AN ABSTRACT OF THE DISSERTATION OF

Dylan Charles Kesler for the degree of Doctor of Philosophy in Wildlife Science presented on December 19, 2005.

Title: Population Demography, Resource Use, and Movement in Cooperatively Breeding Micronesian Kingfishers

Abstract approved:

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Susan M. Haig

Island systems and species are susceptible to extinction because of their small

population size and an ecological naiveté from an evolutionary past lacking strong

competition and predation. For example, only one-fifth of the world's bird species

occur on islands, yet more than 90% of the avian extinctions witnessed during

historic times were island forms. Introduced predators and competitor species are

among the major conservation issues facing insular systems. On the island of

Guam, brown tree snakes (*Boiga irregularis*) are responsible for the local

extinction of twelve native forest birds. The endangered Guam Micronesian

Kingfisher (*Todiramphus cinnamominus cinnamominus*) is one of the species

affected by the introduced snake, as the bird remains only in captive breeding

institutions on the U.S. mainland. In addition to Guam, the islands of Pohnpei and

Palau host endemic subspecies of Micronesian Kingfisher (*T. c. reichenbachii* and *T. c. pelewensis* respectively) that are similarly threatened with extinction.

Previous investigations into the behavioral ecology of the Pohnpei subspecies of Micronesian Kingfisher yielded observations of cooperative social behaviors. Over the past three decades, much research has focused on cooperatively breeding species, which are commonly characterized by non-breeding individuals that delay dispersal and assist others with reproduction. Research addressing cooperative breeding suggests that the behavior is a complex response to interacting factors including life history characteristics, demography, resources, movement, and behavior.

The dearth of information available about critically endangered Micronesian Kingfishers, combined with their potential to provide new insights into cooperative social behaviors, inspired the research presented in this dissertation. The aims were two-fold; results were intended to bolster our understanding of cooperative social behaviors while simultaneously providing vital information to conservation practitioners. Methodology for determining the sex of study individuals is presented in chapter two, which facilitated investigations that followed.

Chapter three addressed the interaction between kingfishers and resources at both the landscape and home range scale. Higher population densities are associated with lowland mangrove, marsh forested habitats, and open vegetation types at the landscape scale. Results further indicated that at the home range scale,

birds selectively used late succession forested habitats in higher proportions than their availability, and forest areas were entirely utilized in study areas where territories were packed boundary-to-boundary. Together these suggested that forested areas and the resources they contain might be limited for Micronesian Kingfishers.

Movement and space use in Micronesian Kingfishers were the focus of chapter four. Within territories, the home ranges of birds overlapped, although not entirely. Birds of all ages and social classes made extraterritorial prospecting movements, but they appear to serve different functions. Juveniles and helpers were observed dispersing from natal areas, but only after repeated extraterritorial homesteading movements. The timing and destinations of adult prospecting suggested that the behavior might provide opportunities for covert reproduction.

Population demography was addressed in chapters five and six, which concluded with the development of a population projection model that will be useful in kingfisher conservation efforts throughout the Pacific. Nestlings on cooperative territories had higher estimated survival rates than those on pair territories. Further, the timing of nestling disappearances and a modified nestling mandible suggested that mortalities were caused by siblicidal nest-mates. In chapter six, post-fledging vital rates were estimated for Micronesian Kingfishers and a population projection matrix model was developed. Vital rate parameters were then varied, and the model was used in a simulation analysis to evaluate the apparent influence of each parameter on population dynamics across a range of

potential values. The exercise was intended to lend insight into the dynamics of Micronesian Kingfisher populations and to form a base model for management of the other eleven endangered Pacific *Todiramphus* species.

In summary, information presented in this dissertation lends insight into factors important to understanding population demography, resource use, and movement in cooperatively breeding Micronesian Kingfishers. Results illustrate that, like other cooperatively breeding species, the birds on Pohnpei are highly territorial and dispersal options may be limited by territory vacancies and forest resources. Extraterritorial prospecting movements have been observed in many cooperative species, and these results illustrate that they may serve multiple purposes. Siblicide is also a phenomenon present in resource-limited species and its occurrence in Pohnpei Micronesian Kingfishers underscores the importance of resources to the evolutionary history of the birds. Results from demographic analyses and modeling suggest that conservation efforts for Micronesian Kingfishers, and the other eleven *Todiramphus* species, should be broadly focused on all life history stages.

POPULATION DEMOGRAPHY, RESOURCE USE, AND MOVEMENT IN
COOPERATIVELY BREEDING MICRONESIAN KINGFISHERS

by
Dylan Charles Kesler

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APPROVED:

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Major Professor, representing Wildlife Science

_____

Head of the Department of Fisheries and Wildlife

_____

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Dylan Charles Kesler, Author

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CONTRIBUTION OF AUTHORS

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TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF TABLES

LIST OF TABLES (continued)

This dissertation is dedicated to my parents

for their enthusiasm and support.

**POPULATION DEMOGRAPHY, RESOURCE USE,
AND MOVEMENT IN COOPERATIVELY BREEDING
MICRONESIAN KINGFISHERS**

1. INTRODUCTION

1.1. ISLANDS

Studies of insular biota have profoundly influenced our understanding of the

biological world. Islands are simpler microcosmic versions of their larger

continental counterparts, and as such, investigations of insular fauna and the

processes underlying island ecosystems have inspired some of the most

fundamental theories in ecology. Experiments on island community structure

(Simberloff and Wilson 1968, Komdeur 1994, Komdeur and Pels 2005), natural

and human-caused changes and catastrophes (van Riper et al. 1986, Savidge 1987,

Steadman 1989, Steadman 1995), and evolutionary time (Darwin 1859, Wallace

1881, Grant 2001) have become the backbone of modern ecology. 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.

Insular systems and species are highly susceptible to extinction (Moors 1993). Both stochastic and deterministic forces greatly affect island populations because of their small size and an ecological naiveté from an evolutionary past often lacking competition and predation (King 1993). Although some refute the assertion that insular species are predisposed to extinction (Simberloff 1995), staggering losses of biodiversity have led most to conclude otherwise (MacArthur and Wilson 1967, Myers 1983, Steadman 1989, Johnson and Stattersfield 1990, Wiles et al. 2003). For example, only one-fifth of the world's bird species occur on islands, yet more than 90% of the avian extinctions witnessed during historic times were island forms (Johnson and Stattersfield 1990). Nonetheless, extinctions are also occurring on continents and there is the possibility that islands are simply exaggerated versions of a catastrophe yet to unfold among continental biota.

The effects of introduced alien species are among the major conservation issues currently facing island systems (Elton 1958, Carlquist 1974, Drake et al. 1989, Brown 1989, Richardson 1992, Atkinson 1993, D'Antonio and Dudley 1995). Guam's experience with introduced brown tree snakes (*Boiga irregularis*) is an oft-cited example of a catastrophe caused by an invasive species (Savidge 1984, Savidge 1987, Engbring and Fritts 1988, Reichel et al. 1992, De Bell and Whitesell 1993, Wiles et al. 2003). The snakes severely affected seventeen of eighteen native birds, and twelve were likely extirpated as breeding residents (Wiles et al. 2003).

1.2. THE MICRONESIAN KINGFISHER

The Guam Micronesian Kingfisher (*Todiramphus cinnamominus cinnamominus*) is one of the species affected by the introduced brown tree snake. Kingfisher populations declined over several decades, and threats to the birds were finally recognized in 1984 when they were listed as endangered (U.S. Fish and Wildlife Service 1984). Twenty-nine individuals were subsequently captured and placed in a captive breeding program in U.S. institutions as they went extinct in the wild (reviewed in Haig and Ballou 1995, Bahner et al. 1998). Attempts to breed the birds in captivity have met with limited success since that time and fewer than 80 individuals are currently extant (B. Bahner, personal communication, August 2005).

Reasons for the stymied breeding program are not altogether clear, but some have suggested that a lack of knowledge about nutrition, microclimate, nesting resources, and breeding behavior have been hindrances (Bahner et al. 1998, Baltz 1998, Kesler 2002, Kesler and Haig 2004, Kesler and Haig 2005a, Kesler and Haig 2005b). Few publications addressed the birds before their extinction from the wild, so those charged with the kingfisher's recovery had little information upon which to base management. The Micronesian Kingfishers were known to occupy mature forest, agricultural forest, mangrove, and open habitat before their demise (Marshall 1949, Jenkins 1983, Pratt et al. 1987). They nested in tree cavities or

cavities excavated from the soft material of arboreal termite nests, or termitaria (Marshall 1989).

