

AN ABSTRACT OF THE THESIS OF

Dylan C. Kesler for the degree of Master of Science in Wildlife Science presented on 12 March 2002.

Title: Nest-site Selection in Cooperatively Breeding Pohnpei Micronesian Kingfishers (*Halcyon cinnamomina reichenbachii*): Does Nest-site Abundance Limit Reproductive Opportunities?

Abstract Approved: *Redacted for Privacy*
Susan M. Haig

Despite their inherent importance and utility as ecological examples, island species are among the most endangered and least studied groups. Guam Micronesian Kingfishers (*Halcyon cinnamomina cinnamomina*) exemplify the plight of insular biota as a critically endangered and understudied island bird that went extinct in the wild before they could be studied in their native habitat. Guam kingfishers currently exist only as a captive population in U.S. zoos. Using radio telemetry and visual observations of a wild subspecies of Micronesian Kingfisher (*H. c. reichenbachii*) from the island of Pohnpei, this study examined factors critical for the persistence of both the Guam and Pohnpei kingfishers.

Behavioral observations indicated that the birds employ a cooperative social system, which included non-parent individuals that assisted in reproductive attempts of others. Because resource limitations have been cited as a potentially important factor in the evolution of cooperative behaviors and in conservation, this

investigation assessed the characteristics and availability of a potentially limited nesting resource, arboreal termite nests. First, the characteristics of termite nests, or termitaria, selected by Micronesian Kingfishers for use as nest sites were modeled. Results suggested that Micronesian Kingfishers selected termitaria that were higher from the ground and larger in volume than unused termitaria. Further, there was little evidence that birds selected from among termitaria based on proximity to forest edges and foraging areas, placement on a tree, vegetation characteristics, or microclimate. Second, the number of termitaria with characteristics indicative of nest sites was assessed to determine if reproductive opportunities might be limited by the abundance of suitable termitaria. Results from this analysis suggested that although fewer termitaria existed with characteristics similar to those used for nesting, reproductive opportunities did not appear to be limited by their abundance. Therefore, while conservation strategies should be directed towards providing ample and appropriate nesting substrates, I found no evidence suggesting that termitaria abundance played a role in the evolution of cooperative breeding in Pohnpei Micronesian Kingfishers. Findings presented here will hopefully enhance our understanding of cooperative behaviors, as well as improve conservation efforts for Micronesian Kingfishers and other insular avifauna.

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NEST-SITE SELECTION IN COOPERATIVELY BREEDING POHNPEI MICRONESIAN
KINGFISHERS (*HALCYON CINNAMOMINA REICHENBACHII*): DOES NEST-SITE
ABUNDANCE LIMIT REPRODUCTIVE OPPORTUNITIES?

By
Dylan C. Kesler

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This thesis is dedicated to my Grandmother Kesler
for always encouraging science and curiosity.

Nest-site Selection in Cooperatively Breeding Pohnpei Micronesian Kingfishers (*Halcyon cinnamomina reichenbachii*): Does Nest-site Abundance Limit Reproductive Opportunities?

1. INTRODUCTION

1.1. INTRODUCTION

The unique species, communities, and systems on oceanic islands have inspired some of the most fundamental and insightful theories in ecology and evolution. That Charles Darwin and Alfred Russell Wallace first developed the theory of evolution after observing assemblages of unique insular species is no coincidence (Darwin 1859, Wallace 1881). And although it has been aptly applied to continental “habitat islands”, MacArthur and Wilson’s (1967) Theory of Island Biogeography was the result of much time studying oceanic islands. The unique characteristics of island species also render them susceptible to anthropogenic influences, which have resulted in an extinction rate twelve times that of mainland species (Halliday 1978, Steadman et al. 1984, Steadman and Olson 1985, Steadman 1989, Vartanyan et al. 1993, and others).

The effects of introduced alien species are among the major conservation issues currently facing island systems. While there is debate about whether insular species are more susceptible to invaders than mainland species, few question the

empirical evidence illustrating that alien invasions have impacted islands to a greater extent (Elton 1958, Carlquist 1974, Simberloff 1986, Brown 1989, Richardson 1992, D'Antonio and Dudley 1995). Guam's experience with introduced Brown Tree Snakes (*Boiga irregularis*), an avian predator, is an oft-cited example of a catastrophe caused by an invasive species. Of the 12 forest bird species indigenous to Guam (Jenkins 1983), all but four are extinct from the wild and the remnant populations are declining (Savidge 1984, 1987; Engbring and Fritts 1988; Reichel 1992; De Bell and Whitesell 1993).

The Guam Micronesian Kingfisher (*Halcyon cinnamomina cinnamomina*) is among the species impacted by Brown Tree Snakes. Kingfisher populations declined over several decades, and in 1984, the birds were U.S. listed as “*Endangered*” (USFWS 1984). Subsequently, twenty-nine individuals were captured and placed in the Micronesian Kingfisher Species Survival Plan (SSP) captive breeding program as they went extinct in the wild (reviewed in Bahner et al. 1998, Haig et al. 1995). Since that time, attempts to breed captive kingfishers have met with limited success and recovery efforts have stagnated because information about their natural history was so limited. What little is published, documents that Micronesian Kingfishers occupied mature forests, agro-forest, mangrove, and open habitats (Coultas 1931, Baker 1951, Marshall 1956, Ralph and Sakai 1977, Engbring et al. 1990) and nested in cavities excavated from soft-

wooded trees and arboreal termitaria prior to their extinction from Guam (Jenkins 1983, Beck and Savidge 1985, Marshall 1989).

Micronesian Kingfishers are one of 36 members of the genus *Halcyon*, 19 of which are island endemic species that have garnered little previous attention from international and local conservation organizations and government agencies (Fry and Fry 1992). Thus, like the Guam kingfishers, there is a lack of information regarding the extant populations of Micronesian Kingfishers on the islands of Pohnpei and Palau (*H. c. reichenbachii* and *H. c. pelewensis* respectively). Pohnpei Micronesian Kingfishers inhabit several small islands, approximately 1,700 km southeast of Guam, and the Palau kingfishers occur on the Palau islands 1,300 km to the southwest. The two extant Micronesian Kingfisher subspecies are also similar to Guam kingfishers in that recent information indicate drastic population declines (Buden 2000; Kesler and Haig, pers. obs).

1.2. COOPERATIVE BREEDING IN MICRONESIAN KINGFISHERS

In 1998, an investigation into the behavioral ecology of Pohnpei Micronesian Kingfishers was initiated to facilitate conservation and recovery efforts for all Micronesian Kingfisher subspecies. Because so little had been published about these birds, initial fieldwork focused on various aspects of their life history including social behavior, phenology of events over the annual cycle, distribution, and abundance. Among the most interesting observations collected

during the early phases of the project, and perhaps those with the most bearing on the recovery of the Guam birds, were observations of cooperative social behaviors.

Cooperative behaviors occur when non-parent individuals assist in the reproductive attempts of others (Skutch 1961). Many researchers have hypothesized about why non-parents, often referred to as helpers, forgo reproductive opportunities for what appears to be the benefit of others (for review see Brown 1987; Stacey and Koenig 1990; Ligon 1999). Two of the more accepted hypotheses include the *ecological constraints hypothesis* (Emlen 1982, 1984) and the *benefits-of-philopatry hypothesis* (Stacey and Ligon 1987, 1991; Waser 1988). Both suggest that the evolution of cooperative behaviors is an adaptation to limited resources and the intraspecific competition for them. They hypothesize that environmental resource availability and distribution limits breeding opportunities, so that the best option for young and inexperienced individuals is to remain on natal territories and assist in their parents' reproductive attempts until resources become available, or until they can inherit natal breeding resources.

Resource availability can functionally limit reproductive opportunities in two ways. First, a resource can be limited in *abundance* if the landscape provides fewer resources than are required by the number reproductively capable pairs of birds present. Alternatively, even if a resource is not restricted in abundance, reproductive opportunities can still be limited if all resources are defended by territorial conspecifics and fewer territories are available than reproductively

capable pairs. Under this second scenario breeding opportunities are limited not because there are too few resources in a given area, but rather because *access* to those resources is limited. Therefore, resources can limit reproductive opportunities and potentially lead to cooperative behaviors if they are limited in *abundance*, or if there is limited *access*.

1.3. OBJECTIVES

If some cooperative social systems are evolutionarily adapted to limited resources, it stands to reason that changes in resource availability may influence reproductive success, life history traits, and ultimately, future evolutionary pathways. Consequently, identifying which resources might limit reproductive opportunities is important for conservation. One way to begin this task is to conceptualize each resource and limitation-function combination (e.g. access to food or abundance of nest-sites) as an alternative null hypothesis to be disproved through research.

The goal of this thesis is to test one of the hypotheses by elucidating the relationship between Micronesian Kingfishers and the abundance of a potential limiting resource, suitable nest-sites. Pohnpei Micronesian Kingfishers construct nest cavities inside the nests of arboreal termites (*Nasutitermes* sp.), or termitaria. Termitaria resemble earthen masses attached to tree stems and branches, and range in size, structure, and placement (Lubin et al. 1977). Thus, the first objective was to identify a model describing the characteristics of termitaria used by nesting

Micronesian Kingfishers. The second objective was to use the model for assessing the abundance of termitaria similar to those selected for nesting, and determine if reproductive opportunities might be limited by suitable nest-site availability.

Although the initial analyses were informative, results were inconclusive with respect to the importance of microclimate. Thus, an additional assessment was conducted to clarify the relationship between nest sites selected by Micronesian Kingfishers and the associated thermal characteristics of surrounding microhabitats. It is my hope that results from these studies provide information that improves the conservation situation facing wild Micronesian Kingfishers, the success of captive recovery efforts, and planning and completion of a timely reintroduction of Guam Micronesian Kingfishers back to their natural habitat.

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2. NEST-SITE SELECTION IN COOPERATIVE BREEDING MICRONESIAN KINGFISHERS: THE INFLUENCE OF SITE CHARACTERISTICS ON SELECTION AND AVAILABILITY OF A POTENTIALLY LIMITED RESOURCE

2.1. ABSTRACT

Delayed dispersal and cooperative breeding are proposed to be adaptive strategies for overcoming limited breeding resources. The recent discovery of cooperative breeding in Micronesian Kingfishers (*Halcyon cinnamomina*) on the island of Pohnpei, Federated States of Micronesia, led to an investigation into the selection and use of a potentially limited nesting resource, arboreal termite nests, or termitaria. I used logistic regression and Akaike's Information Criterion (AICc) to fit and rank seven models describing potential nest-site selection strategies. Results provided little support for models based on vegetation characteristics, proximity to foraging areas and forest edge, and termitarium substrate. However, results did indicate that Micronesian Kingfishers nested in termitaria that were higher from the ground and larger in volume than unused termitaria. This is consistent with the hypothesis that birds selected nest sites inaccessible to terrestrial predators and termitaria with structural characteristics suitable for nest cavity excavation. Results further suggested that termitaria with height and volume characteristics selected for nesting were not limited in number, and were therefore unlikely to restrict reproductive opportunities for Micronesian Kingfishers.

