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Limited nest-site availability appears to be an important factor in the evolution of delayed dispersal and cooperative breeding in some cavity-nesting species. The cooperatively breeding Pohnpei subspecies of Micronesian Kingfisher *Todiramphus cinnamominus* reichenbachii excavates nest cavities from the nests of arboreal termites *Nasutitermes* spp., or termitaria. In this first published description of nest-sites for this subspecies, we used surveys, remote sensing and radiotelemetry to evaluate the relationship between nest-site availability and co-operation. Results illustrate that nest termitaria are higher in the forest canopy, larger in volume and occur in areas with more contiguous canopy cover than unused termitaria. Nest termitaria were selected independently of the proximity to forest edges and territory boundaries, and we found no difference in characteristics of termitaria used by cooperative groups and breeding pairs. Logistic regression modelling indicated that termitaria with nest-like characteristics were not limited in abundance, suggesting that neither the prospects of inheriting nesting resources nor limited nest-site abundance are probable explanations for delayed dispersal in the Pohnpei subspecies of Micronesian Kingfisher.

The Micronesian Kingfisher *Todiramphus cinnamominus* is a terrestrial forest species that historically occurred on the Pacific islands of Miyako, Guam, Pohnpei and Palau (Baker 1951). In the last century, however, the subspecies from Miyako and Guam (*T. c. miyakoensis* and *T. c. cinnamominus*, respectively) have become extinct in the wild, and the remaining populations appear to be declining on the islands of Pohnpei and Palau (*T. c. reichenbachii* and *T. c. pelewensis*, respectively; Buden 2000, our pers. obs.). Despite their dire conservation status, prior publications about Micronesian Kingfishers include only anecdotal descriptions (Baker 1951, Pratt *et al.* 1987, Fry & Fry 1992) and observations from some of the last breeding pairs on Guam (Marshall 1989, Beck & Savidge 1985). Although cooperative breeding was previously unreported for this species, we observed groups of three adults participating in nest construction, nest-site defence and territorial defence in the subspecies from Pohnpei (Kesler 2002, Kesler & Haig 2004). Further observations of colour-banded kingfishers confirmed that the auxiliary birds, or helpers, were offspring that delayed dispersal to assist with future reproductive attempts (our unpubl. obs.).

Several hypotheses about the evolutionary origins and maintenance of delayed dispersal are based on environmental limitations in resources. The 'benefits of philopatry hypothesis' (Stacey & Ligon 1991, Ligon 1999) suggests that potential dispersers benefit by delaying dispersal and waiting to inherit more or higher quality resources, and the 'ecological constraints hypothesis' (Emlen 1982) suggests that potential breeders are prevented from dispersing because of environmental limitations in resources necessary for survival and reproduction. Despite the prominence of resources-based hypotheses, however, only a few notable attempts have been made to evaluate the relationship between resources and cooperative behaviour (Komdeur 1992, Walters *et al.* 1992, Balshine *et al.* 2001, Leisler & Winkler 2002).

Nest-site availability often appears limited for species that use cavities (Scott 1979, Newton 1994, Holt & Martin 1997, Aitken *et al.* 2002), and cavity limitations have been identified as a potential factor in the evolution of delayed dispersal and cooperative

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breeding in Red-cockaded Woodpeckers *Picoides borealis* (Walters *et al.* 1992) and Green Woodhoopoes *Phoeniculus purpureus* (Ligon & Ligon 1990). As in these species, reproduction in cooperatively breeding Micronesian Kingfishers may also be limited by nest-site availability because the birds excavate cavities from a specialized resource – the nests of arboreal termites, or termitaria. Although use of termitaria for nesting is apparently common in many tropical species and up to 45% of all kingfisher species (Fry & Fry 1992, Brightsmith 2000), we could find only one previously published study of the use of termitaria by birds (Brightsmith 2000), and no previous descriptions of the nest cavities excavated from termitaria.

