness, slope, TPI, stream distance, and stand age. The quadratic term for stand age was also included as histograms suggested *M. ryukyuana* might prefer intermediate values. Canopy cover was not included as inclusion did not affect relative model performance, and only four roost sites and seven random sites had values <100%. We were unable to include understory cover as we did not have random site values. All explanatory variables were sufficiently uncorrelated (Spearman correlation coefficient <0.6). All covariates were centered before modeling. We used Akaike’s information criterion corrected for small sample size (AICc) to assess model fit (Burnham & Anderson, 2002). We considered ΔAICc ≤ 4.0 to be supported by the data and examined well-supported models for uninformative parameters (Arnold, 2010). Data were too scant to repeat this process for *M. yanbarensis*.  

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Myotis yanbarensis

Random

Dunn’s test comparisons

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Murina ryukyuana roosts were found in a similar variety of plant species (n = 17; Appendices S2 and S4) but more often in cavities compared with nonmaternity roosts (Figure 2). All foliage maternity roosts were in stands ≥57 years old. Cavity maternity roosts were in stands ≥61 years old, and all but one were located in stands ≥61 years old. Cavity maternity roosts were found in a similar variety of plant species (n = 10, 21, respectively; Appendix S2). Two small tree cavities were used as nonmaternity roosts.

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Table 1: Models for roost site selection by Murina ryukyuana including degrees of freedom (K), difference in AICc relative to the model most supported by the data (∆AICc), Akaike weights (w), and Nagelkerke’s R^2

| Hypothesis                  | Model                                      | K   | ∆AICc | w_0 | R^2  |
|-----------------------------|--------------------------------------------|-----|-------|-----|------|
| Global model                | All variables excluding stand age^2        | 7   | 0.00  | 0.59| 0.45 |
| Warm-tall-old               | –canopy height + stand age + SWness        | 4   | 1.97  | 0.22| 0.40 |
| Warm-tall-intermediate      | –canopy height + stand age + stand age^2 + SWness | 5   | 2.38  | 0.18| 0.41 |
| Mature structure            | –canopy height + stand age                | 3   | 9.08  | 0.01| 0.33 |
| Intermediate structure      | –canopy height + stand age + stand age^2   | 4   | 10.26 | 0.00| 0.34 |
| Typical tree cavity roost   | –canopy height + stream distance + stand age | 4   | 11.17 | 0.00| 0.33 |
| Solar radiation             | –SWness + TPI                             | 3   | 13.35 | 0.00| 0.30 |
| Wetter the better           | –stream distance + SWness + TPI           | 4   | 15.45 | 0.00| 0.30 |
| Concealed habitats          | –TPI                                      | 2   | 22.85 | 0.00| 0.22 |
| Typical foliage roost       | –canopy height                            | 2   | 26.25 | 0.00| 0.19 |
| Null                        | –1                                        | 1   | 47.07 | 0.00| 0.00 |
| Streams                     | –stream distance                          | 2   | 47.78 | 0.00| 0.01 |
| Slopes                      | –slope                                    | 2   | 49.03 | 0.00| 0.00 |

Table 2: Summary of unique visually confirmed roost site and random site characteristics (mean ± SE)