2.2 INTRODUCTION

Micronesian Kingfishers (*Halcyon cinnamomina*) are a forest species that historically occurred on the four pacific islands (Baker 1951). The kingfishers from Miyako (*H. c. miyakoensis*) are completely extinct, and the Guam kingfishers (*H. c. cinnamomina*) are extinct in the wild and currently only exist as a captive population in U.S. zoos. On the islands of Pohnpei and Palau, the last remaining wild Micronesian Kingfishers appear to be declining (*H. c. reichenbachii* and *H. c. pelewensis* respectively; Buden 2000; D. Kesler, S. Haig, pers. obs.). Despite their status, prior publications about Micronesian Kingfishers include only anecdotal descriptions (Baker 1951, Pratt et al. 1987, Fry and Fry 1992) and observations from some of the last breeding pairs on Guam (Jenkins 1983, Beck and Savidge 1985, Marshall 1989).

Although previously unreported for this species, I observed cooperative breeding in Pohnpei during 1999 and 2000, when non-parent individuals assisted in the reproductive attempts of others. On 53% of regularly observed territories (n=15), color-banded and radio-marked Micronesian Kingfishers were observed maintaining territorial boundaries and participating in nest activities as cooperative groups comprised of a breeding pair and one non-breeding adult male helper. Groups remained together across breeding attempts and years. In some species, cooperative social behaviors seem to be an evolutionary adaptation to limited resources (Emlen 1982, Brown 1987; Stacey and Koenig 1990), suggesting that

changes in resource availability have the potential to influence reproductive success, life history traits, and ultimately, future evolutionary pathways.

Consequently, understanding species-resource interactions not only lends insight into the evolution of cooperative breeding, but is paramount to conservation of endangered species like Guam Micronesian Kingfishers (USFWS 1984).

Resources can functionally limit reproductive opportunities in two ways. First, if the landscape provides fewer resources than pairs of birds that are physiologically capable of reproduction, resource *abundance* can restrict reproductive opportunities. Second, even if there adequate resources to support reproduction by all capable reproducers, *access* to those resources may be denied to non-territory holding individuals like young dispersers if all available habitat is completely defended by territorial conspecifics.

Nesting and roosting cavities have been identified as the limited resource potentially responsible for the evolution of cooperative breeding in Red-cockaded Woodpeckers (*Picoides borealis*; Walters et al. 1992) and Green Woodhoopoes (*Phoeniculus purpureus*; Ligon and Ligon 1990). Like these cooperative species, reproduction in Micronesian Kingfishers may be limited by cavity availability, so I evaluated whether the abundance of nesting resources available in Pohnpei rainforests might limit reproductive opportunities for Pohnpei Micronesian Kingfishers.

Kingfisher nest cavities are excavated inside the nests of arboreal termites (*Nasutitermes* sp.), or termitaria, which resemble earthen masses ranging in size from a few centimeters to nearly a meter in height and width (Fig. 2.1). Little is known about site and vegetation characteristics associated with nest-site selection in Micronesian Kingfishers (see Marshall 1989), so my first objective was to model the characteristics of sites selected by Micronesian Kingfishers for nesting.

To determine if the number or type of termitaria available to Micronesian Kingfishers limits reproductive opportunities, two additional objectives were addressed. The abundance of termitaria can limit reproduction if there are fewer termitaria than reproductively capable Micronesian Kingfishers. Hence, my second objective was to compare kingfisher and termitaria densities. Termitaria can also limit opportunities if certain site and structural characteristics render only a subset of the available termitaria suitable for nesting, and the number of suitable sites is restricted. Thus, my third objective was to determine if termitaria with characteristics similar to those selected as nest sites were limited in abundance.

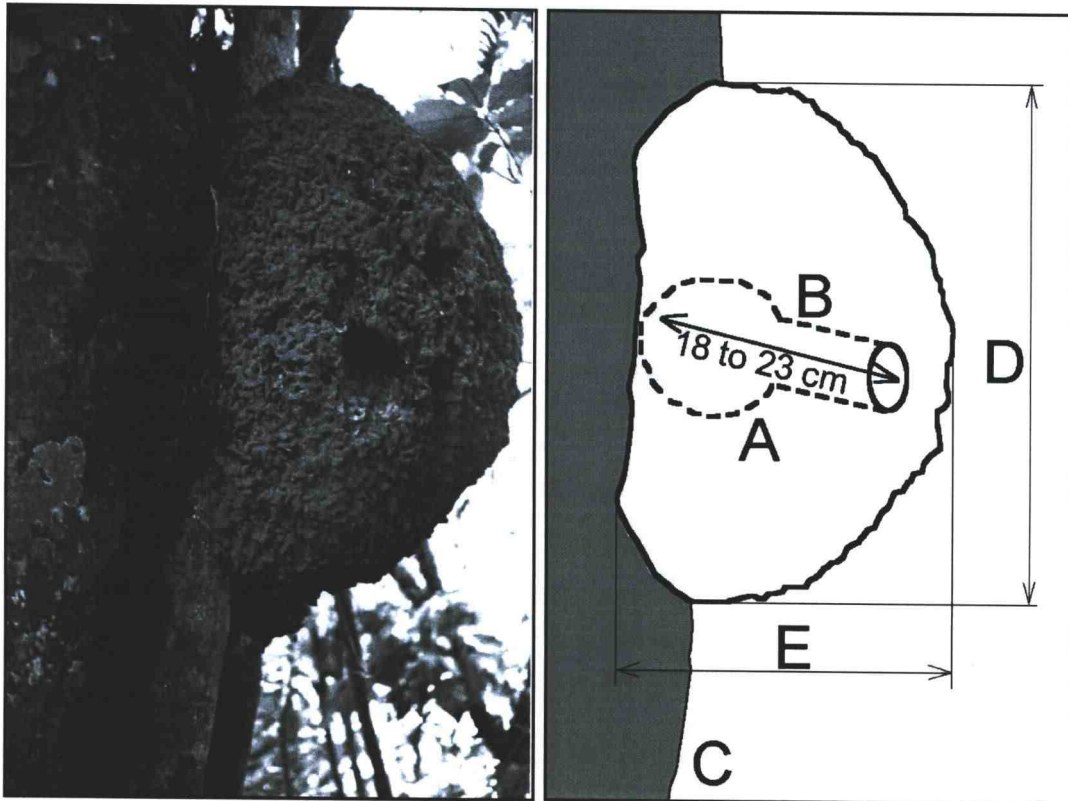


Figure 2.1. Left: photograph of typical nest termitarium used by Micronesian Kingfishers on Pohnpei. Right: schematic diagram depicting arboreal termitarium (A), shape of internal nest cavity (B), and the tree to which the termitarium is attached (C). Length (D), depth (E), and width (not illustrated) were assessed for each termitarium and used to calculate overall termitarium volume. Nest cavities constructed by Pohnpei kingfishers are relatively similarly sized and shaped, with spherical nest chambers averaging 12.7 ($SD \pm 1.5$) cm in diameter. Chambers are connected to the termitarium surface by a tunnel 5.1 (± 0.5) cm in diameter and 10.6 (± 2.2) cm long ($n=32$ measured cavities).

2.3. METHODS

2.3.1. *Study Area*

Research was conducted on the island of Pohnpei, Federated States of Micronesia (158.22° east, 6.88° north; Fig. 2.2). Pohnpei is a relatively 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. Previous descriptions of Pohnpei separate vegetation into four broad cover-types including mangrove forests, strand vegetation, secondary growth of lowlands, and rainforest/secondary growth of the uplands (Glassman 1952).

Three study areas were selected for the investigation. In the Nett municipality, the Ranch study area is a private landholding (158.21° east, 6.95° north); in Sokhes, the College of Micronesia (COM) area was located on the national campus (158.16° east, 6.91° north); and the Palikir study area was located on the Federated States of Micronesia federal government complex (158.16° east, 6.92° north). Each site is characterized by strand vegetation and secondary-growth lowland rainforest (Glassman 1952), pasture, grassland, urban vegetation, and agroforest.