In addition to the Guam Micronesian Kingfisher, the islands of Pohnpei and Palau also host endemic subspecies (*T. c. reichenbachii* and *T. 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 extant Micronesian Kingfisher subspecies are similar to Guam kingfishers in that recent information indicates drastic population declines (63% on Pohnpei, Buden 2000). Despite the fact twelve of the twenty-one members of the genus *Todiramphus* are threatened or in danger of extinction (Clemets 2000, IUCN 2004), there is little information to draw from related species because they have received so little research focus.

1.3. COOPERATIVE BREEDING

In 1998, an investigation into the behavioral ecology of the Pohnpei subspecies of Micronesian Kingfisher was initiated to facilitate conservation and recovery efforts for Micronesian Kingfishers and other Pacific *Todiramphus* species. Initial work focused on various aspects of their life history because so little had been published about the birds previously. Observations of cooperative social behaviors, which occur when individuals put themselves at risk for the benefit of others, were among the most interesting collected during the early phases of the project. They led to

several investigations into the relationship between nesting resources and social behaviors in the birds (Kesler 2002, Kesler and Haig 2005a, Kesler and Haig 2005b).

Over the past three decades, much research has focused on cooperatively breeding species, which are commonly characterized by non-breeding individuals that delay dispersal and assist others with reproduction (*for review see* Brown 1987, Stacey and Koenig 1990, Stacey and Koenig 1990, Stacey and Koenig 1990, Ligon 1999, Koenig and Dickinson 2004). While there are examples of cooperative breeding throughout the world, and in taxonomic groups as diverse as ants (order Hymenoptera; Reeve and Ratnieks 1993) and hawks (e.g., *Buteo galapagoensis*; Faaborg and Bednarz 1990), the behavior remains relatively rare among vertebrates. Brown (1987) surveyed the literature and concluded that approximately 2.5% of birds were cooperative breeders.

Researchers have studied why non-parents, often referred to as helpers, delay reproduction for what appears to be the benefit of others. Several generalized pathways to increased fitness have been identified. For helpers, delayed dispersal is thought to be associated with a combination of ecological factors. The *ecological constraints hypothesis* (Emlen 1982, Ligon 1999, Perrin and Lehmann 2001) suggests that potential dispersers cannot depart because of environmental limitations in resources necessary for reproduction, including territories (i.e., *habitat saturation hypothesis*; Selander 1964, Brown 1974, Gaston 1978, Stacey

1979, Emlen 1982). By delaying dispersal, the non-breeding individuals are also poised to inherit resources in their immediate vicinity (e.g., Komdeur 1994). If the delay results in the eventual inheritance of natal or nearby territories containing superior resources, the benefit of waiting may come to fruition with increased lifetime reproductive success (i.e., *benefits of philopatry hypothesis*; Stacey and Ligon 1987, Stacey and Ligon 1991).

Delayed dispersers might also derive fitness benefits from helping with the reproductive attempts of others. These "helpers" are frequently closely related to dominant individuals and can therefore receive indirect fitness benefits from raising siblings (i.e., *kin selection theory*; Hamilton 1964, McCarthy et al. 2001; e.g., Whittingham et al. 1997, Langen and Vehrencamp 1999). Studies using molecular tools (see Hughes 1998) have provided evidence that helpers also receive occasional opportunities for reproduction (e.g., Rabenold et al. 1990, Beck 1990, Keller and Reeve 1994, Richardson et al. 2001). Distribution of reproduction among group members is a relatively recent finding for most cooperatively breeding species, so the mechanisms controlling the so-called reproductive "skew" remain a topic of debate (Koford et al. 1990, Vehrencamp 1993, Keller and Reeve 1994, Whittingham et al. 1997, Johnstone and Cant 1999, Keller and Chapuisat 1999, Clutton-Brock et al. 2001, Haydock et al. 2001, Cant and Reeve 2002).

1.4. OBJECTIVES

Research addressing cooperative breeding suggests that the behavior is a complex

response to interacting factors including life history characteristics, demography,

landscape resources, movement, and behavior. An understanding of these same

factors is paramount to successful conservation management for any species. The

dearth of information available about critically endangered Micronesian

Kingfishers, combined with their potential to supply new insights into cooperative

social behaviors, inspired the research presented herein. The goal of this

dissertation is therefore two-fold; results are intended to provide vital information

to conservation practitioners while simultaneously bolstering our understanding of

cooperative social behaviors.

The studies summarize data collected during six field seasons and more

than twenty-four months of fieldwork on the island of Pohnpei. Challenges were

omnipresent since the beginning in 1998. For example, simply discerning the sex

of study birds was one of the initial challenges because so little was published

about the Pohnpei Micronesian Kingfishers. Morphological measures and tissue

samples were collected throughout fieldwork with the hope that they would be

useful for deriving methodology for sex determination. In the second chapter, I

present results from quantitative and molecular analyses of these data.

Information about how individuals interact with landscape resources is

paramount to both understanding factors underlying cooperative behaviors and to

conservation management. The third chapter discusses the relationship between landscape vegetation structure and the distribution of Micronesian Kingfishers on Pohnpei. Additionally, interactions between individuals and vegetation resources are addressed at the home range scale, and comparisons are made between resources on cooperative and pair-breeding territories. Since delayed dispersal is a behavior at the heart of cooperative breeding theory, understanding movement is fundamental to investigations of cooperative social behaviors. The study of distribution and dispersal in cooperative and pair-breeding kingfishers is the focus of the fourth chapter, which presents radio telemetry data and results in a comprehensive representation of kingfisher movement.

Population demography provides direct insights into the factors influencing individual fitness and underlying evolutionary theory. Thus, the fifth and sixth chapters address the demographic characteristics of Micronesian Kingfishers. Chapter five investigates nestling survival in Micronesian Kingfishers. During analyses, results suggested that there were profound differences in nestling survival on cooperative and pair territories and patterns of mortality and morphological characteristics indicated that aggression between brood-mates was an important force to consider. Chapter six also addresses demography in Micronesian Kingfishers by presenting additional vital rate analyses and using results to structure a population projection matrix model. The model is then perturbed in

simulation analyses to evaluate its potential utility to other endangered

kingfishers in Oceania.

Micronesian Kingfishers are but one of many cooperative breeders, and

they are only one of the hundreds of endangered insular birds. Chapter six

summarizes results and the broader implications of this work. Suggestions are also

made as to where additional investigations might further clarify the information

presented here.

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2. SEX DETERMINATION IN POHNPEI MICRONESIAN KINGFISHERS USING MORPHOLOGICAL AND MOLECULAR GENETIC TECHNIQUES

2.1. ABSTRACT

Conservation-oriented investigations of Micronesian Kingfishers (*Todiramphus cinnamominus*) have been hindered by a lack of basic natural history information, despite the Guam subspecies' (*T. c. cinnamominus*) status as one of the most endangered species in the world. I used tissue samples and morphometric measures from museum specimens and wild-captured Pohnpei Micronesian Kingfishers (*T. c. reichenbachii*) to develop methods for sex determination. I present a modified molecular protocol and a discriminant function that yields the probability that a particular individual was male or female. Results indicated that females were significantly larger than males, and the discriminant function correctly predicted sex in 73% (30/41) of the individuals. Eighty-six percent (18/21) of individuals were correctly assigned sex when a moderate reliability threshold was set. Sex determination through molecular genetic techniques was more reliable than methods based on morphology. Results will facilitate recovery efforts for the critically endangered Guam Micronesian Kingfisher and provide a basis for sex determination in the 11 other endangered congeners in the Pacific.

2.2. INTRODUCTION

Three subspecies of the Micronesian Kingfisher (*Todiramphus cinnamominus*)

have been described from the islands of Guam (*T. c. cinnamominus*), Pohnpei (*T. c.*

reichenbachii), and Palau (*T. c. pelewensis*). The Guam birds are extinct in the

wild (Haig and Ballou 1995, Bahner et al. 1998, U.S. Fish and Wildlife Service

2004), drastic declines have been observed on Pohnpei (63%, Buden 2000), and

little is known about the status of the Palau kingfishers. The Pohnpei Micronesian

Kingfishers represent a wild population that has been used for surrogate studies to

address knowledge-gaps and facilitate recovery efforts for all three subspecies

(*e.g.,* Kesler and Haig 2004, U.S. Fish and Wildlife Service 2004). However,

recent and ongoing investigations of distribution, resource use, behavior, and

movement have been stymied by a lack of natural history information and research

tools. A means for sex determination is among the field research methods

desperately needed for the Pohnpei and Palau subspecies of Micronesian

Kingfisher, which do not exhibit sexually dimorphic plumages (Pratt et al. 1987,

Fry et al. 1992).