| Variable                   | Murina ryukyuana   | Myotis yanbarensis | Random     | Dunn’s test comparisons |
|-----------------------------|--------------------|--------------------|------------|-------------------------|
|                             | NM (n = 56)        | M (n = 17)         | All Myo (n = 10) | (n = 73) M v NM | M v Myo |
| Roost height (m)            | 2.3 ± 0.5          | 4.3 ± 0.6          | 2.7 ± 0.5 | NA                      | ***     | n.s. | n.s. |
| Understory cover (%)        | 84.9 ± 2.2         | 86.5 ± 3.3         | 51.5 ± 8.5 | NA                      | n.s.    | **   | **   |
| Canopy cover (%)            | 99.2 ± 0.5         | 98.5 ± 1.5         | 100.0 ± 0.0 | 96.9 ± 1.6             | n.s.    | n.s. | n.s. |
| Canopy height (m)           | 14.6 ± 0.5         | 17.6 ± 0.8         | 16.8 ± 0.8 | 12.1 ± 0.5             | **      | n.s. | n.s. |
| Southwestness               | 1.49 ± 0.07        | 1.14 ± 0.13        | 1.22 ± 0.27 | 1.03 ± 0.08          | *       | n.s. | n.s. |
| Slope (°)                   | 30.7 ± 1.2         | 33.9 ± 2.6         | 29.6 ± 3.1 | 31.0 ± 1.2             | n.s.    | n.s. | n.s. |
| TPI                         | −0.71 ± 0.12       | −0.77 ± 0.19       | −1.39 ± 0.40 | 0.07 ± 0.11         | n.s.    | n.s. | n.s. |
| Stream distance (m)         | 58.7 ± 6.0         | 36.3 ± 7.7         | 7.2 ± 3.9  | 62.2 ± 5.6             | n.s.    | ***  | *    |
| Stand age (yrs)             | 51.9 ± 1.8 (n = 51)| 70.9 ± 2.0         | 86.7 ± 2.9 | 66.3 ± 2.2             | ***     | ***  | n.s. |
| DBH (cm)                    | 15.8 ± 7.8 (n = 5) | 22.8 ± 4.8 (n = 13)| 18.4 ± 3.7 (n = 8) | NA          | NA      | NA   | NA   |
| Entrance area (cm^2)        | 25.35 (n = 2)      | 69.8 ± 11.3 (n = 13)| 27.4 ± 7.1 (n = 8) | NA          | NA      | NA   | NA   |
| Cavity volume (cm^3)        | 360, 243 (n = 2)   | Unconfirmed        | 354.1 ± 110.6 (n = 8) | NA          | NA      | NA   | NA   |

Note: Unique M. yanbarensis roosts were pooled due to low sample size (n = 10). Only one record of the M. yanbarensis roost used as both a nonmaternity and maternity roost was included. Significance levels of Dunn’s tests with Bonferroni correction are indicated with asterisks (p < .05*, .01**, .001***). DBH, cavity entrance area, and cavity volume were not statistically compared due to small sample sizes.

Abbreviations: M, maternity M. ryukyuana roosts; Myo, Myotis yanbarensis roosts; NM, nonmaternity Murina ryukyuana roosts.

3.1 | Roost characteristics

Solitary M. ryukyuana of all age classes and reproductive status utilized a variety of roost types and plant species as nonmaternity roosts (n = 56; Figure 2, Appendices S2 and S3). Nonmaternity roosts were most often in the dead or living foliage of understory plants, with some roosts in the fallen foliage of canopy species (Appendix S3). The foliage of many common trees was notably not used (e.g., Castanopsis sieboldii and Pinus ryukyuana), while the foliage of two common understory species, Blechnum orientale and Alpinia intermedia (Appendix S3A, B), represented 55% of all unique nonmaternity roosts (n = 10, 21, respectively; Appendix S2). Two small tree cavities were used as nonmaternity roosts.

Murina ryukyuana maternity roosts were found in a similar variety of plant species (n = 17; Appendices S2 and S4) but more often in cavities compared with nonmaternity roosts (Figure 2). All foliage maternity roosts were in stands ≥57 years old. Cavity maternity roosts were in stands ≥61 years old, and all but one were located in stands ≥61 years old. Cavity maternity roosts were found in a similar variety of plant species (n = 10, 21, respectively; Appendix S2). Two small tree cavities were used as nonmaternity roosts.

Murina ryukyuana maternity roosts were found in a similar variety of plant species (n = 17; Appendices S2 and S4) but more often in cavities compared with nonmaternity roosts (Figure 2). All foliage maternity roosts were in stands ≥57 years old. Cavity maternity roosts were in stands ≥61 years old, and all but one were located in stands ≥61 years old. Cavity maternity roosts were found in a similar variety of plant species (n = 10, 21, respectively; Appendix S2). Two small tree cavities were used as nonmaternity roosts.
Castanopsis sieboldii (Appendix S2). Mean DBH of cavity maternity roosts was 22.8 ± 4.8 cm (n = 13). The mean minimum number of individuals per maternity roost ranged from 2 to 15 (mean 6 ± 1). Maternity roost entrances were larger (mean 70 cm²; n = 4) than for nonmaternity roosts (25 and 35 cm²), but we were unable to measure internal dimensions.