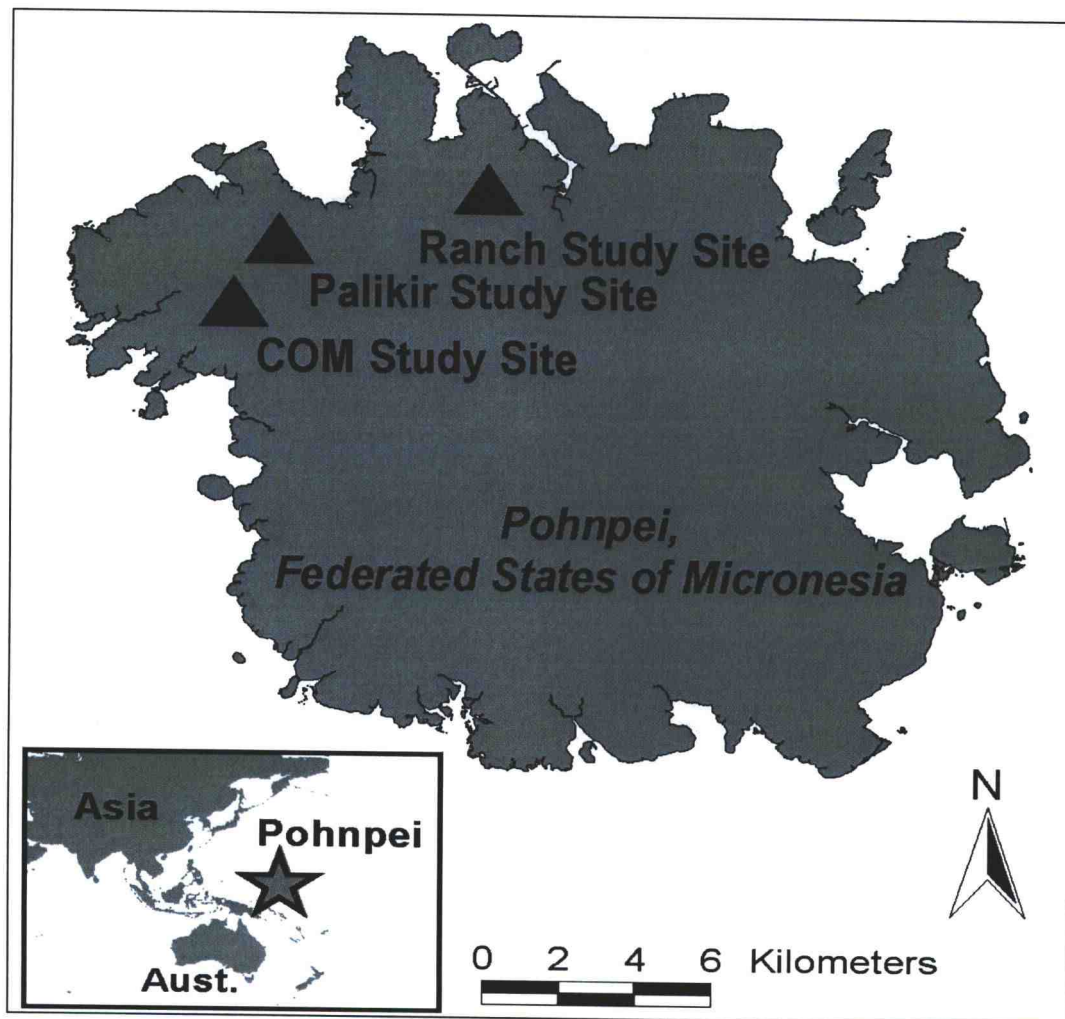


Figure 2.2. Study site locations on Pohnpei, Federated States of Micronesia.

2.3.2. Study Population

A study population was established in the Ranch and COM study areas from January to July 1999. The Palikir study area was added in 2000 and Micronesian Kingfishers were observed in the three study areas from April to September of that year. Radio-transmitters and colored leg bands were used to identify and follow individuals to nest-sites. Adult, yearling, and juvenile Micronesian Kingfishers were captured using mist nets and outfitted with a 1.8g telemetry package (Holohil Systems, Ltd., Ottawa, Canada) using the leg-harness design described by Rappole and Tipton (1991), and a unique combination of colored leg bands and a numbered aluminum USFWS band. I observed no adverse effects from transmitters or leg bands and assumed that they did not alter behavior of study individuals.

2.3.3. Nest-site Characteristics

Environmental factors with the potential to influence nesting success and nest-site selection were identified during fieldwork and from the literature. Reproductive success may suffer if nest termitaria are too small to contain a nest cavity without falling apart, or if termitarium walls are too thin to provide insulation (e.g., Martin 1992, Clark and Shutler 1999). Reproductive success might also be reduced if nest termitaria are accessible to predators such as domestic cats (*Felis domesticus*), humans (*Homo sapiens*), or monitor lizards (*Varanus indicus*;

e.g., Lack 1954 and others); too far from foraging areas (e.g., Li and Martin 1991, Rosenberg and McKelvey 1999); or located in sites where microclimates are too extreme for incubation and brood rearing (e.g., Ricklefs and Hainsworth 1969, Austin 1976, Wiebe and Martin 1998). I hypothesized that Micronesian Kingfishers select nest termitaria that mitigate the effects of these factors. Termitarium and site characteristics that might serve this purpose were then identified and assessed during a termitaria census.

2.3.4. *Termitaria Census*

Termitaria were located by direct observation and systematic searches of forested areas used by 16 Micronesian Kingfisher family groups (Kesler and Haig, *in prep*). Nests were evident from both telemetry and visual observation because birds called frequently and spent a great deal of time at nest locations prior to and during incubation. I believe that all nests initiated by radio-marked individuals during fieldwork were located. Termitaria available to Micronesian Kingfishers within each study area, but not selected as nest-sites, were located during transect searches conducted between May and September 2000. A compass and the track-log function of the Garmin GPS II+ (Garmin Ltd. Olathe, KS) global positioning system (GPS) were used to walk parallel transects approximately 10m apart in the forested portions of the three areas. To ensure complete coverage, I quantified effort by setting the GPS unit to automatically record observer locations during census periods and then compared the search coverage to aerial photographs.

Three variables were measured directly from termitaria: termitarium *attachment type* (under-hanging from a branch or to the side of a tree), termitarium *height*, and termitarium *volume* (Fig. 2.1). When termitaria were too high to directly measure, a measuring tape was extended alongside and measurements were recorded using binoculars from a short distance away. To summarize termitarium dimensions, termitarium volume was estimated by assuming an ellipsoid shape and using the physical dimensions as radii, as has been done previously (Lubin et al. 1977, Brightsmith 2000). Locations of all termitaria were recorded with a March III (Corvallis Microtechnologies Inc.) or Garmin GPS II+ GPS. To reduce error, more than 20 recorded points were averaged for each termitarium.

Using remote sensing, variables associated with vegetative characteristics were assessed for each termitarium in two steps. First, high-resolution aerial photographs were ortho-rectified and used to construct vegetative coverages for the study areas. Then, vegetative coverages and GPS information for termitaria locations were used together to assess vegetation and habitat variables for each termitarium.

For the three study sites, high-resolution (< 1 M/pixel) aerial photographs were scanned and digitally ortho-rectified using ERDAS Imagine 8.4 (ERDAS Inc., Atlanta, GA) and positioning information collected with the GPS during fieldwork. Resolution of each photograph was reduced from 0.6 to 1 meter/pixel during the resample phase of the correction process to standardize images. ERDAS Imagine

was further used to divide the visual spectrum into 10 habitat classification signatures on each image with an unsupervised habitat classification. After excluding urban development, these signatures were manually combined until their application in a supervised classification resulted in three habitat coverages depicting: 1) grassy area; 2) primary growth and brushy vegetation; and 3) mature forest vegetation. Accuracy was determined by comparing results from the classification process with field notes and GPS data depicting habitat boundaries.

Micronesian Kingfishers were often observed foraging in open grassy patches at least 10M across, so the distance from each termitarium to contiguous grassy area $>100 \text{ M}^2$ was measured to index distance to foraging areas (*forage* hereafter). Nest predators have previously been shown to be associated with forest edges (Gates and Gysel 1978, Johnson and Temple 1996, Wilson et al. 2001). Termitarium proximity to contiguous grassy patches $>1000 \text{ M}^2$ was used as an index of termitarium proximity to forest edge (*edge* hereafter) because forest openings of this size constitute substantial breaks in the forest canopy. Arc Info 8.0 (Environmental Systems Research Institute Inc., Redding CA) was used to calculate distance values for the two variables.

Finally, values for two microclimate variables were calculated by assessing vegetation surrounding each termitarium. A circular area surrounding each termitarium with a diameter of 15M was chosen as an assessment area because it approximated the crown diameter of a mature tree in the Pohnpei rainforest.

Reasoning that less light and cooler temperatures characterized sites in denser portions of the rainforest, the proportion of area surrounding each termitarium classified as mature forest (*% forest*) was assessed as an index of cool microclimate. The proportion of area within 15M of each termitarium classified as grassy vegetation was assessed as an index of warmer microclimate because it represented areas where the forest floor was exposed to light penetration (*% grass*).

2.3.5. Statistical Analysis and Model Selection

Seven models reflecting alternative nest-site selection strategies potentially used by Micronesian Kingfishers were identified (Table 2.1). Models were developed in a multiple logistic regression format for binomial responses. SAS Version 8 (SAS Institute Inc., Cary, NC) was used to fit the models. The models were ranked by their relative ability to account for deviance and their efficient use of explanatory variables using Akaike's Information Criterion AICc (Anderson et al. 1994, Burnham and Anderson 1998). The model with the lowest AICc value ranked first and models with sequentially higher AICc values received correspondingly poorer rankings. The difference between the top-ranked (first) model and subsequent models was then assessed using the difference in AICc (Δ_i) values and "Akaike weights" (w_i ; see Burnham and Anderson 1998, p126).

Table 2.1. Hypothesized nest-site selection strategies potentially employed by Micronesian Kingfishers on Pohnpei and related candidate logistic regression models.

<i>Model</i>	<i>Hypothesized Selection Strategy</i>	<i>Logistic Regression Model</i>
1. Termitarium Volume	Greater volume provides sturdy substrate for cavity construction.	$\beta_0 + \beta_1 \ln(\text{volume})$
2. Distance to Foraging Areas	Termitaria selected near grassy foraging areas.	$\beta_0 + \beta_1 \text{forage}$
3. Microclimate 1	Termitaria selected with greater proportion of mature forest nearby and under-hanging termitarium provide cooler nest-site.	$\beta_0 + \beta_1 \%forest + \beta_2, \beta_3 \text{attachment type}$
4. Microclimate 2 and Volume	Termitaria selected with reduced exposure to sun for cooler site and greater volume for sturdy substrate.	$\beta_0 + \beta_1 \%grass + \beta_2 \text{volume}$
5. Predator Model 1	High termitaria are not accessible to predators and humans.	$\beta_0 + \beta_1 \text{height}$
6. Predator Model 2	Termitaria selected far from forest edge and high from ground to limit predator and human access.	$\beta_0 + \beta_1 \text{edge} + \beta_2 \text{height}$
7. Predator 1 and Volume	High termitaria with large volume are selected for protection from predators and greater volume for sturdy substrate.	$\beta_0 + \beta_1 \ln(\text{volume}) + \beta_2 \text{height}$

2.3.6 *Termitarium Availability*

Termitaria abundance was assessed to determine if the number of nest sites available might limit kingfisher reproduction. The number of breeding pairs within the census area was compared to the number of termitaria to test whether the raw number of termitaria limited reproductive opportunities. The top-ranked model from the model selection process was then used as an inferential model to determine if there were a limited number of termitaria with characteristics necessary for nesting.

As applied here, the form of a logistic regression model is as follows:

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

where π is the predicted probability of selection as a nest, and $\beta_0, \dots, \beta_p$ represent parameter estimates for variables $X_1, \dots, X_p$. 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 would indicate that there were unused termitaria with characteristics similar to nest termitaria and that nesting resources were not saturated. On the contrary, if analyses resulted in 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 were saturated.