We undertook an investigation of nesting resources and behaviour in Micronesian Kingfishers because of the lack of information about termitaria nesting, the importance of the information to understanding cooperative breeding, and the paramount importance to conservation efforts for the Guam, Palau and Pohnpei kingfishers. Our first objective was to describe the nest cavities, and to compare habitat characteristics of used and unused termitaria. Furthermore, nest termitaria used by cooperative groups of kingfishers were compared with those used by breeding pairs to determine whether the possibility of inheriting higher quality termitaria might be enticing potential dispersers to delay. We then modelled nest-site characteristics with logistic regression and assessed availability to determine whether the abundance of suitable nests might limit dispersal opportunities.

METHODS

Study area

Research was conducted on the island of Pohnpei, Federated States of Micronesia (6°52.8′N, 158°13.2′E; Fig. 1). Pohnpei is a more or less circular volcanic island with an approximate diameter of 20 km circumscribing the highest peak in the Micronesian chain (nearly 800 m, Engbring *et al.* 1990). Extensive lowland coastal plateau and mangrove swamps surround the inner mountain range, which is characterized by dense tropical rainforests. Three study areas were selected for this investigation (Fig. 1), the Ranch study area (6°57.5′N, 158°12.5′E), the College of Micronesia study area (COM; 6°54.6′N, 158°9.6′E) and the Palikir study area (6°55.3′N, 158°9.6′E). Each site is characterized by strand vegetation and secondary-growth lowland rainforest, grassland, urban vegetation and agroforest (Glassman 1952).
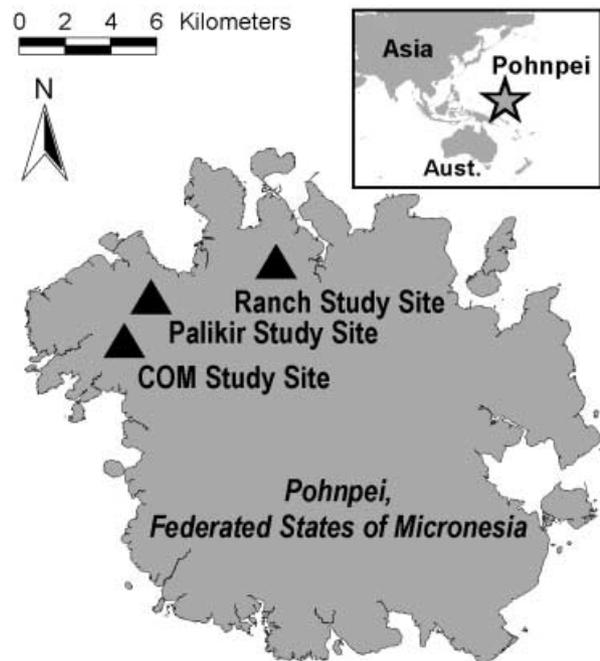

Figure 1. Map and geographical location of Pohnpei Island, and the three study areas.

Termitarium and nest survey

We located termitaria available to Micronesian Kingfishers within each study area using transect searches conducted between May and September 2000. A compass and global positioning systems (Garmin GPS II+; Garmin Ltd, Olathe, KS, USA) were used to walk parallel transects approximately 10 m apart in the forested portions of the three areas. For each arboreal termitarium encountered, we recorded structural measures (termitarium length, width and depth), height in the forest canopy and geographical location. For 25 nests in the study areas and six from surrounding forests, we recorded nest cavity and entrance-tunnel height, width, depth, presence or absence of termites and detritus material, and approximate moisture level. Nest stage was determined by floating eggs. Fourteen nest termitaria were re-visited approximately 1 year after nest discovery to re-evaluate their condition.

Nest-site characteristics

Previous studies suggest that factors with the potential to influence nest-site selection include substrate characteristics, site microclimate (e.g. Ricklefs & Hainsworth 1969, Austin 1976, Martin 1992, Wiebe

& Martin 1998, Clark & Shutler 1999), predators (e.g. Ricklefs 1969) and proximity to foraging areas and conspecifics (e.g. Li & Martin 1991, Rosenberg & McKelvey 1999). Thus, we utilized seven variables to compare used and unused termitaria: termitarium volume (log-transformed and assuming an ellipsoid shape; Lubin *et al.* 1977, Brightsmith 2000); height in canopy; proximity to foraging areas (defined as the distance to a patch of grassy habitat > 100 m^2), forest edge (defined by the interface of forest and grassy areas > 1000 m^2) and territory boundaries (defined below); and proportion of mature forest and open forest canopy within 15 m (see below). Variables for the proportion of open canopy and mature forest within 15 m of sites were arcsin square root transformed (Zar 1984, p. 238) to normalize proportion distributions.