All ten unique Murina yanbaren sis roosts were in gulch bottoms, usually directly next to flowing water, and almost entirely in small tree cavities (Figure 2, Appendix S5). One nonmaternity roost included two adults, while all others were used by solitary individuals. Two nonmaternity roosts were in snags, one in a liana cavity, one in an overhanging root cavity, and one in a tree fern frond tube. A pregnant female roosted with 2–3 other individuals in an old Okinawa woodpecker (Sapheopipo noguchi) roost in an unidentifiable snag (Appendix S5B), and a lactating female roosted once with a fledged juvenile in a live Toxicodendron succedaneum cavity (Appendix SSC). DBH for all Murina yanbaren sis roosts was 18.4 ± 3.7 cm. Cavities were generally small; entrance area was 27.4 ± 7.1 cm², and cavity volume was 354.1 ± 110.6 cm³. The first maternity roost was 844 cm above ground level, but only four Murina yanbaren sis were found in more than one roost. Maximum roost-switch distance among Murina yanbaren sis (n = 17) was 178 ± 32 m (range 8–480 m). Roost fidelity was higher for Murina yanbaren sis (2.7 ± 0.5 days per roost) than for M. ryukyuana, but only four Murina yanbaren sis were found in more than one roost. Maximum roost-switch distance among Murina yanbaren sis (n = 4) was 701 ± 580 m (range 35–2,436 m).

### 3.2 Murina ryukyuana roost site selection

The only model supported by the data included canopy height, SWness, and stand age (ΔAICc ≤ 4; Table 1). Although we did not consider the global model ecologically relevant, the fact that it received 59% of the AICc weight suggests that our a priori hypotheses were not strongly supported by the data. The quadratic stand age term in the warm-tall-intermediate model was considered uninformative as it did not improve model fit (Arnold, 2010). According to the remaining warm-tall-old model, the likelihood of a site being used for roosting by Murina ryukyuana increases 85% with each unit increment in SWness (1 unit = 90°), increases 235% with each meter increase in canopy height, and, contrary to our prediction, decreases 60% with each year increase in stand age (Table 3). Odds ratios were similar according to the discarded warm-tall-intermediate model, except that the likelihood of a site being used by Murina ryukyuana increased 152% with each year increase in stand age. On average, SWness was 0.4 units (roughly 45°) greater, canopy height 3 m taller, and stand age 10 years younger at Murina ryukyuana roost sites than at random sites.

![FIGURE 2](image-url) Proportion of roost types among unique roosts of Murina ryukyuana and Myotis yanbaren sis. Murina ryukyuana roosts were divided into nonmaternity or maternity roosts.

| Parameter       | Estimate | SE  | Odds ratio | Upper 85%, OR CI | Lower 85%, OR CI |
|-----------------|----------|-----|------------|------------------|-----------------|
| Intercept       | -0.08    | 0.20|            |                  |                 |
| SWness          | 0.62     | 0.21| 1.85       | 1.38             | 2.54            |
| Canopy height   | 1.21     | 0.27| 3.35       | 2.33             | 5.06            |
| Stand age       | -0.91    | 0.23| 0.40       | 0.29             | 0.56            |

**TABLE 3** Parameter estimates, st. errors (SE), odds ratios (OR), and 85% confidence intervals (CI) for the warm-tall-old model of roost selection by Murina ryukyuana.
FIGURE 3  Circular plot showing phenological periods and records for adult female Murina ryukyuana (circles) and Myotis yanbarenensis (triangles). Records for radio-tracked bats represent the median date during each tracking period. Reproductive period (yellow) includes all capture records of pregnant or lactating females, and maternity roosts (green) include communal roosts of juveniles, reproductive females, or postlactating females. Postlactating bats are not included if roosts were not found. Periods include 14-day buffers at the beginning and end. Includes data from this study (n = 17), Maeda et al., 2001 (n = 2), Funakoshi et al., 2019 (n = 12), and V. Dinets, unpublished (n = 1)