2.4. RESULTS

2.4.1. Nest Termitaria

Among 267 termitaria located, 24 were selected as nest sites and 243 were not (Table 2.2). When termitaria data were fitted to the logistic regression models and the models were ranked, the *Predator I and Volume* model ranked first because it resulted in the lowest AICc value (134.19) and captured 82.3% of the Akaike weight (Table 2.3). Parameter estimates for the *Predator I and Volume* model are as follows:

$$\text{logit}(\pi) = -7.68 + 1.65 \ln(\text{volume}) + 0.33 \text{ height}$$

The *Predator I and Volume* model indicated that there was a positive relationship between *height* and *volume*, and the odds of selection as a nest-site (Fig. 2.3). The parameter estimate further suggests that the odds of selection as a nest-site increase by a factor of 1.39 with each added meter in height from the ground (95% Wald confidence interval from 1.13 to 1.71; 95% CI hereafter). The coefficient for *volume* suggests that for each doubling in termitarium volume, there is a 3.14 fold increase in the odds of selection as a nest-site (95% CI from 1.62 to 6.07). Because

Table 2.2. Characteristic means ($\pm$ SD) of termitaria used and not used by nesting Micronesian Kingfishers on Pohnpei, Federated States of Micronesia.

<i>Termitarium Characteristic</i>	<i>Nest Termitaria (n = 24)</i>	<i>Non-Nest Termitaria (n = 243)</i>
Volume (liters)	31.1 (11.8)	17.7 (15.3)
Height from Ground (meters)	4.36 (2.07)	2.49 (1.82)
Attachment Type (<i>n</i> side, <i>n</i> under branch)	6, 18	97, 146
Grassy Area (%)	0.02 (0.02)	0.06 (0.08)
Mature Forest (%)	0.81 (0.12)	0.75 (0.17)
Distance (meters) to grassy area > 100 M ²	40 (29)	39 (29)
Distance (meters) to grassy area > 1000 M ²	79 (58)	77 (57)

both the parameter estimates and their 95% CIs are greater than 1, resulting in significantly positive ($P < 0.05$) relationships and confirming that all termitaria were not equally desirable to nesting Micronesian Kingfishers.

It has been suggest as a rule of thumb, that Δ_i values ranging from 4-7 constitute a useful cutoff for a set of the top-ranking models (Burnham and Anderson 1998, p123). Therefore, some consideration should be given to the second-ranked *Microclimate 2 and Volume* model because its Δ_i value (3.3) is less

than the 4-7 cutoff range and because the model is within the top 95% of the Akaike weights. The top-ranked and second-ranked models both include the *volume* variable, which may account for their similarity. Nonetheless, the second-ranked model also includes a variable for microclimate, a factor that may be worthy of consideration.

Table 2.3. AICc rankings for Pohnpei Micronesian Kingfisher nest-site selection models.

Rank	Model	Parameters	AICc ^a	Δ_i^b	w_i^c
1	<i>Predator 1 and Volume</i>	3	134.19	--	82.3%
2	<i>Microclimate 2 and Volume</i>	3	137.48	3.3	15.9%
3	<i>Termitarium Volume</i>	2	142.00	7.8	1.7%
4	<i>Predator Model 1</i>	2	148.08	13.9	0.1%
5	<i>Predator Model 2</i>	3	149.40	15.2	0.0%
6	<i>Distance to Foraging Areas</i>	2	162.19	28.0	0.0%
7	<i>Microclimate 1</i>	4	164.34	30.2	0.0%

^a AICc calculated using formula in section 2.4.1 in Burnham and Anderson (1998, p53).

^b Δ_i indicates difference in AICc values between model *i* and top-ranked model.

^c w_i sum to 1 and are suggested by Burnham and Anderson (1998, p129) to represent probability that model *i* is the actual Kullback-Leibler best model.

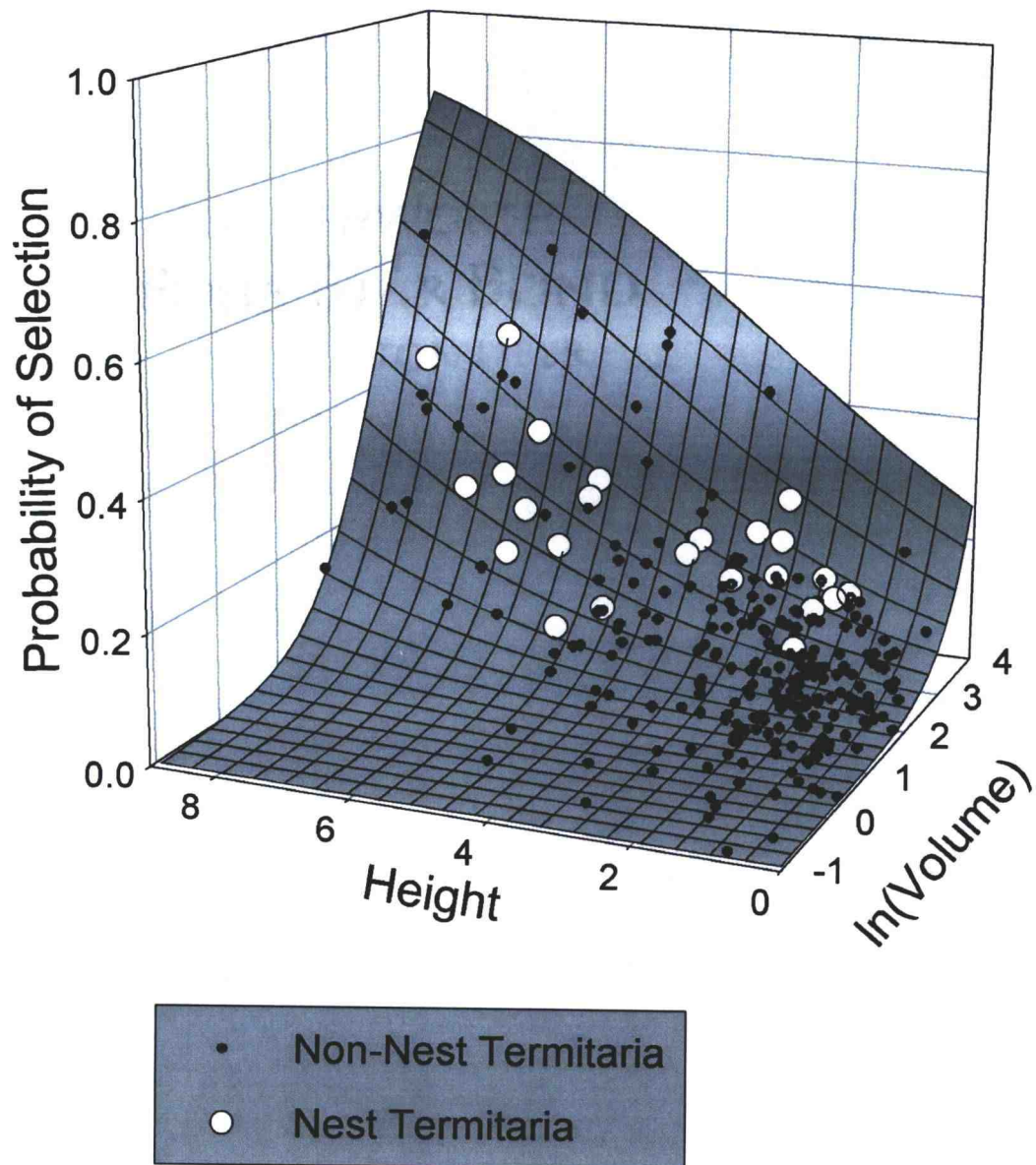


Figure 2.3. The influence of termitarium volume and height on the predicted probability of selection as a Pohnpei Micronesian Kingfisher nest-site. The Predator 1 and Volume model is depicted as the surface. Nest and non-nest termitaria detected during the termitaria census are plotted on top of the model at observed height and volume values.

2.4.2. *Termitarium Availability*

Fewer than 9% of the observed termitaria were used for nesting, suggesting that the raw number of termitaria available does not limit reproductive opportunities for Micronesian Kingfishers. However, only a subset of the termitaria located during the census may be suitable for use by kingfishers because of their height and volume characteristics. Thus, I predicted that if suitable resources were saturated, there should be no unused termitaria with characteristics similar to nest termitaria. To test this prediction, observed values for *height* and *volume* were entered into the inferential model and π_j was calculated for each termitarium. The resulting π_j distributions for used and unused termitaria overlapped substantially (Table 2.4) and 102 of the non-nest termitaria received π_j values at least as great as the lowest π_j for a nest termitarium. This suggests that although termitaria used for nesting are of greater *volume* and increased *height*, termitaria with *height* and *volume* characteristics similar to nest termitaria are not limited in abundance.

Table 2.4. Predicted probability of selection as a Pohnpei Micronesian Kingfisher nest-site (π) for termitaria and unused termitaria. Values are based on the *Predator I and Volume* model. Overlapping distributions for nest and non-nest termitaria indicate the existence of excess termitaria with characteristics similar to nest termitaria and suggest that termitaria suitable for nesting were not limited in abundance.

π_j	Nest Termitaria	Non-nest Termitaria
0-10%	4	184
10-20%	11	38
20-30%	6	7
30-40%	1	6
40-50%	2	5
50-60%	0	1
60-70%	0	2
70-100%	0	0
Total	24	243

2.5. DISCUSSION

2.5.1 *Nest-site Selection*

In this study, Micronesian Kingfishers selected termitaria for nesting that were higher off the ground and larger in volume than termitaria not selected for nesting. In North American species, higher nests have been shown to be subject to lower rates of failure (Li and Martin 1991). Observations from Samoa suggest that Tooth-billed Pigeons (*Didunculus strigirostris*) selected nest sites at increased heights following the introduction of domestic cats to the island (Austin and Singer 1985 *from* Gill 1990). In Pohnpei, higher nest locations may enhance survival and reproductive success by being inaccessible to predators such as domestic cats (*Felis domesticus*), monitor lizards (*Varanus indicus*), and rats (*Rattus* spp.). Additionally, Pohnpei residents destroy Micronesian Kingfisher nests because the birds are considered to be pests and higher nests may suffer less persecution from humans.

All nest cavities encountered during this study had approximately the same dimensions (Fig. 2.1.), despite the volume of the termitaria that contained them. Thus, smaller termitaria containing a nest cavity had thinner walls than larger nest termitaria. And while some termitaria were only slightly larger than the cavities they contain, in most cases, termitaria selected for nesting were at least one order of magnitude larger in volume than the nest cavity.

The reason for selection of what appears to be excessively large termitaria is not clear. One hypothesis worthy of further investigation is that Micronesian Kingfishers are selecting termitaria of greater volume to gain insulation from Pohnpei's tropical temperatures and moisture. Thicker nest walls have been shown to provide greater insulation (Skowron and Kern 1980) and in Northern Flickers (*Colaptes auratus*) cavities excavated from larger trees were found to have more stable temperatures (Wiebe 2001). Additionally, the second-place ranking of a microclimate model provides further support for this hypothesis. An alternative hypothesis for selection of the largest termitaria is based on structural soundness. Unlike non-nest termitaria, nest termitaria often lose their structural soundness and crumble in the months following breeding. If the thinner walls of smaller nest termitaria are more prone to break apart than the thicker walls of larger nest termitaria, choosing smaller termitaria may pose risks to kingfishers, making selection of the largest termitaria available the most adaptive strategy.