Our goal was to facilitate field investigations and conservation-oriented

research by providing methods for sex determination in the Pohnpei Micronesian

Kingfisher. I used tissue samples and morphological measures from museum

specimens and wild-captured birds to test a new protocol for molecular genetic

sexing based on polymerase chain reaction (PCR) of the chromo-helicase-DNA

binding (CHD) gene. Sex results from molecular methods were then

used in combination with multiple measures for museum specimens and wild-

captured birds to derive a discriminate function for sex determination.

2.3. METHODS

Micronesian Kingfishers were investigated on three study areas on the island of

Pohnpei, Federated States of Micronesia, which have been extensively described

elsewhere (Kesler 2002, Kesler and Haig 2005a, Kesler and Haig 2005b). Birds

were captured in mist nets between February and July 1999, March and August

2000, September 2001, September 2002 and January 2003, October and November

2003, and September 2004. Age was determined using breast, belly, and vent

plumage coloration, with adults displaying white underparts and juveniles showing

rufous (Pratt et al. 1987, Fry et al. 1992). Yearlings and juveniles were also

characterized by slight rufous coloration in the flanks, although they were primarily

white throughout the belly and vent (D. Kesler, unpublished data). Tarsus length,

exposed culmen, and wing cord were measured during each capture. Each bird was

weighed using a 100 g hanging pesola scale and approximately 0.1 cc of blood was

drawn from the ulnar vein using a 27-gauge needle. Blood was immediately placed

in storage buffer (100 mM Tris-HCl pH 8.0, 100 mM EDTA, 10 mM NaCl, and

0.5% SDS) and frozen. Morphological measurements were also recorded from

museum specimens at the American Museum of Natural History. D.

Kesler recorded all morphological measures.

2.3.1. Molecular sex determination

I simplified a previously described protocol for sex determination in multiple avian

species (Jensen et al. 2003) by excluding the DNA extraction step and by using

different reagents. DNA was obtained from whole blood stored in buffer following

Khatib and Gruembaum (1996). Approximately 10µl of red blood cells were

disrupted after boiling for 10 min in 12µl of 50mM NaOH at 99ºC. The solution

was neutralized using 22µl of Tris-HCl 1M pH 8.0 and diluted by adding 1:3 (v/v)

proportion of sterile water. This suspension was boiled at 100ºC for 10 min and

used as source DNA.

Fragments of genes CHD-Z and CHD-W located on the avian sex

chromosomes were amplified using the primers P2 and P8 (Griffiths et al. 1998).

The PCR amplification was performed in a final reaction volume of 10µl

containing 1.5 µl of DNA suspension, 1 x PCR buffer (Promega), 3.5 mM $MgCl_2$,

25 mM each dNTP, 25 µg/ml bovine serum albumin (BSA), 0.4 µM each of

primers P2 and P8, and 1 unit of Taq polymerase (Promega). The thermal cycling

program follows: 3 min at 95ºC (denaturation); 35 cycles of 30 sec at 94ºC, 30 sec

at 52ºC, 45 sec at 72ºC (amplification), and 5 min at 72°C (final extension). Sex

was identified through a 1.5% agarose gel electrophoresis visualized using

ethidium bromide. PCR product produced a single band in males

(derivate from the Z chromosome) and two bands in females (Z and W fragments

being amplified). Although previous results indicate the reliability of sex

determination through molecular techniques (Jodice et al. 2000), I repeated

analyses on six samples to ensure accuracy.

2.3.2. *Morphometric analyses*

Morphological analyses were conducted using museum specimens and wild-caught

adult Pohnpei Micronesian Kingfishers. Results from genetic analyses were used

to determine sexes for wild-caught individuals. The sexes of museum birds were

taken from specimen tags. Differences in mean measures of weight, flattened wing

cord, exposed culmen, and tarsus length (Baldwin et al. 1931) were evaluated using

t-tests. Logistic regression was then used in a discriminate function analysis of

morphological characteristics of adult Micronesian Kingfishers to evaluate sex

differences in linear combinations of interval variables. Only data from wild-

caught kingfishers without missing measures were included. Morphological data

were entered into Statistical Analysis Software (SAS SAS Institute 1999) and a

linear combination of morphological measures was fitted to sex using binomial

logistic regression. Once the model equation was developed, it was tested on all

sampled kingfishers, including the subset that had not been used in the derivation

of the equation because of missing weight measures on museum specimens. Unless

otherwise noted, metrics were reported as means $\pm$ (SD), and differences were considered statistically significant at $\alpha < 0.05$.

2.3. RESULTS

Pohnpei Micronesian Kingfisher blood samples ($n = 66$) analyzed with molecular methods showed the expected pattern of two bands in females and one band in males. The size and base pair (bp) difference between the two amplified CHD fragments were similar to those reported for Guam Micronesian Kingfishers (Z-band = 350bp and W-band = 400bp; Jensen et al. 2003). I did not observe unspecific band amplification. To test the reliability of the molecular method, samples collected from the same individuals on different capture occasions were evaluated simultaneously. All six pairs of repeated samples resulted in identical outcomes, verifying reliability of the method.

Morphological measures were assessed for 60 wild-caught and 29 museum specimens of Pohnpei Micronesian Kingfishers. Male Pohnpei Micronesian Kingfishers appeared to be smaller than females because they were significantly lighter, had shorter wing cords, and there was suggestive evidence that their culmen lengths were shorter (Table 2.1). I collected complete measurement data for 41 of the study specimens. Weight measures were missing for the 29 museum specimens and 19 wild-caught individuals were also missing data. The discriminant function resulting from the logistic regression analysis follows:

$$\ln\left(\frac{\pi_i}{1-\pi_i}\right) = 35.34 - 0.07(\text{wing cord}_i) - 0.72(\text{tarsus}_i) - 0.06(\text{culmen}_i) - 0.19(\text{weight}_i)$$

By including all four morphological characters, the mean response of males and females is significantly different (Type III test; P-value = 0.02) and negative parameter estimates also verify that males are smaller than females. The discriminant function can also be solved for π to yield the probability that a particular individual is a male:

$$\pi_i = \frac{e^{(35.34 - 0.07(\text{wing cord}_i) - 0.72(\text{tarsus length}_i) - 0.06(\text{culmen length}_i) - 0.19(\text{weigh}_i))}}{1 + e^{(35.34 - 0.07(\text{wing cord}_i) - 0.72(\text{tarsus length}_i) - 0.06(\text{culmen length}_i) - 0.19(\text{weigh}_i))}}$$

where morphometric measures for individual i are used, and π_i is the probability that the bird is male. The discriminant function correctly predicted the sex of 73% (30/41) of the birds from the set used to derive the equation. Accuracy increased as predicated values approach the extremes of 0 and 1, which is illustrated by an improvement in accuracy to 86% (18 of 21) for the sex of the individuals with $\pi_i <$ 0.30 and > 0.70.

Table 2.1. Results of *t*-tests comparing morphological measures from male and female Pohnpei Micronesian Kingfishers, sampled in the American Museum of Natural History (AMNH) and Pohnpei, Federated States of Micronesia.

Metric	Sample Origin			Mean and Standard Error		
	AMNH	Pohnpei	N(M/F)	Male	Female	*P*-value
Culmen (mm)	28	58	43/43	41.4 (0.2)	42.0 (0.3)	0.07
Tarsus (mm)	27	45	34/38	18.2 (0.2)	18.5 (0.3)	0.20
Wing Cord (mm)	28	57	42/43	99.1 (0.5)	101.0 (0.7)	<0.01
Weight (g)	0	54	27/27	61.8 (0.9)	66.7 (1.3)	<0.001
TOTAL	29	60	46/46	--	--	--

2.4. DISCUSSION

Pohnpei Micronesian Kingfishers exhibited reverse size dimorphism, in that males were smaller than females. Result illustrated that females weighed more than males, had significantly longer wing cords, and longer culmens. Additionally, the negative parameter estimates and statistical significance of the discriminant function provided further evidence that males were smaller than females. Reverse size dimorphism has also been documented in Laughing Kookaburras (*Dacelo novaeguineae*; Legge 2000b). Laughing Kookaburras are also in the family Alcedinidae, and their cooperative breeding system is similar to that in Pohnpei Micronesian Kingfishers (Legge 2000a, Kesler 2002), which suggests that similar evolutionary forces may underlie size dimorphism in these birds. Legge (2000a)

hypothesized that the size difference may give female kookaburra

nestlings an advantage in a species with extreme sibling aggression.