Remote sensing was used to evaluate the proximity to forest edge and foraging areas, as well as the proportion of mature forest and open canopy within 15 m of termitaria. High-resolution (1 m/pixel) aerial photographs were scanned and digitally orthorectified using ERDAS Imagine 8.4 (ERDAS Inc., Atlanta, GA, USA) and positioning information was collected with the GPS during fieldwork. The software was also used to conduct an unsupervised habitat classification, which divided the visual spectrum of each photograph into ten signatures using a clustering algorithm (Avery & Berlin 1992). After excluding urban development, we manually combined the signatures in a supervised classification, which incorporated information about areas of known vegetation types (Avery & Berlin 1992). The process resulted in three habitat coverages depicting grassy vegetation, early succession and agroforest vegetation, and mature forest vegetation. Grassy areas included pastures and fallow fields. Early succession and agroforest vegetation were characterized by lower canopy (2–20 m high) Hibiscus *Hibiscus tiliaceus*, Bananna *Musa sapientum*, Coconut *Cocos nucifera*, Breadfruit *Artocarpus altilis* and Sakau *Piper methysticum*. Mature forests had a higher canopy (25–30 m high) and were dominated by Mango *Mangifera indica*, Dohng *Campnosperma brevipetiolata*, Sadak *Elaeocarpus carolinensis*, Karara *Myristica insularis*, Ais *Parinari laurina*, and tree ferns *Cyathea* spp. (see Mueller-Dombois & Fosberg 1998, Buden 2000). We verified vegetation classifications by comparison with aerial photographs, and vegetation coordinate information recorded via GPS during fieldwork.

Results from radiotelemetry analyses were used to assess termitarium proximity to territorial boundaries.

A study population of 33 radiomarked adult Micronesian Kingfishers was established and monitored for approximately 16 weeks each between January 1999 and January 2003. Birds were captured by mist-netting and fitted with a 1.8-g telemetry package (Holohil Systems, Ltd, Ottawa, Canada) using the leg-harness design described by Rappole and Tipton (1991) and a unique combination of coloured leg bands and a numbered aluminium USFWS band. We used hand-held Yagi antennae, compasses and GPS (March III; Corvallis Microtechnologies Inc., Corvallis, OR, USA) to record directional bearings of Micronesian Kingfishers. The best maximum likelihood estimates of bird locations were calculated using LOAS (Ecological Software Solutions; $n = 65 \pm 22$ sd mean estimated locations per individual). Most birds were located once daily, and we never recorded locations more frequently than once in each 2-hour interval to avoid autocorrelation. We used the ArcView animal movement extension (Hooge & Eichenlaub 1997) to conduct a kernel density analysis (White & Garrott 1990) of telemetry locations, and the 95% use contours for the home-ranges of adults on each territory were amalgamated to delineate 16 territorial boundaries.

Statistical analysis and model selection

The characteristics of termitaria used by kingfishers were compared with unused termitaria with a two-sample *t*-test (Ramsey & Schafer 1997, p. 43). Similarly, characteristics of termitaria used by cooperative groups were compared with those used by breeding pairs for nests in which social information was available.

We modelled the characteristics of termitaria used by Micronesian Kingfishers for nesting using logistic regression (Hosmer & Lemeshow 2000). All 127 possible linear combinations of the seven explanatory variables were included as competing models, which were fitted to the data by using a binomial nest/non-nest response variable. We ranked models by using Akaike's Information Criterion for limited sample sizes (AICc). This model selection technique accounts for both the number of variables and the model fit, and provides advantages over other model-ranking techniques, such as stepwise regression, which perform differentially depending on the order of variables and lose applicability when explanatory variables are correlated (Burnham & Anderson 1998). Adequacy of the model fit was evaluated using a deviance goodness of fit test (Ramsey & Schafer 1997, p. 607).