3.3 | Phenology

Capture and radio-tracking records for adult female and juvenile M. ryukyuana from this and prior studies demonstrated a minimum reproductive period (pregnant or lactating) between 14 April and 20 July (Figure 3). Murina ryukyuana maternity roosts have been found from 2 May to 13 November. In this study, three adult female and three juvenile M. ryukyuana used maternity roosts (and sometimes solitary nonmaternity roosts) between 2 May and 12 July, while three postlactating females roosted only solitary between 23 April and 22 October. The three reproductive females from this study were captured between 21 April and 7 July. All M. yanbarenensis records were from this study. A pregnant M. yanbarenensis was captured on 5 May and tracked to the same maternity roost on 11 and 12 May, while another maternity roost was used on 19 June by a lactating M. yanbarenensis caught on 16 June.

4 | DISCUSSION

Our radio-tracking results represent the first descriptions of natural M. ryukyuana and M. yanbarenensis maternity day roosts, as well as the first documented breeding on Okinawa. Our results support two of our primary hypotheses; both species roosted only in forests, and M. ryukyuana roosted in both foliage and cavities. M. yanbarenensis roosted only in old-growth forests, primarily in woody cavities but also in one tree fern frond tube. The degree to which M. ryukyuana maternity roosts are reliant on cavities and stands >50 years is unclear. Myotis yanbarenensis showed a strong preference for roosting along gulch bottoms and streams, and both species roosted remarkably low off the ground throughout the year. Our analysis of roost site selection by M. ryukyuana was inconclusive, particularly regarding stand age, but suggests that the importance of southwesterly aspects and taller canopies should be investigated further. The poor fit of our models may be due to small sample sizes or biases in the data structure (e.g., pooling of both nonmaternity and maternity roost sites). We also may have missed an important variable; we suspect that understory cover may better explain M. ryukyuana roost site selection and recommend further investigation.

Murina ryukyuana in particular may be negatively impacted by understory foliage removal. Most roosts were only 1–2 m high, including three foliage maternity roosts, similar to examples from Tokunoshima and other Murina species (Fukui et al., 2012; Funakoshi et al., 2013, 2016). Though its diet is unknown, the low wing aspect ratio and faint frequency-modulated echolocation of M. ryukyuana (Funakoshi et al., 2019; Norber & Rayner, 1987; Schnitzler et al., 2003), as well as the diet of congenerics (Ma et al., 2008; Schulz & Hannah, 1998), suggest that this species likely forages in clutter. Therefore, understory removal probably temporarily destroys both roosting and foraging habitats.

Myotis yanbarenensis roosted primarily in woody cavities along gulch bottoms and streams through forests >70 years old. This roost specialization may be a limiting factor for M. yanbarenensis populations that also raises the risk of extinction (Sagot & Chaverri, 2015). A handful of M. yanbarenensis have been observed in tunnels (Asari et al., 2021) and rock crevices along streams (H. Tamura, personal communication), and these potentially important roosts warrant investigation. Many tree-roosting bats prefer to roost near water, presumably to reduce commuting time to foraging grounds (Campbell, 2009; Kalcounis-Rüppell et al., 2005). The higher wing aspect ratio of M. yanbarenensis relative to M. ryukyuana and the relatively low understory cover around M. yanbarenensis roosts suggest that M. yanbarenensis prefers relatively uncluttered corridors within forests (Norber & Rayner, 1987). Dietary information would help clarify the foraging habitat of this species. On Amami Oshima, individuals have been captured over roads through old-growth forest (Asari & Kimoto, 2016; Funakoshi et al., 2019), and streambeds may simply be the only flyways through old-growth forest on Okinawa.

Old-growth forests appear to be important breeding habitats for both M. ryukyuana and M. yanbarenensis. Only old-growth forests were used by maternity colonies of both species even when tracked bats traveled through younger stands very close by. This preference for mature stands has been reported for other cavity-roosting bats (e.g., Burgar et al., 2015; Perry et al., 2007) and may be related to higher cavity densities in older stands (Matsumoto et al., 2015).
Also like other cavity-roosting bats (e.g., Dietz et al., 2018), both *M. ryukyuana* and *M. yanbarenensis* utilized old woodpecker cavities, and the recovery of woodpeckers in the central Ryukyu Archipelago bodes well for these bats (Kotowska et al., 2020). Our results are inconclusive as to the importance of roost tree diameter or cavity volume, but *M. ryukyuana* may utilize more cavity roosts during pup-rearing or cold winter months for their insulating benefits (Klug et al., 2012).