Despite the statistical differences in mean measures, distributions

overlapped substantially for all metrics. This prevented intuitive determinations of

sex during fieldwork and necessitated other methods. Single morphological traits

can provide useful tools for determining the sex of an individual in other species

(e.g., Zavalaga and Paredes 1997), but none of the individual metrics that I

assessed provided a reliable means for sex determination in Pohnpei Micronesian

Kingfishers. As a linear combination, however, the four characteristics of culmen

and tarsus lengths, wing cord, and weight resulted in a useful discriminant function

for sexing birds in the field. The discriminant function's reliability may also be

enhanced through additional sampling and the inclusion of alternate morphological

metrics.

Despite the utility of the discriminant function, results indicated that the sex

of Pohnpei Micronesian Kingfishers was most reliably determined using molecular

genetic techniques. Results confirmed the wide applicability of the primers P2 and

P8 described by Griffiths et al. (1998). Furthermore, the modified avian blood

DNA extraction protocol provided a simplified and low-cost method for obtaining

high-yield and high-quality DNA.

With the simplification of molecular methods and recently increased

numbers of commercial and research laboratories, molecular sexing is now

available to most field researchers for low costs. Blood and feather

samples can be sent from study sites using overnight mail, and sexing results can

typically be accessed by telephone or internet within two days. Given the

importance of accurate sex determination to most research projects, captive

breeding programs, and conservation efforts such as translocations and

reintroductions, the use of molecular sexing techniques currently seems

underutilized.

2.5. ACKNOWLEDGEMENTS

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3. MULTI-SCALE RESOURCE USE AND SELECTION IN COOPERATIVELY BREEDING MICRONESIAN KINGFISHERS.

3.1. ABSTRACT

Information about interactions between behavior and landscape resources is key to understanding ecology and directing conservation management for endangered species. I studied multi-scale occurrence, habitat use, and resource selection in a cooperatively breeding population of Micronesian Kingfishers on the island of Pohnpei. At the landscape level, point transect surveys were conducted throughout the island and results indicated that kingfisher detection frequencies were higher than those reported in 1994, although they remained 15% to 40% lower than 1983 indices. Integration of spatially explicit vegetation information with survey results indicated that kingfisher detections were positively correlated with the amount of wet forest and grass-urban vegetative cover and negatively associated with agricultural forest, secondary vegetation, and upland forest cover types within 250 m of observers. At the home range scale, radio telemetry and remote sensing were used to assess vegetative cover utilized by individual kingfishers on three study areas. A comparison of resources in Micronesian Kingfisher home ranges with those in randomly placed polygons illustrated that birds used more forested areas than were randomly available. Further, the home ranges of kingfishers in cooperative groups included more forested area than those in pairs. Study areas

were saturated with territories, which suggests that forest resources are

limited for Micronesian Kingfishers on Pohnpei, and therefore might play a role in

maintaining delayed dispersal. Results also provide useful information to

conservation practitioners working to restore Micronesian Kingfishers to native

ranges on the island of Guam where they are currently extinct, as well as those

managing bird populations on the islands of Pohnpei and Palau.

3.2. INTRODUCTION

Three subspecies of Micronesian Kingfisher occur on the islands of Guam

(*Todiramphus cinnamominus cinnamominus*), Pohnpei (*T. c. reichenbachii*), and

Palau (*T. c. pelewensis*) and all are facing perilous conservation situations. The

Guam Micronesian Kingfisher is among the most endangered species in the world,

as it is extinct in its native range (Haig and Ballou 1995) and now exists only as a

captive population of fewer than 90 birds (Bahner et al. 1998; B. Bahner, personal

communication, August 2005). The Micronesian Kingfisher population on Pohnpei

has declined drastically over the last two decades (63%; Buden 2000) and the status

of the Palau population remains unclear.

Despite their dire conservation status, little research has addressed even the

most basic natural history characteristics of Micronesian Kingfishers. Early

publications include mostly anecdotal descriptions (Stophlet 1946, Marshall 1949,

Baker 1951, Baker 1951, Jenkins 1983, Fry et al. 1992) and observations from the

last breeding pairs on Guam (Beck and Savidge 1985, Marshall 1989,

Haig and Ballou 1995, Haig et al. 1995). Several studies addressed aspects of the

captive breeding program for the Guam subspecies (Baltz 1998, Kesler and Haig

2004, Sanchez and Murray 2005) and nest site selection in the wild (Marshall 1989,

Kesler 2002, Kesler and Haig 2005a, Kesler and Haig 2005b). Additionally,

investigators have assessed movement and territoriality (Kesler and Haig *in review

a*), reproductive success and demography (Kesler and Haig *in review b*, Kesler and

Haig *in review c*), and morphological and genetic methods for sex determination

(Kesler et al. *in review*) in the Pohnpei subspecies.

Knowledge about habitat selection and use can be vital to conservation

efforts for endangered species, but this information is not available in many cases.

For example, those working to reintroduce Guam Micronesian Kingfishers back to

their native range are hindered by a severe lack of information about the birds'

habitat requirements. Many tropical islands in the Pacific share similar "strand

forest" vegetation communities (Glassman 1952, Mueller-Dombois and Fosberg

1998), but areas hosting Micronesian Kingfishers are among the largest and most

ecologically complex of the Micronesian islands. Surveys have shown that

Micronesian Kingfisher densities vary greatly among regions and vegetation types

on the islands they inhabit (Engbring and Ramsey 1984, Engbring et al. 1990,

Buden 2000), which suggests that particular habitat features may provide

differential resources.

Resources also have the potential to strongly influence social and breeding behavior. For example, among cooperatively breeding species the *ecological constraints hypothesis* (Emlen 1982; for review see Brown 1987, Ligon 1999, Hatchwell and Komdeur 2000, Perrin and Lehmann 2001, Koenig and Dickinson 2004) suggests that potential dispersers do not depart from natal areas because of environmental limitations in resources necessary for successful reproduction (i.e*., habitat saturation hypothesis*; Selander 1964, Brown 1974, Gaston 1978, Koenig and Pitelka 1981; e.g., Walters et al. 1992). The *benefits of phylopatry hypothesis* (Stacey and Ligon 1991) further suggests that delayed dispersers remain on natal areas to inherit parental resources or resources in surrounding territories. Despite the close theoretical tie between resources and cooperative social behaviors, however, logistic restraints have led to only a few empirical evaluations of resources used by cooperative breeders (see Walters et al. 1992, Clarke and Fitz-Gerald 1994, Burt 1996, Langen and Vehrencamp 1998, Hale et al. 2003, Carmen 2004).

Recently, cooperative breeding was described in Pohnpei Micronesian Kingfishers when groups of three adults were observed participating in nest construction, nest site defense and territorial defense, and when young delayed dispersal for multiple years (Kesler 2002, Kesler and Haig 2005b). Micronesian Kingfishers exemplify what may be the most common form of cooperative breeding, where several individuals socialize as a group and work cooperatively

during reproductive attempts (Kesler and Haig *in review a*, Brown 1987,

Stacey and Koenig 1990, Ligon 1999). Dominant individuals exhibit a majority of

the mating behaviors, while helpers remain close by and assist with parental care

and nest and territorial defenses.

Johnson (1980) defined resource selection at four scales, including the

geographic, landscape, home range and microsite scales. Here, I assess

Micronesian Kingfisher occurrence, habitat use, and selection at two of these scales

(2nd and 3rd order scales; Johnson 1980). At the landscape scale, I evaluated the

relationship between kingfisher occurrence and vegetative cover throughout the

island of Pohnpei using point transect surveys and spatially referenced vegetation

coverages. These data allowed me to compare detection frequencies with previous

surveys and assess the relationship between kingfishers and vegetative cover. At

the home range scale, I assessed resource selection using remote sensing data and

movement information from Micronesian Kingfishers marked with radio telemetry.

3.3. METHODS

3.3.1 Study area

Research was conducted on the island of Pohnpei, Federated States of Micronesia

(6º52' N, 158º13' E; Fig. 1). Pohnpei is a circular 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. Transect surveys were conducted

throughout the island and in all elevation zones. Telemetry work occurred

primarily at three locations, the Ranch (6º57' N, 158º12' E), College of Micronesia

(COM; 6º54' N, 158º9' E), and Palikir (6º55' N, 158º9' E) study areas.

Characteristics of the island and study sites are addressed extensively below and

they have been described elsewhere (McClean et al. 1998, Buden 2000, Kesler

2002, Kesler and Haig 2004, Kesler and Haig 2005a, Kesler and Haig 2005b).