The top-ranked model was then utilized as an inferential model to determine whether there was a limited number of termitaria with nest-like characteristics within the study areas. As applied here, the form of a logistic regression model is as follows:

$$\text{logit}(\pi) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p$$

where π is the predicted probability of selection as a nest, and $\beta_0, \ldots, \beta_p$ represent parameter estimates for variables $X_1, \ldots, X_p$. When observed values from a single termitarium, j, are entered into the model, it yields a predicted probability of its selection as a nest-site (π_j).

A measure of similarity among multiple termitaria can then be inferred by comparing π_j values. Similar π_j values for nest and non-nest termitaria indicate that there were unused termitaria with characteristics similar to nest termitaria and that nesting resources were not saturated. By contrast, if results show two distinct sets of π_j, with unused termitaria receiving low values and nest termitaria receiving high values, results would suggest that there were no excess termitaria with nest-like characteristics and that nesting resources in the study areas were limited in abundance. Unless otherwise noted, nest cavity metrics are reported as means with standard deviations in parentheses. Logistic regression parameter estimates are reported as means with 95% Wald confidence intervals (CI), and differences are considered statistically significant at $\alpha \leq 0.05$.

RESULTS

Nest cavities

Nest cavities ($n = 31$) excavated by Micronesian Kingfishers were similar in volume and shape (Fig. 2). Cavities had spherical nest chambers averaging 12.7 (1.5) cm in diameter, which were connected to the termitarium surface by a tunnel 5.1 (0.5) cm in diameter and 10.6 (2.2) cm long. Termites were observed inside cavities during the excavation process, but their presence subsided shortly before laying, and they were never observed inside the nest cavity during incubation or brood rearing. Two termitaria were re-used by birds during subsequent nesting attempts. In all but one of the observed nest termitaria, termite colonies appeared to remain active throughout the kingfisher nesting period, and visits 1 year after nesting showed that ten cavities had been re-filled with new termitarium material
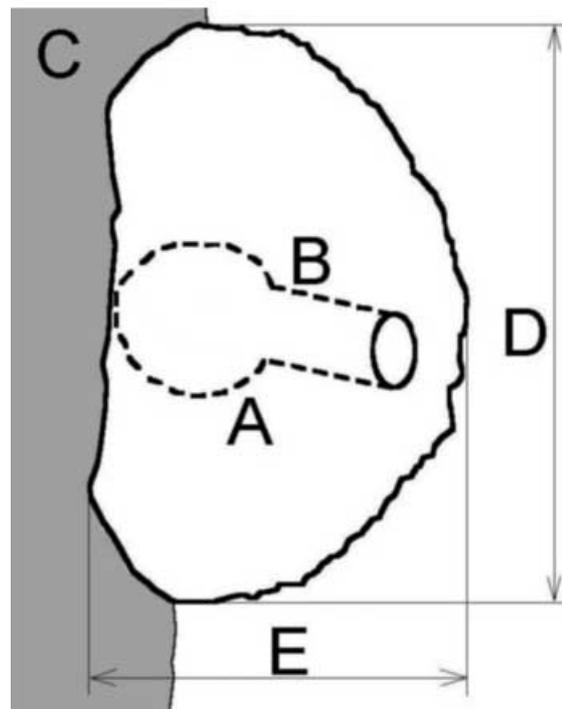

Figure 2. Photograph and schematic of nest termitarium used by Micronesian Kingfishers on Pohnpei, Federated States of Micronesia. Schematic depicts arboreal termitarium (A), shape of internal nest cavity (B) and the tree to which the termitarium is attached (C). Length (D), depth (E) and width (not shown) were used to calculate overall termitarium volume.

and four had not been re-filled. Faecal material and moisture accumulated in nest chambers following hatch, as did an associated musty odour that was detectable from several metres away. Micronesian Kingfishers were never observed foraging on termites.