Existing records suggest that pregnancy and lactation in *M. ryukyuana* and *M. yanbarenensis* occur from April to at least mid-July. Two reproductive female captures, ten maternity roosts, and three nonmaternity female roosts for *M. ryukyuana* were found in the literature. These included maternity roosts found in artificially placed leaves in August–November on Tokunoshima (Funakoshi et al., 2019), lactating females caught on Tokunoshima in late July (Maeda et al., 2001), and a night roost of mothers and infants seen 8 May on Amami Ōshima (V. Dinets, unpublished). The latter is the only record of a gravid *M. ryukyuana* and suggests that bats are heavily pregnant in April. Insect parts observed in the feces of juveniles indicated successful foraging by early June. However, continuing lactation suggests that offspring are reliant on mothers to some degree until at least mid-July (Maeda et al., 2001). Juveniles and postlactating females have been observed together on Tokunoshima between August–November (Funakoshi et al., 2013, 2019), indicating that communal roosting continues beyond the lactation period. It is uncertain whether networks of related individuals are maintained throughout the breeding season, but fluctuating colony sizes and frequent roost-switching in *M. ryukyuana* suggest a fission–fusion social system common among plant-roosting bats (Patriquin & Ratcliffe, 2016). Records are far fewer for *M. yanbarenensis*, but reproductive timing appears similar. Although roosts were not located, a postlactating female was captured in October (Preble et al., in press), and postlactating females were caught on Amami Ōshima in mid-July (Asari & Kimoto, 2016).

We found too few roosts to explain the apparent rarity of *M. yanbarenensis*. Based on our limited results, we surmise that *M. yanbarenensis* occurs in lower numbers in a relatively restricted range due to a combination of greater roost specialization (mentioned previously) and a lower reproductive rate compared with *M. ryukyuana*. When perfect counting was possible (9 of 23 records), *M. ryukyuana* maternity colonies tended toward a ratio of one adult to two juveniles (e.g., Appendix S4C), suggesting that *M. ryukyuana* may birth 1–3 pups per year similar to other *Murina* species (Kuramoto & Uchida, 1981, Garbino et al., 2021). Conversely, our only record of an *M. yanbarenensis* mother and pup (Appendix S5D) suggests that this species is monotypic like other *Myotis* species and most other Chiroptera (Racey & Entwistle, 2000). Differences in the current rarity of *M. ryukyuana* and *M. yanbarenensis* may thus partially reflect differences in population growth following severe declines experienced during periods of large-scale clear-cutting such as the 1950s post-WWII reconstruction period. The higher capture rate of *M. yanbarenensis* on Amami Ōshima (Funakoshi et al., 2019; Preble et al., in press) may reflect the longer period since large-scale clear-cutting compared with Okinawa and the resulting larger areas of suitable old-growth breeding habitat. Clarifying the extent of range restriction in *M. yanbarenensis* and the ecological causes (e.g., habitat requirements and life history) should be a high priority for future research to avoid inadvertently destroying critical habitat.

### 4.1 Management implications

Given their roosting habits and the lack of evidence of other threats, forest degradation is likely the greatest threat to *M. ryukyuana* and *M. yanbarenensis* (Fukui & Sano, 2019a, 2019b). Local forestry guidelines already attempt to mitigate impacts to other threatened taxa and could be updated to also reduce negative impacts to bats. Based on our results, we make the following suggestions:

1. **Retain understory vegetation to preserve** *M. ryukyuana* **habitats and to avoid disturbing the low roosts of both** **bat species.** Understory removal in Yambaru is already of conservation concern due to adverse impacts on native biodiversity (Azuma et al., 1997; Ito et al., 2000).