3.3.2 Landscape scale

Point transect surveys were used in combination with vegetation coverage

information to model the relationship between Micronesian Kingfisher occurrence

and landscape features. During the middle portion of the 2002 breeding season for

Pohnpei Micronesian Kingfishers (April and May), observers traversed 20 transect

routes and conducted 184 point-transect surveys (Buckland et al. 1993). Transects

were distributed throughout the island and they occurred at all elevations (Figure

3.1). Along each transect route, surveys were conducted at locations separated by

>200 m, which were determined using global positioning systems (GPS; Garmin

Ltd., Olathe, Kansas). Observers recorded visual observations or calls of
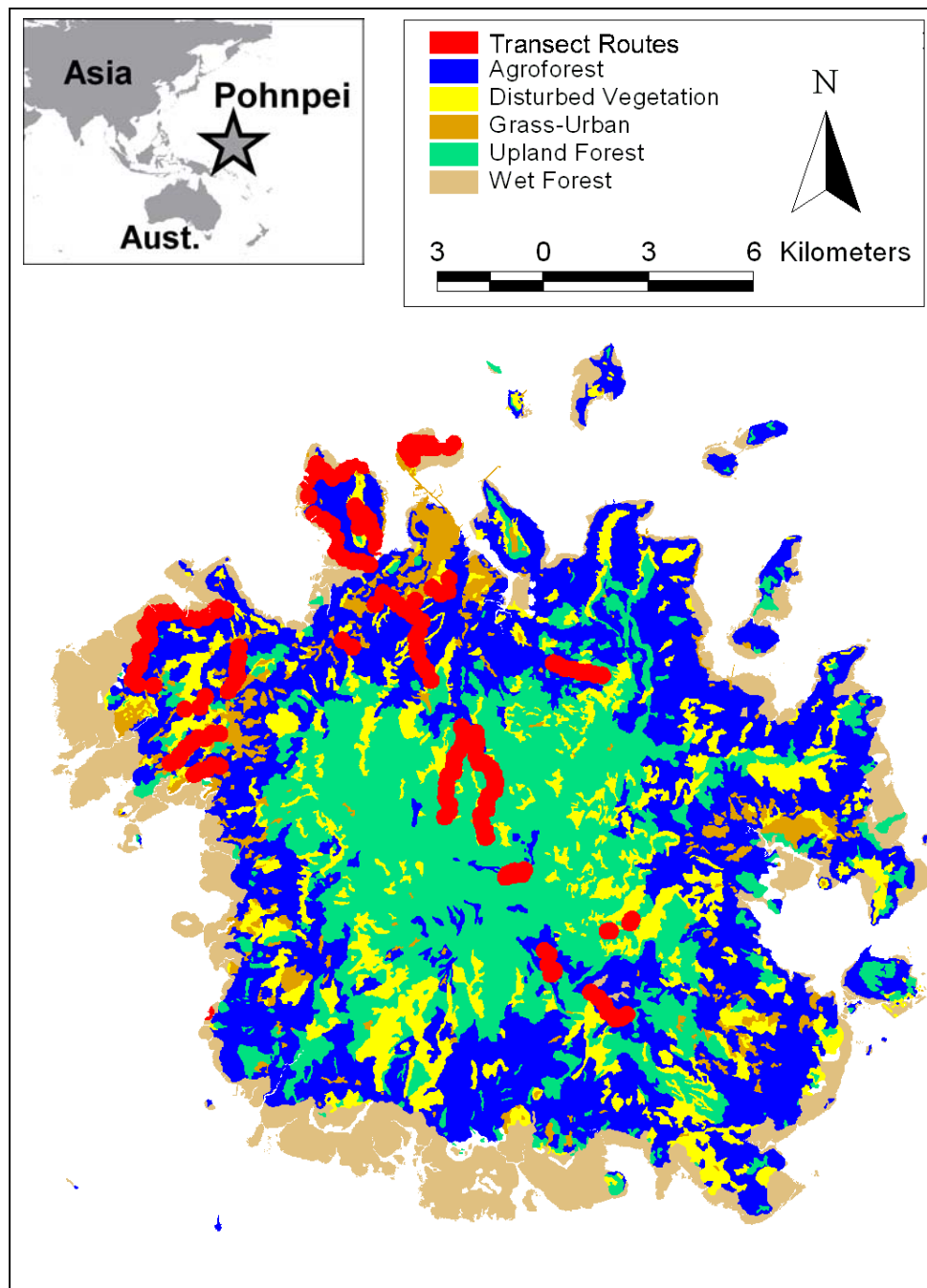
Figure 3.1. Map of point transect locations and vegetation cover types on the island of Pohnpei, Federated States of Micronesia.

Micronesian Kingfishers during 10-minute periods between 0600 and

1000hrs. Micronesian Kingfishers rarely move off home territories (Kesler and

Haig *in review a*), so detections made during transect surveys likely reflected

resident individuals and thus provide an index of local population densities.

The vegetation composition of areas within 250 m of observers was

assessed using a geographic information system (GIS) to evaluate the relationship

between Micronesian Kingfisher occurrence and habitat characteristics. Previously

published habitat coverages (Newsome et al. 2003) were used to represent

vegetative cover. Sixteen vegetation classifications occurred within transect areas

including agroforestry, forest with *Albizia* sp., barren, cropland, coconut forest,

dwarf forest, grassland, freshwater marsh, mangrove forest, saltwater marsh, ivory-

nut palm forest, palm forest, secondary vegetation, swamp forest, urban vegetation,

and upland forest (see Newsome et al. 2003). I aggregated vegetation polygons

into five coverage classifications based on vegetative structure, which included

agricultural forest (agroforestry, cropland, coconut forest, and palm forest),

disturbed vegetation (secondary vegetation and forest with *Albizia* sp.), *wet forest*

(mangrove, saltwater marsh, and freshwater marsh), *upland forest* (dwarf forest,

ivory nut palm forest, upland forest), and *grass-urban* (barren, grassland, and urban

vegetation). ArcView (ESRI, Redlands California) and XTools software extension

(Oregon Department of Forestry, Salem) were used to evaluate the amount of area

within 250 m of observers that was comprised of each vegetation cover type. I

used two-sample *t*-tests to compare the amount of each vegetation type

within 250 m of observers at point transects where birds were detected and point

transects where birds were not detected. Additionally, the number of birds detected

at each point was regressed against the amount of each habitat type within 250 m of

observers to model the influence of vegetation on kingfisher detections. All

additive linear combinations of the five vegetation variables were fitted to survey

responses using Poisson regression (SAS Institute 1999). Models were ranked

using second order Akaike's Information Criteria (AICc; Burnham and Anderson

2002) and model-averaged parameter estimates were derived for models

comprising the top 90% of AICc weight.

3.3.3. Home range scale

3.3.3.1. Study population

I radio-marked and color-banded a population of Micronesian Kingfishers on the

three study areas between January 1999 and November 2004. Birds were captured

in mist nets, marked with a unique combination of colored leg bands, and fitted

with a 1.8g telemetry package (Holohil Systems, Ltd., Ottawa, Canada) using the

leg-harness design (Rappole and Tipton 1991). The age and sex of each bird was

determined using molecular analyses and morphological characteristics (Kesler et

al. *in review*). Radio-marked birds were observed from January to July 1999,

March to September 2000, and September 2002 to January 2003. Because

observers were present on study areas daily, I believe that the social class

of all individuals was known. Hereafter, I follow the terminology of recent

literature (e.g., Haydock and Koenig 2002) by using "dominant" to refer to the

putative breeders on a territory and "helper" for offspring that have delayed

dispersal through subsequent parental reproductive attempts. Additionally, I use

"juvenile" to describe progeny for the most recent breeding season.

3.3.4.2 Radio telemetry and home range

Radio-telemetry and GIS analyses were used to assess the home range

characteristics of Micronesian Kingfishers. During each telemetry session, I used

hand–held Yagi antennas, compasses, and global positioning systems (GPS; March

III, Corvallis Microtechnologies Inc., Corvallis, OR) to record bearing groups of

two to five directional bearings for each Micronesian Kingfisher. If birds were

visually observed, I recorded their actual location using the offset function of the

GPS. Most birds were located once daily and all observations were separated by $\geq$

2 hrs. to avoid autocorrelation. I further avoided biasing results (see Porter and

Dooley 1993, Porter and Dooley 1993, Koenig et al. 1996, Koenig et al. 1996,

Koenig et al. 2000) by locating birds every time I attempted to find them, with the

exception of several sessions cut short by factors unrelated to bird movement (e.g.,

weather and equipment failure). Because previous work indicated that birds do not

move substantially between sunset and sunrise (Kesler and Haig *in review a*), I also

balanced sampling equally during each 2-hour time block between 06:00 and 18:00 hrs.