Despite lower rankings for models based on vegetative characteristics, proximity to foraging areas, and proximity to forest edge, these factors should not be considered unimportant to nesting Micronesian Kingfishers because this comparison is limited to sites selected first by arboreal termites and only then by kingfishers. Arboreal termites are likely susceptible to driving rain, predation by lizards, overheating, and a host of other environmental factors that may affect termitarium placement. If the same environmental factors affect termites and

Micronesian Kingfishers, the use of termitaria for nesting may be an adaptive mechanism employed by the birds to avoid unsuitable conditions.

Other studies concerning selection of arboreal termitaria by nesting birds are limited to work conducted in Amazonian Peru that focused on parakeet and trogon species (*Brotogeris cyanoptera*, *B. sanctithomae*, and *Trogon melanurus*; Brightsmith 2000). Nonetheless, results reported here are remarkably similar. Both investigations conclude that higher and larger volume termitaria are selected for nesting and overall occupancy rates do not indicate saturated nesting resources. 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 multiple species using termitaria. In Pohnpei, Micronesian Kingfishers appear to be the only species using arboreal termitaria for nesting however.

During this work, I was unable to completely explore the relationship between Micronesian Kingfishers and arboreal termites. Research into whether the interaction between kingfishers and termites is parasitic, mutualistic, or a predator-prey relationship may add valuable insight into our understanding of nest-site selection in Pohnpei. Furthermore, expanded sampling and alternative modeling approaches might provide better fitting models for the relationship between height and volume and the probability of selection as a nest-site. Clark and Shulter (1999) suggest that investigations of nest-site characteristics are a first step in the

investigation of the process of natural selection. Thus, another logical next-step in the study of Micronesian Kingfishers might be to investigate the influence of nest-site selection patterns on nest success.

2.5.2. Are Termitaria Limiting Reproductive Opportunities?

Many researchers have asked why non-parent helper individuals delay dispersal and forgo reproduction in cooperative social systems like the one employed by Micronesian Kingfishers. In many cases, cooperation seems to be an evolutionary adaptation to limited resources that are necessary for reproduction (Emlen 1982, Brown 1987, Stacey and Koenig 1990, Koenig et al. 1992, Ligon 1999, Hatchwell and Komdeur 2000). In these situations, resource availability is hypothesized to be so low that the most adaptive behavior for a helper may be to remain on a natal territory until future opportunities arise for acquisition of the limited resource. Here, I assessed whether either the abundance of termitaria or the abundance of suitable termitaria might limit reproductive opportunities for Micronesian Kingfishers.

The literature provides several examples of nest-site limitations in non-cooperative cavity nesting species (e.g., Cline et al. 1980, Raphael and White 1984, *but see* Walters et al. 1990). Walters et al. (1992) artificially increased breeding bird densities and illustrated that the number of available cavities limited reproduction in cooperative Red-cockaded Woodpeckers. However, the low rate of termitaria occupancy found here (9%) and predicted probabilities of selection from

the inferential model suggest that neither the sheer number of termitaria available nor the number of termitaria with characteristics typical of nests are limited in abundance for Micronesian Kingfishers.

Prior to their extinction from Guam, Micronesian Kingfishers were observed nesting in both arboreal termitaria and dead and decaying trees (Marshall 1989). In Pohnpei, however, neither the literature nor reports from island residents provided evidence that the Pohnpei subspecies uses decaying trees for nesting. Nonetheless, if Pohnpei kingfishers used alternative resources for nesting in addition to arboreal termitaria, the behavior would only strengthen conclusions that the number of nest sites available is unlikely to limit reproductive opportunities.

This study lends insight into the relationship between Micronesian Kingfishers and nest-site availability by rejecting hypotheses that the abundance of termitaria limited reproduction or that the abundance of termitaria with nest-like characteristics limited reproductive opportunities. However, the possibility that nest termitaria limit reproduction in Micronesian Kingfishers cannot be completely rejected without determining whether the excess numbers of termitaria identified here were available for use by non-reproductive individuals. Although excess termitaria with nest-like characteristics occurred on the study areas, they may not have been available by non-territory-holding helpers if space is saturated by territorial conspecifics that restrict access to those termitaria.

Nothing has previously been published describing territoriality and space use in Micronesian Kingfishers, but our anecdotal observations of Pohnpei kingfishers suggest that they are highly territorial. If the kingfishers can defend territories against intrusions by conspecifics, and if the territories are distributed in the Pohnpei rainforest so that all available habitat is defended by territorial individuals, helpers might not have had an opportunity to disperse and breed. Thus, further insight into the relationship between cooperation in Micronesian Kingfishers and resource availability can be gained through an investigation into Micronesian Kingfisher space use, territoriality, and territory and resource distributions. Similarly, alternative hypotheses about other resources such as food and cover potentially limiting reproductive opportunities also warrant further investigation.

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3. THE ROLE OF THERMAL CHARACTERISTICS IN NEST-SITE SELECTION BY COOPERATIVELY BREEDING POHNPEI MICRONESIAN KINGFISHERS.

3.1. ABSTRACT

Pohnpei Micronesian Kingfishers (*Halcyon cinnamomina reichenbachii*) excavate nest cavities from the nest structures of arboreal termites (*Nasutitermes* sp.), or termitaria. Previous research indicated that birds selected higher and larger termitaria for nesting, but was inconclusive with regard to microclimate. Here, thermal characteristics of microhabitats where nest termitaria occurred were compared to those of unused termitaria and random locations in the forest to clarify the importance of microclimate to nesting kingfishers. I examined average daily high and low temperatures, overall temperature fluctuation, and the proportion of time temperatures were low enough to metabolically stress adult birds. No significant differences were found between temperatures in microhabitats where nest termitaria occurred and those where non-nest termitaria occurred. Significant differences were identified for all four temperature metrics in microhabitats surrounding termitaria and random sites in the forest. However, after considering the small magnitude of differences and relating findings to physiological requirements of adult kingfishers, results did not provide convincing evidence to support the hypothesis that selection of nest sites was based on microhabitat temperatures. Results clarify the relationship between nest-site selection and

microhabitat thermal characteristics as well as provide ambient temperature guidelines for the captive population of the critically endangered Guam Micronesian Kingfishers (*H. c. cinnamomina*).

3.2. INTRODUCTION

Most avian species expend great amounts of energy and are restricted to a single site during nesting, which increases vulnerability to environmental factors that often pose less of a threat during other life history phases (Ricklefs 1969, Martin 1992, With and Webb 1993, Gloutney and Clark 1997, Reid et al. 2002). To reduce these risks, birds have evolved a broad range of strategies for choosing locations and constructing nests with characteristics likely to enhance reproductive success (Ricklefs 1969, Walsberg 1985, Sheldon and Winkler 1999). Some species have been shown to alter nest construction and select nest sites in response to microclimate (e.g., Austin 1974, van Riper et al. 1993, Weibe 2001). Suitable microclimates have the potential to reduce metabolic costs to incubating adults (reviewed in Gloutney et al. 1996, Williams 1996, Thomson et al. 1998) and protect eggs and chicks from mortality and developmental problems (Quinney et al. 1986). Even in regions with generally mild climates where benefits of microclimate selection are not as intuitively apparent, nest-site selection has been linked to microhabitat temperature, exposure to sunlight, prevailing wind, and moisture (e.g., van Riper et al. 1993).

One way to assess the influence of microclimate on reproducing birds is to compare ambient temperatures to their thermoneutral zone. The thermoneutral zone includes the range of temperatures within which birds can thermoregulate by adjusting posture or plumage. When ambient temperatures are outside this zone, birds must expend additional energy to maintain body heat (see Calder and King 1974, Robins 1993). The effects of disparate ambient temperatures and thermoneutral zones can be exacerbated for birds during reproduction when metabolic energy is already invested in incubating eggs and brooding chicks (Williams 1996, Gloutney et al. 1996, Thompson et al. 1998). This has caused some to suggest that selection of nest sites more closely aligned with the zone may result in increased fitness and survival (With and Webb 1993, Gloutney and Clark 1997, Reid et al. 2002).

Guam Micronesian Kingfishers (*Halcyon cinnamomina cinnamomina*) are extinct in the wild and only exist as a captive population (Haig et al. 1995, Bahner et al. 1998). To facilitate recovery of these birds to a point where reintroduction might occur, I previously studied nest-site characteristics selected by the closely-related cooperatively breeding Pohnpei Micronesian Kingfisher (*H. c. reichenbachii*). The Pohnpei kingfishers excavate nest cavities from the nests of arboreal termites (*Nasutitermes* sp.), or termitaria, which resemble earthen masses attached to trees. Results indicated termitaria used for nesting were higher from the

ground and larger in volume than unused termitaria, but results were inconclusive with regard to the importance of microclimate.

Life history characteristics of Micronesian Kingfishers may render them more susceptible to thermal stresses than other taxa. As members of the Order Coraciiformes, Micronesian Kingfishers hatch as altricial chicks and lack the downy stage of development present in other orders (Fry and Fry 1992). Eventually, nestlings grow feather-spines, which unfurl into feathers approximately three weeks post-hatch. Down feathers provide young in other species with insulation for the maintenance of body heat, but because young Micronesian Kingfishers are covered only by skin or feather-spines during the first several weeks of growth, they may be more susceptible to thermal stresses and require more parental attention than species with downy chicks.

Temperatures on Pohnpei range from 16°C to 35°C (NOAA 2001) and suggest potential thermal stress and possible survival and reproductive benefits associated with the selection of thermally buffered nest microclimates. While daily high temperatures do not appear likely to stress Micronesian Kingfishers, average daily low temperatures during the kingfisher breeding season (mid-March to November) may stress incubating parents and chicks with developing feathers (mean daily high $31.1 \pm 1.4^{\circ}\text{C}$ SD, mean daily low $23.1 \pm 1.23^{\circ}\text{C}$ SD; NOAA 2001).