2. **Riparian trees, including mature trees and snags, should not be removed,** particularly in old-growth forests, **given the rarity of** *M. yanbarenensis* **and its apparent reliance on these habitats.** Local forestry guidelines already recommend retaining riparian corridors for wildlife, but currently only advise against removing underground and small diameter trees (Okinawa Prefecture Department of Agriculture, Forestry, & Fisheries, 2013). Riparian exclusion zones are a common forestry practice for maintaining biodiversity, including bats (Lloyd et al., 2006, Law et al., 2016), and the natural succession of riparian trees likely produces more snag cavities than thinning (Pollock & Beechie, 2014).

3. **Old-growth forest (especially >70 years old) should be preserved to provide ample cavity roosts, and some mature trees and snags should be retained in harvested or thinned forests.** Although the exact cavity densities required by each species are unknown, both bat species formed small maternity colonies and switched roosts regularly, suggesting that they require high roost availability (Russo et al., 2005).

4. **To avoid disturbing maternity roosts, trees and understory foliage should not be removed between April and mid-July, when bats are pregnant or lactating.** Current forestry guidelines advise against harvesting during the Okinawa woodpecker breeding season between March and June (Okinawa Prefecture Department of Agriculture, Forestry, & Fisheries, 2013). Extending this period through July would be a relatively simple way to accommodate the area’s endangered plant-roosting bats.

We are cautiously optimistic about the outlook of *M. ryukyuana* and *M. yanbarenensis* given current low levels of logging and increasing interest in sustainable management across their range. Still, further research is needed, particularly concerning *M. yanbarenensis*, and these...
species should be incorporated into forest management plans rather than just listed as threatened. We hope that this study serves as a reference for both local conservation planning and further roosting ecology research in Asia.

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CONFLICT OF INTEREST

We have no competing interests to declare.

AUTHOR CONTRIBUTION

Jason H. Preble: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). Christian E. Vincenot: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Resources (equal); Supervision (lead); Writing-review & editing (supporting). Kazuhiko Saito: Data curation (equal); Formal analysis (supporting); Investigation (supporting); Writing-review & editing (supporting). Nobuhito Ohte: Funding acquisition (equal); Resources (equal); Supervision (supporting); Writing-review & editing (supporting).

ETHICAL APPROVAL

This research was carried out under permits from Aha Dam Office, Kunigami Village Office, University of the Ryukyus Experimental Forest Yona Field, Okinawa Regional Forest Office, Okinawa Prefectural Government Hokubu Agriculture, Forestry and Fisheries Promotion Center, and the Japanese Ministry of the Environment. Animal research was also permitted by Kyoto University (permits Inf-K17008 and Inf-K19007).

DATA AVAILABILITY STATEMENT

Raw data and R scripts are available on Figshare (https://doi.org/10.6084/m9.figshare.16528209).