Bearing groups were used to estimate the best maximum likelihood locations with default settings in LOAS (Ecological Software Solutions, http://www.ecostats.com/). Bearing groups were excluded if LOAS failed to identify a location, or if locations had a 95% error ellipses $> 5,000$ m^2 (approximately 10% of the area of a mean Micronesian Kingfisher home range). Additionally, I eliminated locations that were within 15 m of nest sites because kernel density analyses can be biased by clusters of locations during the breeding season (White and Garrott 1990). Micronesian Kingfishers also occasionally depart from home areas on extraterritorial forays, and the resulting disparate point distributions can substantially enlarge home range estimates. Thus, I eliminated 170 locations that met previously described prospecting criteria (Kesler and Haig *in review a*), including locations that were > 50 m outside territorial boundaries and surrounded by a single kernel island. The process yielded a total of 3,721 locations from which to derive 61 Micronesian Kingfisher home ranges.

3.3.4.1. Resource availability and use

Resources available to Micronesian Kingfishers on each of the three study areas were assessed using vegetation cover maps that have been described extensively elsewhere (Kesler 2002, Kesler and Haig 2005b). In general, high-resolution (1

m/pixel) visual spectrum aerial photographs were used to conduct an

unsupervised habitat classification that divided the visual spectrum of each

photograph into ten signatures using a clustering algorithm (Avery and Berlin

1992). I manually combined signatures in a supervised classification, which

incorporated information about areas of known vegetation types (Kesler,

unpublished data; Avery and Berlin 1992). The process resulted in four habitat

coverages depicting sparse and short grassy vegetation, long grasses and brush,

early succession and agricultural forest vegetation, and mature forest vegetation.

Grassy areas included pastures and fallow fields. Early succession and agricultural

forest vegetation were characterized by lower canopy (2-20 m high) hibiscus

Hibiscus tiliaceus, banana *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

and Fosberg 1998, Buden 2000). I verified vegetation classifications with

comparisons to aerial photographs, and vegetation coordinate information recorded

with a GPS during fieldwork.

I selected five biologically relevant metrics to represent resources used by

breeding Micronesian Kingfishers within their home ranges. Four metrics came

directly from remote sensing visual spectrum analyses, as the kingfishers use short

grass and tall grass areas for foraging, early succession forest for foraging

and loafing, and late succession forests for loafing and nesting (Kesler, unpublished

observations). Additionally, the length of forest edge was evaluated because the

birds often forage near edges. Spatially referenced GIS coverages of each resource

metric were constructed and metric estimates were derived for each home range.

Resource values were log transformed and mixed models ANOVA (Proc Mix; SAS

Institute 1999) was used to compare mean resource areas among social classes.

Models included random effects variables for territory and fixed effects variables

for social classes. A mixed models approach was also employed to compare

between males and females. Linear models (Proc GLM; SAS Institute 1999) were

used to compare resources in the home ranges of breeders and juveniles on

cooperative and pair-held territories. Least squared means estimates were adjusted

with the Bonferroni method (see Ramsey and Schafer 1997) to account for the

influence of multiple comparisons.

To determine whether Micronesian Kingfishers selected or avoided

particular vegetation types, I compared vegetative coverage in kingfisher home

ranges with that in eight randomly placed polygons of similar size and shape (see

Katnik and Wielgus 2005). I hypothesized that if Micronesian Kingfishers were

selecting particular habitat features, then resource distributions in observed home

ranges would differ from those in randomly placed polygons. Observed home

ranges were defined by the 95% use contour from kernel density analyses and

simulated polygons included eight polygons matching the size and shape

of each observed home range. Simulated polygons were shifted away from

observed home range locations in eight random directions, and at random distances

between 100 and 200 m. By retaining simulated polygons within the general

vicinity of the observed home range, I was able to test whether birds were using

resources differently from what was randomly available in the immediately

surrounding area. Within home ranges and simulated polygons, the areas

comprised of each of the four vegetation types and the length of forest edge were

calculated using the GIS. I then compared used and available habitat proportions

with the method of Neu et al. (1974) and the software package Resource Selection

for Windows (Leban 1999), which estimated the difference between resource

values for home ranges and simulated polygons. Bonferroni adjustments were

made to confidence intervals to account for multiple comparisons (Ramsey and

Schafer 1997, p 156). Statistical tests used for each analysis, 95% confidence

intervals (CI), and least squared mean parameter estimates are presented whenever

appropriate. Unless otherwise noted, estimates are reported as means ($\pm$SD).

Differences are considered suggestive at $\alpha \leq 0.10$ and statistically significant at $\alpha \leq$

0.05.

3.4. RESULTS

3.4.1 Landscape scale

Point transect surveys indicated that Micronesian Kingfishers occurred throughout

the island and on all transect routes. A total of 480 Micronesian Kingfishers were

detected at 79% of the 184 survey stations. The mean detection frequency was

15.65 birds per hour for all surveys, 8.05 birds per hour in high elevations (above

400m), and 17.82 birds per hour in low elevations.

I evaluated the relationship between Micronesian Kingfisher occurrence

during point transects and the amount of each vegetative cover type within 250 m

of observers. When compared to point transects where Micronesian Kingfishers

were not detected, those with kingfishers had a mean of 1.9 (0.7 SE) ha. more wet

forest, 6.1 (1.2 SE) ha. less upland forest, and 2.3 (0.7 SE) ha. more grass-urban

habitat within 250 m of observers (respectively, $F_{1,182}$ 7.38, $F_{1,182}$ 26.06, $F_{1,182}$

10.25; $P < 0.01, < 0.0001, < 0.0001$).

The number of kingfishers detected at each station was then modeled

against vegetative cover within 250 m of observers using Poisson regression and

models were ranked using AICc . The model ranking process indicated that there

was a strong relationship between vegetative cover and the number of kingfishers

detected at each point transect location. All five vegetation cover variables

occurred in the top 12 models, which encompassed 90% of the overall AICc weight

(w_i; Table 3.1). Parameter inclusion and w_i estimates from the set of 12

indicated that the order of variable influence was agricultural forest < upland forest

< grass-urban < disturbed vegetation < wet forest (see Burnham and Anderson

2002, p168; cumulative w_j 0.76, 0.75, 0.58, 0.57, 0.52 respectively). Model

averaged unconditional parameter estimates indicated a positive relationship

between the number of bird detections at each station and wet forest (0.28 ± 0.20

SE change in log transformed bird detections for each 10 ha of wet forest habitat

added). There was a similar relationship between bird detections and grass-urban

cover (0.31 ± 0.18 SE change in log transformed bird detections for each 10 ha of

grass-urban habitat added). To the contrary, results indicated that agricultural

forest, secondary vegetation, and upland forest were all negatively correlated with

the number of bird detections. Respectively, there were 0.44 ± 0.19 SE, $0.06 \pm$

0.19 SE, and 0.53 ± 0.22 SE fewer kingfisher detections for each 10 ha of these

habitats added.

3.4.2. *Home range scale*

I used observations from radio-marked Micronesian Kingfishers to better

understand the interaction between resources, movement, and habitat use at the

home range scale. I estimated the home ranges of 60 Micronesian Kingfishers

(White and Garrott 1990) using a mean of 61 (20 SD, range 13-97) observations.

All three social classes were represented in the study population,

including 34 dominants on both pair (8M:10F) and cooperative (9M:7F) territories.

Eleven

Table 3.1. Results of model selection analysis for models relating the number of Micronesian Kingfishers detected during point transects with vegetation cover within 250 m of observers on the island of Pohnpei, Federated States of Micronesia. The 12 top-ranked models are depicted.

Rank	Model	k	AICc	Δw_i	sum w_i
1	*Ag. forest + Disturbed Veg. + Upland Forest*	4	1039.6	0.18	0.18
2	*Ag. forest + Wet Forest + Upland Forest + Grass-urban*	5	1040.1	0.14	0.31
3	*Ag. forest + Disturbed Veg. + Upland Forest + Grass-urban*	5	1040.7	0.10	0.42
4	*Ag. forest + Upland Forest + Grass-urban*	4	1041.2	0.08	0.50
5	*Disturbed Veg. + Wet Forest + Grass-urban*	4	1041.2	0.08	0.58
6	*Ag. forest + Wet Forest*	3	1041.5	0.07	0.64
7	*Ag. forest + Disturbed Veg. + Wet Forest + Upland Forest*	5	1041.6	0.06	0.71
8	*Disturbed Veg. + Wet Forest + Upland Forest + Grass-urban*	5	1041.8	0.06	0.77
9	*Ag. Forest + Disturbed Veg. + Wet Forest + Upland Forest + Grass-urban*	6	1042.2	0.05	0.82
10	*Ag. Forest + Upland Forest*	3	1042.4	0.04	0.86
11	*Ag. forest + Disturbed Veg. + Wet Forest + Grass-urban*	5	1042.7	0.04	0.90
12	*M + Upland Forest + Grass-urban*	4	1042.9	0.03	0.93

(8M:3F) helpers, and 16 hatch year birds from pair-held (3M:6F) and

cooperative (3M:4F) territories were observed.