I conducted this study to determine if microclimate plays a role in nest-site selection by Micronesian Kingfishers because of the need for this information for captive management and planning a release of the captive Guam birds into the wild, and because of a lack of understanding about avian use of arboreal termitaria (Brightsmith 2000). I predicted that if ambient temperatures affect nest-site selection, the microhabitats where nest termitaria occur should exhibit thermal characteristics more closely aligned with the thermoneutral zone of adult Micronesian Kingfishers than unused termitaria. Guam Micronesian Kingfishers used rotten trees and termitaria for nesting, while Pohnpei Micronesian Kingfishers appear to be obligate termitaria nesters. If the apparent obligate use of termitaria is an adaptive trait in Pohnpei birds, the behavior may have arisen because microclimates where termitaria occur exhibit more suitable thermal properties than the microhabitats of other potential cavity substrates. Thus, I also compared microhabitat temperatures at locations where termitaria occur with random locations in the Pohnpei rainforest.

3.3. METHODS

3.3.1. Study Area

Research was conducted on the island of Pohnpei, Federated States of Micronesia (158.22° east, 6.88° north; Figure 1). Pohnpei is a relatively 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. Previous descriptions of Pohnpei separate vegetation into four broad cover-types including mangrove forests, strand vegetation, secondary growth of lowlands, and rainforest/secondary growth of the uplands (Glassman 1952). Because of its proximity to the equator and location in the Pacific Ocean, Pohnpei is a tropical island, which receives an average of 473 cm of precipitation per year.

Two study areas located approximately six km apart were selected for microclimate analyses. The Ranch study area is a private landholding in the Nett municipality (158.21° east, 6.95° north) and the College of Micronesia (COM) area in Sokehs is located on the national college campus (158.16° east, 6.91° north). The areas ranged in elevation from 50 to 100M and were characterized by strand vegetation and secondary-growth lowland rainforest and have been described previously (Kesler and Haig, *in review*; Glassman 1952).

3.3.2. Thermoneutral Zone

The thermoneutral zone includes the range of temperatures within which birds can thermoregulate by adjusting posture or plumage, while additional metabolic energy must be dedicated to thermoregulation and reproduction when temperatures are outside the zone (Calder and King 1974, Robins 1993, Gloutney et al. 1996). The upper limit of the thermoneutral zone, or the upper critical

temperature (T_{uc}), averages $38 \pm 3^\circ\text{C}$ for most avian species (Aschoff 1981). I estimated the lower limit of the zone, or the lower critical temperature (T_{lc}), for adult Micronesian Kingfishers to be 23.8°C using a formula for inactive non-passerine birds (Robbins 1993):

$$T_{lc} = T_b - 38.3 X^{0.31}$$

where T_b is body temperature (estimated as 39.6°C ; King and Farner 1961), and X is body weight (58.3g; unpub. data). For some species, adjustments to T_{lc} need to be made to include the energetic costs of incubation, but I made no adjustments because Micronesian Kingfishers do not fit the criteria suggested by Robbins (1993; the total weight for the one to two egg clutch is between 14% and 28% of the average adult body weight, and the birds nest inside thermally buffered cavities).

3.3.3. *Termitaria Census*

Termitaria available to Micronesian Kingfishers, but not selected for nesting, were located during transect searches conducted between May and September 2000. A compass and the track-log function of the Garmin GPS II+ (Garmin Ltd. Olathe, KS) global positioning system (GPS) were used to walk parallel transects approximately 10 M apart in forested portions of the study areas. GPS units were set to automatically record observer locations every 30s during census periods and those records were compared to aerial photographs to ensure

complete coverage. Radio-marked (Holohil Systems, Ltd., Ottawa, Canada) Micronesian Kingfishers ($n = 26$) were subsequently followed to monitor termitaria use. Twenty-one nest and 234 non-nest termitaria were identified in the 43.4 ha search area and entered into an ArcView (ESRI, Redlands, CA) geographic information system (GIS) database.

3.3.4. Microclimate Assessment

The goal of this study was to compare temperatures in the microhabitat immediately surrounding (≤ 10 cm) nest termitaria, non-nest termitaria, and random locations in the forest (non-termitaria hereafter). An equal number of sample locations within each microhabitat type were selected from the GIS database. All known nest termitaria were selected ($n = 21$). Previous research suggested that Micronesian Kingfishers chose termitaria for nesting that were ≥ 10 L in volume and > 1.8 M from the ground (Kesler and Haig, *in review*). Thus, 21 non-nest termitaria were randomly selected from a candidate list of 107 termitaria fitting these criteria. Similarly, 21 non-termitaria locations were randomly selected from a 1 X 1 M grid placed over the census search areas. Because height from ground may affect temperatures, each non-termitaria sampling location was randomly assigned a height from the height distribution of nest termitaria.

Records indicate that temperatures in Pohnpei are extremely stable both within and among years (mean daily temperature $27.2 \pm 0.99^{\circ}\text{C}$ SD; NOAA 2001). This thermal stability suggested that even short-duration monitoring would likely

be representative of overall thermal patterns characteristic of each microhabitat type. Thus, seven nest, non-nest, and non-termitaria sample locations were randomly assigned to each of three assessment periods beginning on 6, 10, and 14 September 2001.

On the first day of each assessment period, 21 StowAway temperature loggers (Onset Computer Corp. Pocasset, MA) were placed at the assigned sample locations by 1900 hrs. The loggers recorded ambient temperatures at six minute intervals for 3.5 days. Then, after 0700 hrs on 10 and 14 September, loggers were collected and re-distributed to the sample locations in the subsequent assessment period. Temperature loggers were placed ≤ 5 cm below the base of nest and non-nest termitaria and on the same side of the tree. At non-termitaria sample locations, temperature loggers were attached to the nearest tree ≥ 15 cm diameter breast height (approximate minimum diameter tree supporting nest termitaria), at the assigned height, and in a random orientation.

3.3.5. Statistical Methods

Four biologically relevant thermal metrics were identified to assess temperatures recorded in each microhabitat type. Daily extreme temperatures have the potential to thermally stress birds, so mean daily high temperatures (T_{max}) and mean low temperatures (T_{min}) were assessed. Some have suggested that birds seek nest sites with stable temperatures (With and Webb 1993, Gloutney and Clark

1997), so percent coefficients of variation (arcsine square root transformed; T_{flux}) were used to compare temperature stability among microhabitat types.

Micronesian Kingfishers are most likely to be metabolically stressed when ambient air temperatures are outside their thermoneutral zone. Historic records suggest that ambient air temperature is unlikely to go above the kingfisher thermoneutral zone (0.02% daily high temperatures, NOAA 2001) but quite likely to fall below (73% hourly observations, NOAA 2001), so the proportion of observations that fell below T_{lc} (% below T_{lc}) was also compared among site types. I chose to treat all variables separately and to present correlation coefficients and 95% confidence intervals (95% CI) for parameter estimates because the response variables are potentially correlated.

Mixed Models ANOVA (SAS Analyst, SAS Institute Inc., Cary NC) was used to fit models to each of the response variables. Microhabitat type (nest, non-nest, or non-termitaria) was included as a fixed effect. A block (observation period 1, 2, or 3) and a block by microhabitat type interaction were included as random effects. Sample location height was also included as a covariate to account for temperature differences associated with layers in the forest canopy. Estimates for least squares means were then used in two orthogonal linear contrasts (Ramsey and Schafer 1996) to compare microhabitat thermal characteristics of nest termitaria

with non-nest termitaria and all termitaria with non-termitaria. Values are reported as means $\pm$ SD unless otherwise noted and differences are considered statistically significant if $P \leq 0.05$.

3.4. RESULTS

Data were collected at 18 nest termitaria, 19 non-nest termitaria, and 21 non-termitaria microhabitat sample locations during the assessment period, for a total of 48,720 observations (Table 3.1). Sample sizes differed from *a-priori* assignments because a landowner restricted access to two pre-assigned nest and two non-nest sample locations, and vegetation was cleared from another nest location. Additionally, data from one nest and two non-nest sample locations were lost when a temperature logger was stolen. To mitigate losses, one nest and two non-nest termitaria located during 2001 fieldwork were added to the sampling regime.

A single T_{max} observation from a non-termitaria microhabitat stood as an outlier. The observation was probably the result of logger heated by direct sunlight because an extreme temperature bout lasted approximately one hour and exceeded the maximum capabilities of the unit (38°C). All observations within 30 min of the spike (11 observations) were removed from the data set because the intent of this study was to assess ambient air temperatures rather than solar insolation, and because the temperature spike had the potential to influence conclusions.

Table 3.1. Temperature observations from microhabitats where Micronesian Kingfisher nest termitaria and non-nest termitaria occur, and random sites in the forest on Pohnpei during three assessment periods in September 2001. Periods beginning at 19:00 hrs on the first day and ending at 07:00 hrs on the last day.

	6-10 Sept.		10-14 Sept.		14-18 Sept.	
Site Type	sites	obs.	sites	obs.	sites	obs.
Nest	6	5040	5	4200	7	5880
Non-Nest	7	5880	6	5040	6	5040
Forest	7	5880	7	5869	7	5880
Total	20	16800	18	15109	20	16800

Temperatures in all microhabitat types generally followed similar patterns (Fig. 3.1). Beginning shortly after sunrise (~ 0700 hrs), temperatures climbed to a mid-day peak at approximately 1000 hrs. As expected, daily high temperatures ($29.4 \pm 1.9^{\circ}\text{C}$) remained below the T_{uc} (approximately $38 \pm 3^{\circ}\text{C}$). Afternoon temperatures fluctuated and began to fall at approximately 1500 hrs. Nocturnal temperatures fell to an average low of $22.8 \pm 0.7^{\circ}\text{C}$. The low temperature trough lasted from approximately 0000 hrs to 0730 ($25.1 \pm 5.5\%$ for each 24 hr period).

The correlation matrix for response variables shows strong correlation between T_{max} and T_{flux} , and between T_{min} and % below T_{lc} (Table 3.2). T_{min} at all sites was nearly stable across time and locations, so the strong correlation between

T_{max} and T_{flux} is not surprising. Similarly, because T_{min} observations were so close to the T_{lc} for Micronesian Kingfishers, the duration of time required for temperatures to drop to T_{min} , and then climb back above T_{lc} (% below T_{lc}) were strongly correlated. The existence of the correlations suggests that although analyses presented here concern different microhabitat thermal aspects, all thermal metrics were somewhat similarly affected by the daily microhabitat temperature regimes.

Table 3.2. Correlation matrix for average daily maximum temperature (T_{max}), average daily minimum (T_{min}), percent coefficient of variation (T_{flux}), and proportion of observations when temperatures were below the thermoneutral zone for adult Micronesian Kingfishers (arcsine square root transformed; % below T_{lc}). Observations were recorded in microhabitats surrounding arboreal termitaria used by nesting by Pohnpei Micronesian Kingfishers, termitaria that were not used, and at random sites in the rainforest. Correlations were averaged for each of three assessment periods, SD are presented below the diagonal.