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REFERENCES

Altringham, J. D. (2011). Bats: From evolution to conservation. Oxford University Press.
Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike’s information criterion. Journal of Wildlife Management, 74, 1175–1178. https://doi.org/10.2193/2009-367
Asari, Y., & Kimoto, Y. (2016). Bat species found during capturing and acoustic surveys in Amami-Oshima Island, Japan. Fauna Ryukyuana, 26, 5–7.
Asari, Y., Kimoto, Y., & Noda, K. (2021). Five day-roosts of Myotis yambarensis and Murina ryukyuana in Amami-Oshima Island, Kagoshima, Japan. Mammalian Science, 61(1), 49–54.
Azuma, S., Sasaki, T., & Itö, Y. (1997). Effects of undergrowth removal on the species diversity of insects in natural forests of Okinawa Hontō. Pacific Conservation Biology, 3(2), 156–160. https://doi.org/10.1071/PC970156
Beers, T. W., Dress, P. E., & Wensel, L. C. (1966). Aspect transformation in site productivity research. Journal of Forestry, 64, 691–692.
Brunet-Rossini, A. K., & Wilkinson, G. S. (2009). Methods for age estimation and the study of senescence in bats. In T. H. Kunz, & S. Parsons (Eds.), Ecological and behavioral methods for the study of bats, 2nd ed. (pp. 315–328). The Johns Hopkins University Press.
Burgar, J. M., Craig, M. D., & Stokes, V. L. (2015). The importance of mature forest as bat roosting habitat within a production landscape. Forest Ecology and Management, 356, 112–123. https://doi.org/10.1016/j.foreco.2015.07.027
Burnham, K. P., & Anderson, D. R. (2002). Model selection and multi-model inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag.
Campbell, S. (2009). So long as it’s near water: Variable roosting behaviour of the large-footed myotis (Myotis macropus). Australian Journal of Zoology, 57(2), 89–98.
Carr, A., Weatherall, A., & Jones, G. (2020). The effects of thinning management on bats and their insect prey in temperate broadleaved woodland. Forest Ecology and Management, 457, 117682.
Carter, T. C., & Menzel, J. M. (2007). Behavior and day-roosting ecology of North American foliage-roosting bats. In M. J. Lacki, J. P. Hayes, & A. Kurta (Eds.), Bats in forests: Conservation and management (pp. 83–128). The Johns Hopkins University Press.
Conenna, I., Rocha, R., Russo, D., & Cabeza, M. (2017). Insular bats and research effort: A review of global patterns and priorities. Mammal Review, 47(3), 169–182. https://doi.org/10.1111/mam.12090
De Conno, C., Nardone, V., Ancilotti, L., De Bonis, S., Guida, M., Jorge, L., Scarpa, U., & Russo, D. (2018). Testing the performance of bats as indicators of riverine ecosystem quality. Ecological Indicators, 95(1), 741–750. https://doi.org/10.1016/j.ecolind.2018.08.018
Dietz, M., Brombacher, M., Erasmy, M., Fenchuk, V., & Simon, O. (2018). Bat community and roost site selection of tree-dwelling bats in a well-preserved European lowland forest. Acta Chiropterologica, 20(1), 117–127. https://doi.org/10.3161/1508109acc2018.20.1.008
Fabianek, F., Simard, M. A., & Desrochers, A. (2015). Exploring regional variation in roost selection by bats: Evidence from a meta-analysis. PLoS One, 10(9), e0139126, 1–21. https://doi.org/10.1371/journal.pone.0139126
Frack, W. F., Kingston, T., & Flanders, J. (2019). A review of the major threats and challenges to global bat conservation. Annals of the New York Academy of Sciences, 1469(1), 5–25. https://doi.org/10.1111/nyas.14045
Fukui, D., Matsumura, S. (2012). Maternity roosts and behaviour of the Ussurian tube-nosed bat (Murina ussuriensis). Acta Chiropterologica, 14(1), 93–104. https://doi.org/10.3161/15081012X654303
Fukui, D., & Sano, A. (2019). Murina ryukyuana. The IUCN Red List of Threatened Species 2019, e.T29485A22066512. https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T29485A22066512.en
Patriquin, K. J., & Ratcliffe, J. M. (2016). Should I stay or should I go? Fission-fusion dynamics in bats. In J. Ortega (Ed.), Sociality in bats (pp. 65–103). Springer. https://doi.org/10.1007/978-3-319-38953-0_4

Perry, R. W., & Thill, R. E. (2007). Tree roosting by male and female eastern pipistrelles in a forested landscape. Journal of Mammalogy, 88(4), 974–981. https://doi.org/10.1644/06-mamm-a.215r.1

Perry, R. W., Thill, R. E., & Leslie, D. M. (2007). Selection of roosting habitat by forest bats in a diverse forested landscape. Forest Ecology and Management, 238, 156–166. https://doi.org/10.1016/j.foreco.2006.10.008

Pollock, M. M., & Beechie, T. J. (2014). Does riparian forest restoration thinning enhance biodiversity? The ecological importance of large wood. Journal of the American Water Resources Association, 50(3), 543–559. https://doi.org/10.1111/jawr.12206

Preble, J. P., Ohte, N., & Vincenot, C. E. (2021). In the shadow of the rising sun: A systematic review of Japanese bat research and conservation. Mammal Review, 51, 109–126. https://doi.org/10.1111/mam.12226

Preble, J. H., Vincenot, C. E., Hill, D. A., & Ohte, N. (forthcoming). Capturing endangered endemic Okinawan bats with acoustic lures. Journal for Nature Conservation.