Nest-site characteristics

No differences were identified between nests used by cooperative groups ($n = 10$) and pairs ($n = 12$) of Micronesian Kingfishers for any of the seven variables ($P > 0.05$). However, *t*-tests and results of the logistic regression modelling indicated differences between used ($n = 25$) and unused termitaria ($n = 242$). When each of the variables was considered separately, *t*-tests showed significant differences in termitarium volume, height in canopy, proximity to foraging areas, and proportion of open canopy and mature forest canopy within 15 m of nests (Fig. 3; Table 1). The last three of these variables are derived from vegetation characteristics, and are therefore correlated.

Results from the model selection process were considered to determine which of the vegetation-associated variables best explain nest termitaria. The top-ranked model from the AICc model selection process included variables for termitarium volume, termitarium height in canopy and proportion of open forest canopy within 15 m. The deviance goodness-of-fit test provided no evidence of model inadequacy ($\chi_{3,263}$, $P > 0.999$). The form of the top-ranked model follows:

$$\text{logit}(\pi) = -7.32 + 1.38 \ln(volume) + 6.32$$
$$height + (-14.07)open\ canopy.$$

The results indicated a positive relationship between height in canopy and volume, and the chance of selection as a nest-site. Parameter estimates suggested that the chance of selection as a nest-site increased by a factor of 1.38 with each added metre in height (1.11–1.71 CI). The parameter estimate for volume suggested that for each doubling in termitarium volume, there is a 2.60-fold increase in the chance of selection as a nest-site (1.5–4.4 CI). Conversely, a negative relationship between the proportion of open canopy within 15 m of the termitaria and probability

Figure 3. Vegetation coverage and nest locations (crosshairs) for the COM, Palikir and Ranch study sites (top, middle and bottom, respectively). Unshaded areas represent grassy and urban cover, light grey areas show early succession and agroforest vegetation, and dark areas represent mature forest vegetation.
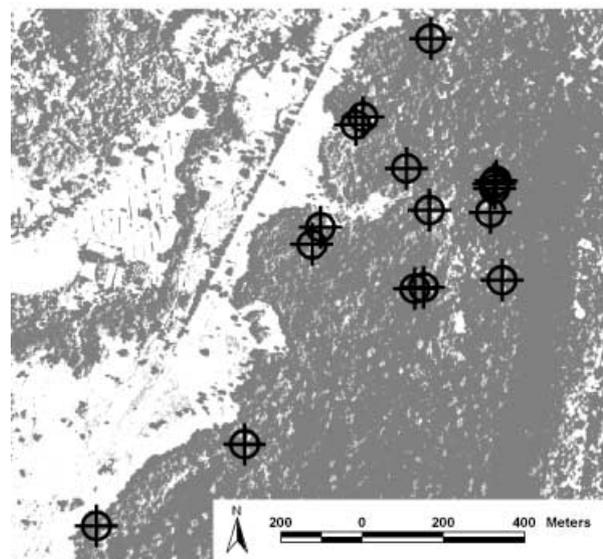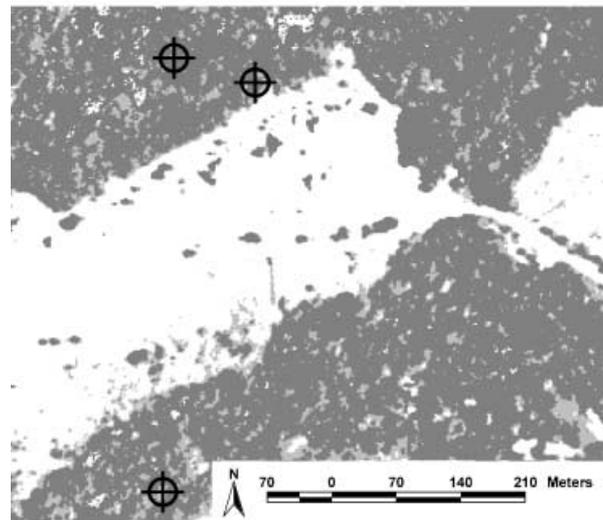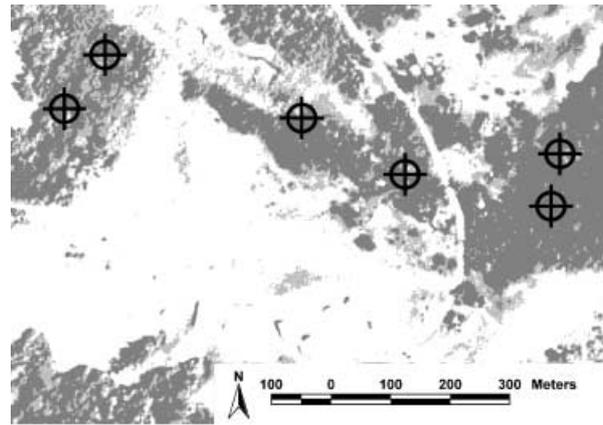
Table 1. Mean site characteristic values (± se) of nest and non-nest termitaria selected by Micronesian Kingfishers on Pohnpei, Federated States of Micronesia. *P*-values are presented for unequal variance *t*-test of nest vs. non-nest termitaria (* denotes variables with statistically significant differences).