<i>Variable</i>	T_{max}	T_{min}	T_{flux}	% below T_{lc}
T_{max}	--	-0.28	0.94	0.21
T_{min}	0.34	--	-0.44	-0.92
T_{flux}	0.02	0.19	--	0.36
% below T_{lc}	0.35	0.05	0.21	--

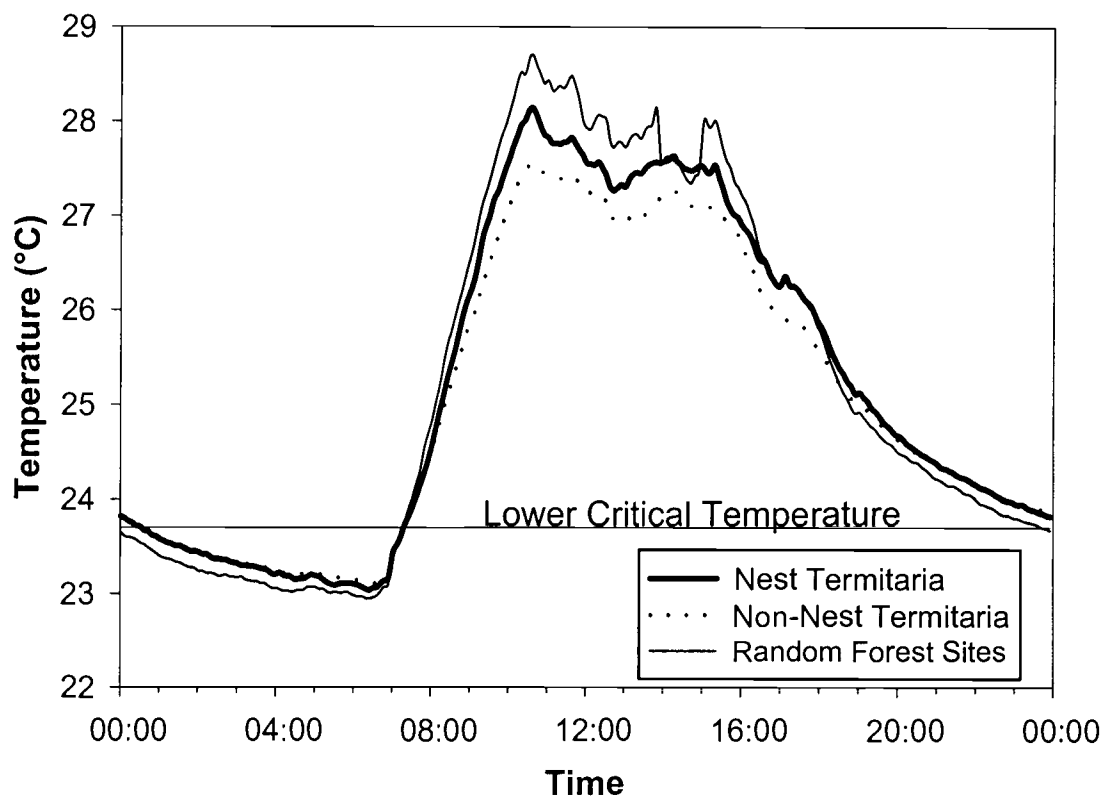


Figure 3.1. Lower critical temperature of adult Pohnpei Micronesian Kingfishers and average hourly temperatures from microhabitats surrounding nest termitaria, non-nest termitaria, and random forest sites in September 2001.

Table 3.3. Least squares means and standard errors for estimated temperatures in microhabitats surrounding Pohnpei Micronesian Kingfisher nest termitaria, non-nest termitaria, and random locations in the forest. Estimates are result of an ANOVA Mixed Model (SAS Analyst, Cary NC) procedure which accounted for assessment period and height from ground. Resulting *P*-values from orthogonal linear contrasts of nest and non-nest termitaria microhabitats, as well as contrasts of all termitaria microhabitats with random locations in the forest are also presented.

Thermal Metric	Nest Termitaria (n=18)	Non-nest termitaria (n=19)	Nest vs. Non-nest Termitaria (<i>P</i>)	Random Locations (n=21)	Termitaria vs. Random Locations (<i>P</i>)
T_{max} (°C)	28.05 (0.41)	27.71 (0.40)	>0.05	28.70 (0.39)	<0.01
T_{min} (°C)	22.86 (0.11)	22.91 (0.11)	>0.05	22.72 (0.11)	<0.01
T_{flux}^a	0.38 (0.06)	0.36 (0.05)	>0.05	0.45 (0.05)	<0.001
% below T_{lc}	28.7 (2.6)	27.3 (2.6)	>0.05	31.7 (2.5)	<0.05

^a T_{flux} values were arcsine square root transformed to normalize the response distributions.

Results from linear contrasts indicate that after accounting for the influence of assessment period and sample location height, there was no significant difference in microhabitats where nest and non-nest termitaria occur for any of the four thermal metrics ($P > 0.05$, Table 3.3). To the contrary, after accounting for the effects of assessment period and height, all four metrics differed significantly between microhabitats where termitaria occurred and non-termitaria microhabitats (Fig. 3.2, Table 3.3). Contrasts of least squares means suggest that the average T_{max} was 0.82°C lower ($P < 0.01$) in termitaria microhabitats than in non-termitaria microhabitats (95% CI 0.24°C to 1.39°C lower). Average T_{min} observed in termitaria microhabitats were significantly warmer ($P < 0.01$) than in non-termitaria microhabitats, however the estimated difference in magnitude was small (0.17°C warmer at termitaria; 95% CI 0.05°C to 0.29°C). Results from the analysis of temperature extremes suggested that in general, temperatures fluctuate less in termitaria microhabitats than in microhabitats where termitaria do not occur, a result corroborated by the significantly lower T_{flux} ($P < 0.01$) in termitaria microhabitats than in non-termitaria microhabitats (0.08 smaller at termitaria, 95% CI 0.03 to 0.13). Similarly, the proportion of time when temperatures were below the T_{lc} was estimated to be 3.69% greater ($P < 0.05$) in non-termitaria microhabitats than in termitaria microhabitats (95% CI 0.57 to 6.81%).

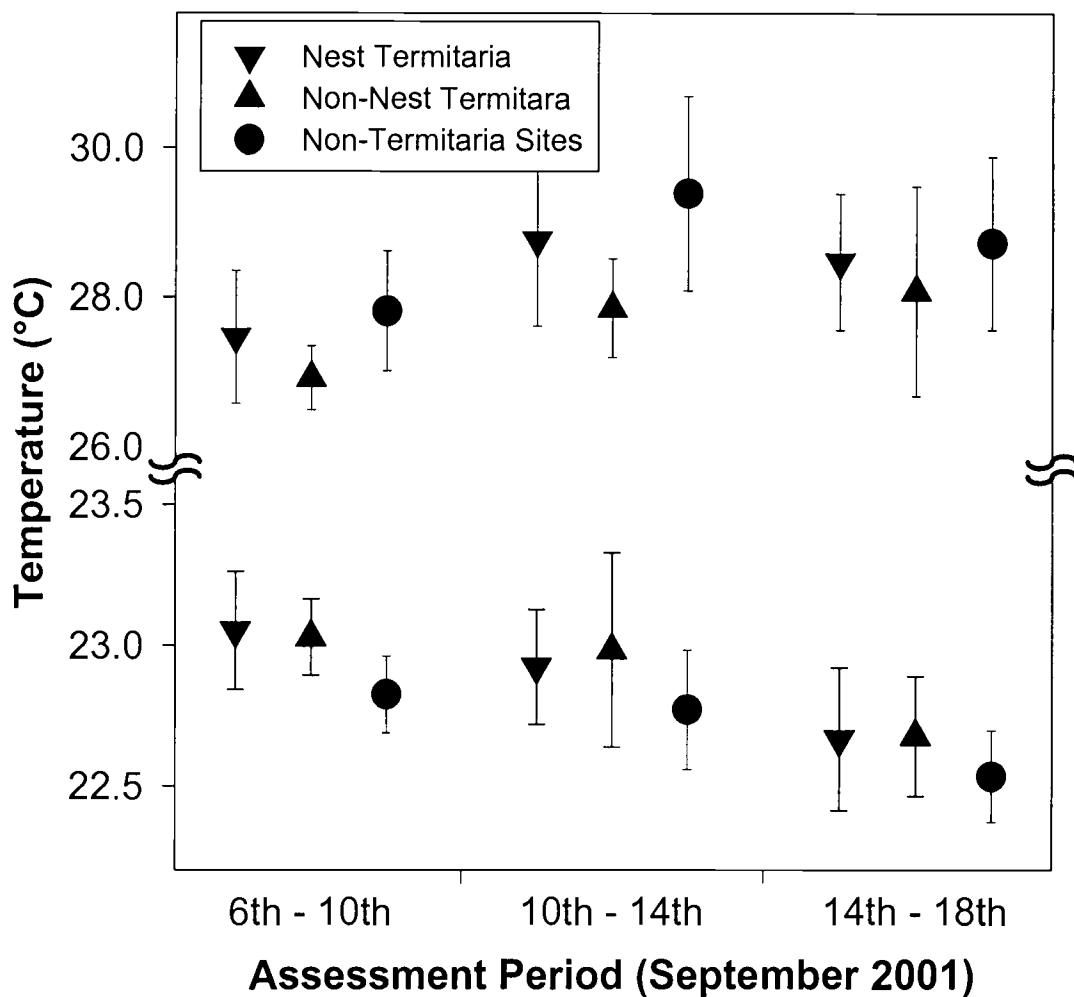


Figure 3.2. Means and SD (error bars) for average daily high and low temperatures in microhabitats surrounding nest termitaria used by Pohnpei Micronesian Kingfishers, non-nest termitaria, and random forest sites in September 2001.

3.5. DISCUSSION

3.5.1. *Temperature Characteristics of Microhabitats Surrounding Termitaria*

Results showing no significant difference in T_{max} , T_{min} , T_{flux} and % below T_{lc} do not support the hypothesis that Micronesian Kingfishers select termitaria for nesting on the basis of microhabitat temperatures. This apparent lack of temperature consideration may be related to the generally suitable temperature range of all termitaria microhabitats, limited temperature variation among termitaria microhabitats, or to the tradeoffs associated with selecting nest sites based on thermal characteristics.