Pryde, M. A., O’Donnell, C. F. J., & Barker, R. J. (2005). Factors influencing survival and long-term population viability of New Zealand long-tailed bats (Chalinolobus tuberculatus): Implications for conservation. Biological Conservation, 126, 175–185. https://doi.org/10.1016/j.biocon.2005.05.006

Racey, P. A. (2015). Bat conservation: Past, present and future. In R. A. Adams, & S. C. Pedersen (Eds.), Bat evolution, ecology, and conservation (pp. 517–532). Springer. https://doi.org/10.1007/978-1-4614-7397-8_25

Racey, P. A., & Entwistle, A. C. (2000). Life-history and reproductive strategies of bats. In E. G. Chrithton, & P. H. Krutzsch (Eds.), Reproductive biology of bats (pp. 363–414). Academic Press.

Russo, D., Billington, G., Bontadina, F., Dekker, J., Dietz, M., Gazaryan, S., Jones, G., Meschede, A., Rebelo, H., Reiter, G., Ruczyński, I., Tillon, L., & Twisk, P. (2016). Identifying key research objectives to make European forests greener for bats. Frontiers in Ecology and Evolution, 4(87), 1–8. https://doi.org/10.3389/fevo.2016.00087

Russo, D., Cistrone, L., & Jones, G. (2005). Spatial and temporal patterns of roost use by tree-dwelling barbastelle bats, Barbastellus barbastellus. Ecography, 28, 769–776.

Russo, D., Cistrone, L., Jones, G., & Mazzoleni, S. (2004). Roost selection by barbastelle bats (Barbastella barbastellus, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: Consequences for conservation. Biological Conservation, 117(1), 73–81. https://doi.org/10.1016/S0006-3207(03)00266-0

Sagot, M., & Chaverri, G. (2015). Effects of roost specialization on extinction risk in bats. Conservation Biology, 29(6), 1666–1673. https://doi.org/10.1111/cobi.12546

Saito, K. (2011). Forest age distribution in Kunigami-village, Okinawa, based on forest register data. Papers on Environmental Information Science, 25, 245–250. https://doi.org/10.11149/ceispapers.ces25.0.245

Sedgeley, J. A., & O’Donnell, C. F. J. (1999). Roost selection by the long-tailed bat, Chalinolobus tuberculatus, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. Biological Conservation, 88, 261–276. https://doi.org/10.1016/S0006-3207(98)00069-x

Schnittler, H. U., Moss, C. F., & Denzinger, A. (2003). From spatial orientation to food acquisition in echolocating bats. Trends in Ecology and Evolution, 18(8), 386–394. https://doi.org/10.1016/S0169-5347(03)00185-X

Schulz, M., & Hannah, D. (1998). Relative abundance, diet and roost selection of the tube-nosed insect bat, Murina florium, on the Atherton Tablelands, Australia. Wildlife Research, 25, 261–271. https://doi.org/10.1038/261637a0

Sugimura, K. (1998). The role of government subsidies in the population decline of some unique wildlife species on Amami Oshima, Japan. Environmental Conservation, 15(1), 49–57. https://doi.org/10.1017/S0376892900028459

Watari, Y., & Funakoshi, K. (2013). Use of dead-leaf foliage as day-roosts by the Ryuku tube-nosed bat, Murina Ryukyuana. Mammalian Science, 53(2), 331–334. https://doi.org/10.1238/mammaliensis.53.331

Webala, P. W., Craig, M. D., Law, B. S., Wayne, A. F., & Bradley, J. S. (2010). Roost site selection by southern forest bat Vespadelus regulus and Gould’s long-eared bat Nyctophilus gouldi in logged jarrah forests: south-western Australia. Forest Ecology and Management, 260, 1780–1790. https://doi.org/10.1016/j.foreco.2010.08.022

Wiles, G. J., & Brooke, A. P. (2009). Conservation threats to bats in the tropical Pacific islands and insular Southeast Asia. In T. H. Fleming & P. A. Racey (Eds.), Island bats: Evolution, ecology, and conservation (pp. 405–459). University of Chicago Press.

Yu, W. H., Csorba, G., & Wu, Y. (2020). Tube-nosed variations—a new species of the genus Murina (Chiroptera: Vespertilionidae) from China. Zoological Research, 41(1), 70–77. https://doi.org/10.24272/jissn.2095-8137.2020.009

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