Site characteristic	Nest (n = 25)	Non-nest (n = 242)	Probability of equal means
Volume (L)*	28.7 (1.1)	11.4 (1.1)	$t_{67.17}$ −8.5, $P < 0.001$
Height in canopy (m)*	4.3 (0.41)	2.5 (0.12)	$t_{28.02}$ −4.21, $P < 0.001$
Open canopy (m²)*	1.5% (0.01)	3.4% (0.03)	$t_{45.11}$ 3.06, $P = 0.004$
Mature forest (m²)*	97.4% (0.02)	91.5% (0.14)	$t_{30.76}$ −2.12, $P = 0.043$
Distance to foraging area (m)*	53 (6)	39 (2)	$t_{28.54}$ −2.19, $P = 0.037$
Distance to forest edge (m)	99 (14)	77 (4)	$t_{27.16}$ −1.54, $P = 0.135$
Distance to territory (m)	30 (5)	21 (1)	$t_{27.70}$ −1.77, $P = 0.089$

Table 2. Predicted probability of termitaria selection as a nest-site by Micronesian Kingfishers, based on the π_i values for the top-ranked logistic regression model.

π_j	Nest termitaria	Non-nest termitaria
0−10%	3	202
10−20%	13	24
20−30%	7	6
> 30%	2	10
Total	25	242

of selection as a nest was also detected. With each increase of 100 m² of open canopy, the results indicate a corresponding decline in the chance of selection as a nest-site by 0.14 (0.02–1.00 CI). Drop in deviance *F*-tests for all three variables yield *P*-values < 0.05, confirming that not all termitaria were equally desirable to nesting Micronesian Kingfishers.

Termitaria abundance

Fewer than 9.5% of the observed termitaria were used for nesting, suggesting that the absolute number of termitaria does not limit reproductive opportunities for Micronesian Kingfishers. However, only a subset of the termitaria located during the census were similar to those used as nest-sites because of their height, volume and surrounding forest canopy structure. Thus, we predicted that if suitable nesting resources were saturated, there should be no unused termitaria with characteristics similar to nest termitaria. Data for all termitaria were entered into the inferential model, and resulting π_j distributions for used and unused termitaria overlapped substantially (Table 2). Overlapping distributions indicate an excess of termitaria with characteristics similar to those used for nesting, and suggest no limitation in nest-site

abundance. One hundred and fourteen unused termitaria had higher predicted probabilities of use than the lowest used termitaria, which suggests that termitaria with characteristics similar to nest termitaria are not limited in abundance.

DISCUSSION

Nest-site selection

Compared with unused termitaria, Micronesian Kingfishers selected termitaria for nesting that were larger in volume, less exposed to open forest canopy and situated higher in the forest. Thicker nest walls have previously been shown to provide greater insulation (Skowron & Kern 1980), and Northern Flicker *Colaptes auratus* nest cavities excavated from larger trees were found to have more stable temperatures (Wiebe 2001). Similarly, the larger termitaria selected by Micronesian Kingfishers probably provide insulation from Pohnpei's tropical temperatures and moisture. The selection of termitaria in portions of the forest with contiguous canopy cover may also reduce the chances of overheating from direct sunlight and increase protection from driving rain.