3.4.2.1. *Resource use*

The home ranges of Pohnpei Micronesian Kingfishers encompassed all vegetation

cover types. Mean home range size was 5.95 (4.17 SD) and 5.54 (2.66 SD) with a

single outlier removed. Within 95% home range contours, birds used a mean of

0.72 (0.12 SE) ha of short grass, 1.87 (0.29 SE) ha of tall grass, 0.84 (0.07 SE) ha

of early succession forest, and 2.52 (0.21 SE) ha of late succession forest (Table

3.2). Additionally, kingfisher home ranges encompassed a mean of 4.7 (0.6 SE)

km of forest edge. Within each territory, resource use differed among social

classes. Bonferroni adjusted results indicated that when compared to helpers and

dominants, juveniles used less short grass (T_{44} 3.25; $P < 0.01$), tall grass (T_{47} 3.07;

$P = 0.01$), early succession forest (T_{48} 3.34; $P < 0.01$), late succession forest (T_{44}

3.25; $P < 0.01$), and forest edge (T_{48} 3.62; $P < 0.01$). Dominants and helpers did

not differ in their use of any of the five resources however. Resource use also

differed among sexes. For breeders, there was suggestive evidence that males used

more short grass area (T_{16} -1.87; $P = 0.08$) and early succession forest (T_{23} -1.81; P

$= 0.08$) than females. Similarly, among helpers there was suggestive evidence that

males used more short grass ($T_{2.01}$ - 4.18; $P = 0.05$) and tall grass ($T_{2.01}$ - 7.42; $P =$

0.02) than females. No differences were identified among any of the

other metrics, or between male and female juveniles ($P > 0.10$ for all).

Resource use was also compared between cooperative and pair-held

territories. Results illustrate that when compared to pairs, dominants on

cooperative territories used more early succession forest ($F_{1,32}$ 7.92; $P < 0.01$),

there was suggestive evidence for greater use of late succession forest ($F_{1,32}$ 3.36; P

$= 0.08$), and their home ranges encompassed more edge habitat ($t_{32} = -2.06$, $P <$

0.05). Dominants on cooperative and pair territories did not differ in their use of

short or tall grass habitats and no resource differences were detected between

juveniles on pair or cooperative territories ($P > 0.10$ for all).

3.4.2.2. Resource selection

I compared vegetative cover in Micronesian Kingfisher home ranges with

that in randomly placed polygons of the same size and shape to determine whether

birds were selecting or avoiding particular vegetation types at the home range

scale. Results indicated that Micronesian Kingfishers selectively use and avoid

particular habitats (Table 3.3). Cover type proportions in kingfisher home ranges

differed from those in randomly placed polygons for all birds considered together

($\chi^2_3 = 140$, $P < 0.001$), breeders alone ($\chi^2_3 = 36$, $P < 0.0001$), helpers alone ($\chi^2_3 =$

54 $P < 0.0001$), and juveniles alone ($\chi^2_3 = 84$, $P < 0.0001$). Results further

indicated that

Table 3.2. Vegetative coverages observed in the 95% kernel density home ranges of Micronesian Kingfishers on the island of Pohnpei, Federated States of Micronesia. Means are presented in hectares (± SE).

| | Birds | Grass | | Forest | | |
		Short Grass	Tall Grass	Early Succession	Late Succession	Edge
Dominant						
Pair	18	0.75 (0.23)	1.48 (0.30)	0.67 (0.09)	2.24 (0.32)	2.76 (0.48)
Cooperative	16	0.96 (0.27)	1.96 (0.44)	1.08 (0.12)	2.94 (0.30)	4.25 (0.54)
Helper						
Cooperative	11	0.80 (0.28)	3.46 (1.30)	1.19 (0.28)	3.35 (0.85)	6.72 (2.50)
Juvenile						
Pair	9	0.30 (0.24)	1.02 (0.32)	0.56 (0.06)	2.08 (0.32)	2.07 (0.38)
Cooperative	7	0.54 (0.43)	1.27 (0.33)	0.51 (0.13)	1.55 (0.16)	1.95 (0.53)

Micronesian Kingfisher home ranges included 3.4% less short grass area

(*95% CI* -4.4 to -2.3%, *P* < 0.0001), 4.0% more tall grass (*95% CI* -5.4 to -2.5%, *P* < 0.0001), and 6.4% more late succession forest (*95% CI* 4.8 to 8.0%, *P* < 0.0001) than randomly placed polygons. The same general pattern held when selection was broken down by social class (Table 3.3). No difference was found in the length of edge habitat in Micronesian Kingfisher home ranges and simulated polygons (*t*-test; t_{59} = 1.93; *P* > 0.05).

Qualitative features of Micronesian Kingfisher home ranges provide further support for habitat selection and avoidance. None of the 95% kernel density home range polygons was circular, which would be the most defensible shape because of reduced perimeter to area ratio. Rather, home ranges were elongated and they often included extensions that encompassed particular habitat features such as trees or avoided large open grassy areas.

3.5. DISCUSSION

Results from point transect surveys and home range analyses suggested that while Micronesian Kingfishers occur throughout Pohnpei, both vegetative cover type and the landscape composition have the potential to affect localized population density. Point transect results showed that kingfisher detections were positively associated

Table 3.3. Habitat selection in Micronesian Kingfisher home ranges as determined by comparing habitat proportions in observed home ranges with those in nearby randomly located polygons of similar size and shape. The method of Neu et al. (1974) was used to make comparisons and Bonferroni simultaneous confidence intervals were utilized to assess significance. A plus (+) symbol represents significantly more of the habitat in observed home ranges than simulated polygons, or selection for the habitat. A minus (-) symbol represents significantly less habitat in observed home ranges, or avoidance. A zero (0) denotes habitat use in proportion to availability.

	short grass	tall grass	early forest	late forest
Juveniles	–	–	0	+
Helpers	–	–	0	+
Dominants	–	0	0	+
All Kingfishers	–	–	0	+

with wet forest and grass-urban cover types, which were comprised of mangrove, saltwater marsh, freshwater marsh, barren, grassland, and urban vegetation. Kingfishers were detected less frequently in secondary vegetation, agricultural forest, and upland forest. With increased elevation, mangroves surrounding Pohnpei at sea level yield to wet forest, grass-urban, agricultural forest, secondary vegetation, and upland forest, so results suggested that bird density was directly related to differences in vegetative structure across elevation (Figure 3.1). In this respect, my results were similar to previous findings from Pohnpei that showed higher Micronesian Kingfisher densities at sea level and decreased densities at upper elevations (Engbring et al. 1990, Buden 1996). To the contrary, Micronesian

Kingfishers on the island of Palau were more abundant in upland forests

than lowlands and mangroves (Engbring 1992). low elevations on Palau are also

inhabited by a larger congener (*T. chloris teraokai*), however, that may

aggressively exclude Micronesian Kingfishers from prime habitats.

At the local scale, Micronesian Kingfisher home ranges included higher

proportions of late succession forests than were available in randomly placed

polygons. Kingfishers excavate nest cavities from the arboreal nests of termites

(*Nasutitermes* spp.), or termitaria (Marshall 1989, Kesler and Haig 2005a, Kesler

and Haig 2005b). The birds select for larger and higher termitaria, and termitaria in

areas with more canopy cover (Kesler and Haig 2005b). Termitaria with these

characteristics are more likely to occur in older portions of the forest with greater

vegetation development. Thus, Micronesian Kingfishers may have selected for late

succession forests because they contained specialized nesting resources.

Home range results showed that the Micronesian Kingfishers used grassy

areas in lower proportions than random availability predicted. Researchers have

previously referred to the disproportionately low use of a particular habitat as

"avoidance" (e.g., Meyer et al. 2005). However, the term seems too strong for the

kingfishers because the birds did not exclude grassy areas from home ranges

altogether. Rather, all radio-marked Micronesian Kingfishers used grassy open

areas for foraging despite the existence of large patches of contiguous forests that

could have contained entire home ranges. Thus Micronesian Kingfishers select a

combination of grassy and forested areas, and among the two, forests

may be limited in availability.