Nest sites in microclimates closely aligned to the thermoneutral zone are more likely to benefit fitness and survival through conservation of metabolic energy (White and Kinney 1974). However, temperatures observed in microhabitats where both nest and non-nest termitaria occurred were generally within the thermoneutral zone for adult Micronesian Kingfishers. Observations suggest that on average, microhabitat temperature at nest and non-nest termitaria never extended above T_{uc} and only dipped below T_{lc} by $< 1^{\circ}\text{C}$ during the coolest portions of the night (24.6% of each 24 hr period; Figure 1). This statistic is similar to 25.2% found for Mallards (*Anas platyrhynchos*) but contrasts with the 50.3% observed for Blue-winged Teal (*A. dicors*; Gloutney and Clark 1997).

Interestingly, a comparison of temperatures at nest and nearby non-nest sites for these species also resulted in insignificant differences in ambient air temperature. The T_{lc} estimate for adult kingfishers is probably conservative because adjustments were not made for the insulation afforded by termitaria. If the insulation provided by termitaria were included in the allometric equation, the resulting T_{lc} would likely be lower than the minimum temperatures observed on Pohnpei, and thus suggest negligible metabolic costs associated nesting Micronesian Kingfishers, regardless of which termitaria were selected.

Even if there were slight reproductive advantages associated with the temperature characteristics of microhabitats where some termitaria occurred, there may also be tradeoffs for selecting those sites. For example, termitaria with greater exposure to sunlight might have increased average temperatures that provide a more suitable microclimate for nesting (e.g. Holway 1991, Gloutney and Clark 1997, Wiebe and Martin 1998, *but see* Colwell 1992). However, the same lack of vegetative cover that increases exposure to sunlight might also make the termitaria more vulnerable to predators and driving rainfall.

3.5.2. Thermal Characteristics of Termitaria and Non-termitaria Sites

Temperatures in microhabitats where termitaria and non-termitaria occurred were significantly different for all four metrics. Locations selected by arboreal termites for the construction of termitaria tend to be in forest areas with slightly

greater canopy development and more overhead vegetative cover than microhabitats without termitaria. This additional cover might reduce the heat gain from exposure to sunlight, or insolation, during the daytime and provide cover to reduce the amount of heat radiated from a site at night. The effects of insolation and radiative cover have been investigated previously (e.g., Calder 1974, Campbell 1977, Walsberg 1981, Weibe and Martin 1998). Calder (1973) estimated a 1-6°C difference in the temperatures of hummingbird nests with and without radiative cover and Gloutney and Clark (1997) suggested that radiative cover kept Blue-winged Teal and Mallard nest sites cool during daylight hours. Similarly, temperatures differed statistically with nest box orientation, which presumably reflects different amounts of solar heat (Hooge et al. 1999). To the contrary, some suggest that the effects of radiative cover are minor when compared to other thermal factors like convective heat loss (Walsberg 1985).

In order for microhabitat thermal differences to affect nest-site selection in Micronesian Kingfishers, the differences should be great enough to alter survival or reproductive success. However, results illustrate that estimated temperature differences between microhabitat types were extremely small ($< 1^{\circ}\text{C}$), and temperatures at all sample locations conformed closely to the thermoneutral zone for adult kingfishers. The slight temperature differences and generally amiable

temperatures suggest that nest-site selection based on microhabitat temperatures is unlikely to provide substantial reproductive benefits to Micronesian Kingfishers on Pohnpei.

3.5.3. Nest-site Selection in Micronesian Kingfishers

Aside from anecdotal descriptions (Baker 1951, Jenkins 1983, Beck and Savidge 1985, Pratt et al. 1987, Fry and Fry 1992), prior publications about the behavior of wild Micronesian Kingfishers are limited (Marshall 1989; Kesler and Haig, *in review*). Kesler and Haig suggest Micronesian Kingfishers selected nest termitaria that were larger in volume and higher from the ground than non-nest termitaria. Results presented here do not indicate that microhabitat temperatures are additionally important in either nest-site selection from among termitaria or in the apparent obligate use of termitaria for nesting.

In this and previous investigations (e.g., Gloutney and Clark 1997), microhabitat thermal characteristics were compared to the thermoneutral zone for adult birds. The use of adult thermoneutral zones for inferences was based on the assumption that incubating and brooding adults ensure eggs and nestlings are kept at optimal temperatures for development, and thereby assume all metabolic responsibilities for thermoregulation. However, simulations by Reid et al. (2002) indicate that incubating birds may not always be capable of maintaining optimal developmental temperatures, suggesting that a comparison of microclimate to optimal developmental temperatures for eggs and chicks may be worthy of

additional consideration. If optimal developmental temperatures for Micronesian Kingfisher eggs or altricial nestlings were used in this investigation, conclusions about differences in the thermal characteristics of nest and non-nest microhabitats would be unlikely to change because temperature regimes were so closely aligned at the three site types. To the contrary, conclusions about the general amenability of Pohnpei's ambient temperatures may be different if a large gap existed between the lowest temperatures observed in the Pohnpei rainforest and optimal egg and chick development temperatures. Although additional research is required to assess the distance between these temperatures, a substantial gap would suggest that birds face environmental pressure to select nest locations with suitable microhabitat thermal characteristics.

In addition to ambient temperature, others have assessed alternative nest-site selection hypotheses based on other thermal characteristics including prevailing wind, insolation, vapor pressure, and moisture (Ricklefs and Hainsworth, 1969, van Riper III et al. 1993, With and Webb 1993, McArthur 1990, Gloutney and Clark 1997). Because of their closed nest structures in the shaded Pohnpei rainforest, prevailing wind and insolation seem less likely to affect Micronesian Kingfishers than other species. However, moisture has the potential to greatly influence heat conductance (Robbins 1993), and Pohnpei's average of 473 cm of rain per year (NOAA 2001) may be detrimental to kingfishers not selecting the driest microhabitats for nesting. Because of the mud-like construction

of arboreal termite nests, they are also susceptible to extreme moisture. Thus, if the insects select drier microhabitats for termitaria construction, Micronesian Kingfishers may derive benefit from the use of the termitaria over other nest sites because of their drier microhabitats as well as general protection afforded by the termitaria.

In conclusion, results illustrate that wild adult Micronesian Kingfishers are rarely exposed to temperatures outside of their thermoneutral zone and do not support the hypothesis that nest-site selection is related to microhabitat temperatures. However, additional research is required to assess optimal temperatures for developing eggs and chicks, and the alternative microhabitat thermal characteristics such as moisture before completely rejecting hypotheses about the influence of microclimate on kingfisher nest-site selection. Finally, these results strongly suggests that captive facilities attempting to propagate Micronesian Kingfishers for conservation purposes should closely match ambient temperatures to temperatures typical of native habitats.

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4. CONCLUSIONS

In an attempt to better understand the reproductive behaviors and resource needs of endangered Micronesian Kingfishers (*Halcyon cinnamomina*), the studies presented here evaluate nest-site selection in the Pohnpei subspecies (*H. c. reichenbachii*). In chapter two, the physical and habitat characteristics of termitaria selected by nesting Micronesian Kingfishers were modeled. Because the modeling analyses were not conclusive with respect to one variable, an additional study presented in chapter three focused on the influence of microclimate on kingfisher nest-site selection. Once a nest-site selection model was identified, it was then used to determine whether the abundance of suitable nest termitaria might limit reproductive opportunities for the cooperative breeding Pohnpei Micronesian Kingfishers.

4.1. NEST-SITE SELECTION IN MICRONESIAN KINGFISHERS

Several nest-site selection models were evaluated in chapter two, each comprised of different combinations of habitat variables and each represented a different nest-site selection strategy. The top-ranked model resulting from the analysis suggested that Micronesian Kingfishers selected nest sites that were higher from the ground and larger in volume than sites that were not selected. The model is consistent with the hypothesis that the birds were selecting termitaria large enough to contain a nest cavity and termitaria occurring in sites with reduced risks

of predation. Predation has long been identified as a major component influencing the evolution of nest-site selection (Ricklefs 1969, Martin 1992) and the adaptive benefit of elevated nest placement has been previously described (Austin and Singer 1985 *from* Gill 1990, Li and Martin 1991).

Results presented in chapter two suggested some support for the importance of microclimate in nest-site selection by Micronesian Kingfishers, so chapter three directly evaluates the importance of microhabitat thermal characteristics. Nest placement differences in response to microclimate have previously been identified for other species (Ricklefs 1969, Martin 1992, Sheldon and Winkler 1999 and others), so it was hypothesized that if temperatures were important to nesting Micronesian Kingfishers, there would be differences in the thermal characteristics of nest and non-nest microhabitats. Although differences were identified in the thermal characteristics microhabitat where termitaria occur and microhabitats without termitaria, the magnitude of the difference was not biologically significant. However, results suggested that nearly all sites in the Pohnpei rainforest exhibit amenable thermal characteristics for adult Micronesian Kingfishers, an important finding with respect to captive management.

4.2. COOPERATIVE BREEDING AND NEST-SITE LIMITATION

Micronesian Kingfishers are a cooperative breeding species, meaning that non-parent individuals assist in the reproductive attempts of others. Many researchers have asked why cooperative behaviors occur, and in at least some

situations, cooperation seems to be an evolutionary adaptation to limited resources that are necessary for reproduction (Emlen 1982, Brown 1987, Stacey and Koenig 1990, Koenig et al. 1992, Ligon 1999, Hatchwell and Komdeur 2000). To determine if suitable nest sites might limit reproductive opportunities in Micronesian Kingfishers, termitaria available on the three study areas were evaluated with the nest-site selection model described above. Results suggested that even though most termitaria did not have the height and volume characteristics selected by Micronesian Kingfishers, suitable termitaria were not limited in number. Therefore, results do not support the hypothesis that reproductive opportunities for Pohnpei Micronesian Kingfishers are limited by the abundance of suitable termitaria.

4.3. CONSERVATION IMPLICATIONS

In conclusion, termitaria with characteristics similar to those selected by Pohnpei Micronesian Kingfishers do not appear to be limited in abundance and therefore seem unlikely to limit breeding opportunities. Micronesian Kingfishers selected higher and larger termitaria for nesting. The birds do not appear to choose nest sites from among termitaria based on microclimate characteristics, proximity to forest edge or foraging areas, or termitaria placement on tree stems.

For the captive population of endangered Guam Micronesian Kingfishers, these results underscore the importance of providing nesting substrate that is large in volume and high from the ground. Additionally, temperature observed in the

Pohnpei rainforest seemed unlikely to cause physiological stress. Therefore, captive breeding facilities should maintain temperatures well within the thermoneutral zone of the Micronesian Kingfishers.

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