Previous work concerning selection of arboreal termitaria by nesting birds appears to be limited to research conducted in Amazonian Peru that focused on Tui and Cobalt-winged Parakeets (*Brotogeris sanctithomae* and *B. cyanoptera*, respectively; Brightsmith 2000). In most respects, results reported here are remarkably similar. The previous and current investigations both conclude that higher-placed and larger-volume termitaria are selected for nesting, and the overall occupancy rates do not indicate that nesting resources are saturated. Brightsmith (2000) suggests that termitaria may be selected at heights corresponding to activities of birds in the canopy and that

larger termitaria may be selected as a niche differentiation mechanism for the many species using termitaria. In Pohnpei, however, Micronesian Kingfishers appear to be the only species using arboreal termitaria for nesting.

In North American species, higher situated nests were subject to lower rates of failure (Downing 1959, Li & Martin 1991). Nest termitaria selected by Micronesian Kingfishers were situated higher in the forest canopy than unused termitaria, which may reduce accessibility to predators such as domestic cats *Felis domesticus*, monitor lizards *Varanus indicus* and rats *Rattus* spp. During our work, the only nest mortality observed was from human Pohnpei residents who smashed nest termitaria with sticks and machetes. Pohnpein residents informed us that Micronesian Kingfishers chase domestic chickens and that they are dubious in local legend, so residents frequently smash nests and kill hatchlings (C. Cantero pers. comm.). Thus, higher situated nests may also reduce mortality caused by humans.

Does termitarium abundance limit reproductive opportunities?

In some species, delayed dispersal appears to be an evolutionary adaptation to limitations in the resources necessary for reproduction. Walters *et al.* (1992) provided one of the most notable demonstrations of a behavioural response to resource limitations by artificially augmenting nesting cavities in a population of Red-cockaded Woodpeckers. The manipulation encouraged dispersal and altered the proportion of the population breeding cooperatively. Here, we investigated whether the abundance of suitable termitaria might provide an ecological constraint to potential dispersers and thereby limit reproductive opportunities for Micronesian Kingfishers. However, our results indicated a low overall rate of termitaria occupancy (< 9.5%) and an abundance of nest-like termitaria in the study areas, suggesting that the availability of termitaria is not limiting for Micronesian Kingfishers.

Although excess nesting resources might be available, young birds may delay dispersal because higher-quality resources can be gained by waiting to inherit resources in natal areas (i.e. 'benefits of philopatry'; Stacey & Ligon 1991). An example of such behaviour came from observations of a newly introduced population of Seychelles Warblers *Acrocephalus sechellensis* on Cousin Island (Komdeur 1991, 1992, 1994). As the population increased in density, cooperative groups formed first on high-quality territories where birds were less likely to disperse. Our inability to identify differences in the characteristics of termitaria used by cooperatively breeding groups and pairs of Micronesian Kingfishers does not support the hypothesis that potential dispersers are delaying dispersal in order to inherit higher quality nest-sites.

In some cooperatively breeding species, territories themselves can be limited when population densities are high and habitat is limited (i.e. 'habitat saturation hypothesis'; Selander 1964, Brown 1978, Stacey 1979). In our analysis, visual inspections of the territory boundaries showed that adjacent territories frequently abutted, and Micronesian Kingfishers defended nearly all forest edges. Together, these suggest that although nest-sites may not be limited in abundance, Micronesian Kingfisher reproduction and dispersal may be limited by resources such as foraging perches on forest edges, food resources or territories themselves. These alternative explanations for co-operation in the Micronesian Kingfishers are worthy of additional research.

In conclusion, nest cavities are similar in structure, regardless of the termitarium in which they occur. The Pohnpei subspecies of Micronesian Kingfisher uses termitaria for nesting that are situated higher in the canopy, larger in volume and occur in more contiguous forest canopy than unused termitaria. Although specialized termitaria are selected by the kingfishers for nesting, termitaria with nest-like characteristics do not appear to be limited in abundance, and are therefore unlikely to be an underlying factor in the evolution and maintenance of delayed dispersal and cooperative breeding in Micronesian Kingfishers.

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