Pohnpei Micronesian Kingfishers provided an opportunity to investigate

resource selection and use in a cooperatively breeding species. Radio-marked

kingfishers maintained territories as breeding pairs and cooperative trios that were

comprised of two breeders and one delayed disperser from a previous brood (see

Kesler and Haig *in review c*). Investigations of other cooperatively breeding

species have shown that members of groups often have more or higher quality

resources than members of pairs (Walters et al. 1992, Komdeur 1992, Komdeur

1994, Burt 1996, Langen and Vehrencamp 1998, Balshine et al. 2001, Hale et al.

2003). Similarly, my results indicated that the home ranges of Micronesian

Kingfishers in cooperative groups included more forested areas than the home

ranges of birds in pairs. When combined with indications of the elevated forest use

in a landscape saturated by territories, results also indicate that the forested areas

might be limited on the Pohnpei study areas.

Cooperative breeding theory suggests that in some species individuals delay

dispersal and become helpers because they are prevented from dispersing into an

environment with limited resources, or that they are better off waiting to inherit

natal resources (Emlen 1982, Stacey and Koenig 1990, Ligon 1999, Koenig and

Dickinson 2004). For some cooperative species, territories can even function as

limited resources with the potential to entice birds to delay dispersal (i.e., *habitat*

saturation hypothesis; Selander 1964, Brown 1974, Gaston 1978, Koenig

and Pitelka 1981 but see Austad and Rabenold 1985). In these species, habitats

suitable for nesting are often described as "saturated" with territories that are

packed boundary-to-boundary. If forests, or forest-associated resources, are limited

on a landscape that is saturated with Micronesian Kingfisher territories, forest

availability may underlie cooperative behaviors in this species.

Cooperative Micronesian Kingfishers have higher reproductive success

(Kesler and Haig *in review a*), which may be a result of increased forest areas

within their territories. I frequently observed dominants, helpers, and juveniles

engaging in territorial disputes with neighbors and intruding birds (Kesler,

unpublished data; Kesler and Haig *in review a*). With more individuals defending

territorial boundaries, groups of Micronesian Kingfishers may be better at

competing for potentially limited resources through the cooperative defense of

territory boundaries (i.e., *group territoriality*; Gaston 1978). Additional

investigations may provide insight into specific forest resources with the potential

to influence reproductive success.

3.6. CONSERVATION IMPLICATIONS

Results from point transect surveys provided an indication of the status of Pohnpei

Micronesian Kingfishers. Encounter rates reported in 1983 were 13.3 detections

per hour above 400 m in elevation and 21.0 below (Engbring et al. 1990). In 1994,

6.2 kingfishers were detected during each survey hour above 400 m and

5.6 were reported below (Buden 1996). Although detections have increased since

1990, my observation rates (8.1 and 17.8 respectively) indicate a decline of 40%

and 15% since 1983.

Multi-scale landscape analyses provide information useful to conservation

efforts for Micronesian Kingfishers. Guam Micronesian Kingfishers are extinct in

the wild, but plans are currently underway for reintroductions to their native range

(U.S. Fish and Wildlife Service 2004). My results suggested that portions of the

landscape may provide higher quality resources and therefore support higher

population densities. Thus, conservation practitioners planning reintroductions on

Guam should consider areas with a combination of late succession forest and open

vegetation that occurs in patches small enough to be encircled by kingfisher home

ranges. On Pohnpei, native forests have declined by >70 % during the last three

decades (Newsome et al. 2003), and similar declines characterize Palau. Although

Micronesian Kingfishers' tolerance for open areas may render them somewhat

resilient to native vegetation conversion, my results indicated that disturbed and

secondary vegetative cover was associated with lower detection frequencies. Thus,

a continued conversion from native forests to introduced and agricultural

vegetation types may negatively impact all Micronesian Kingfisher populations.

3.7. ACKNOWLEDGEMENTS

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4. TERRITORIALITY, PROSPECTING, AND DISPERSAL IN COOPERATIVELY BREEDING MICRONESIAN KINGFISHERS

4.1. ABSTRACT

I investigated territoriality, prospecting, and dispersal behavior in cooperatively breeding Pohnpei Micronesian Kingfishers (*Todiramphus cinnamominus reichenbachii*) throughout the annual cycle using radio telemetry and color-band resights.   Mean home range size was 6.3 hectares (ha) and territories were 8.1 ha. Within territories, Micronesian Kingfishers shared 63% of their home range space with co-territorial occupants, and 3% was shared with extraterritorial conspecifics. Birds on cooperative territories had larger home ranges that overlapped more with co-territory occupants' home ranges, than did birds in pair-held territories. Despite evidence suggesting that resources necessary for survival and reproduction occurred on each territory, Micronesian Kingfishers of all age and sex classes made extraterritorial prospecting movements. Prospecting was rare as it comprised only 4.3% of my observations. When birds did depart on forays, they were gone for approximately 1.9 h. Prospecting birds returned to home territories prior to sunset. Prospecting by dominant birds was temporally correlated with courtship and nest initiation, and birds were observed at neighboring nest sites with opposite sex conspecifics and during the period when females were available for insemination.

Juveniles and helpers prospected throughout the year and made repeated homesteading movements to dispersal destinations prior to dispersing. Mean dispersal distance for radio-marked individuals was 849 m. Results suggest that prospecting in Micronesian Kingfishers is a complex behavior that provides information for dispersal decisions and familiarity with dispersal destinations. Additionally, extraterritorial movements may provide covert opportunities for reproduction, which have potential to profoundly influence the distribution of fitness among helper and dominant Micronesian Kingfishers.

4.2. INTRODUCTION

Knowledge of dispersal and space use is paramount to testing hypotheses about the evolution of sociality in cooperatively breeding species. Predominant theories about cooperative breeding suggest that there are fitness benefits associated with delayed dispersal (*benefits of philopatry hypothesis*; Stacey and Ligon 1991), including the potential to inherit resources when natal or nearby territory vacancies occur. The cost of delaying can be outweighed if the inherited resources provide enhanced fitness when compared to outlying areas (Komdeur 1992, 1994). Timing of dispersal is variable among species, however, and little is know about the proximate factors influencing when and how dispersal occurs.

In many cooperatively breeding species, some individuals disperse as juveniles while others delay for extended periods (Koenig and Pitelka 1981, Brown

1987, Stacey and Koenig 1990, Walters et al. 1992, Ligon 1999, Ekman

et al. 2004). This pattern implies that each individual gathers information about

resource quality, territory occupancy, and breeding vacancies in nearby areas prior

to making dispersal decisions. Some have proposed that birds obtain information

pertinent to dispersal through social interactions along territorial boundaries (Hale

et al. 2003) and by making extraterritorial prospecting movements into the

surrounding landscape (Bowen et al. 1989, Reed et al. 1999, Koenig et al. 2000,

Fedy and Stutchbury 2004). However critical this information is to understanding

sociality in cooperative breeders, prospecting movements are rare and elusive and

attempts at empirical assessments can be mired with methodological biases

(Walters 2000, Johnson and Horvitz 2005Koenig et al. 1992, Koenig et al. 2000).

Thus, few have identified how prospecting relates to dispersal, where prospecting

birds travel, and what information birds acquire while prospecting, despite the

paramount importance of these data to understanding proximate dispersal decisions

in cooperative breeders (Walters 2000; but see Doolan and MacDonald 1996,

Schjorring et al. 1999, Fedy and Stutchbury 2004).

Once delayed dispersal has arisen, the behavior can be maintained by

extrinsic limitations in resources necessary for reproduction (*ecological constraints*

hypothesis; Emlen 1982). Habitats suitable for survival and nesting of cooperative

species are often saturated with territories that are packed boundary-to-boundary

and aggressively defended, which suggests that territory availability can function as

the limited resource that prevents young from dispersing (*habitat*

saturation hypothesis; Selander 1964, Brown 1974, Gaston 1978, Stacey 1979,

Koenig and Pitelka 1981, Koenig and Pitelka 1981). In pair-breeding species,

investigators have identified spatially and temporally variable factors that influence

the distribution of individuals, including environmental conditions, intraspecific

interactions (Brown 1964, Emlen and Oring 1977, Hixon 1980, Schoener 1983,

Schoener 1983, Lima 1984, Stamps and Krishnan 1999), and resource dispersion

and predictability (Brown 1964, Emlen and Oring 1977, Bollmann et al. 1997,

Zwicker and Walters 1999, Clark and Shutler 1999, Tyre et al. 2001). Yet, few

have investigated proximate mechanisms underlying space use and territoriality in

cooperative species (Langen and Vehrencamp 1998, Walters 2000, Breininger and

Oddy 2004, Fedy and Stutchbury 2004).

Each individual bird uses space, which makes up its home range (White and

Garrott 1990), and together the home ranges for a pair or social group comprise a

territory. There is a lack of information about how space is partitioned among

individuals, and the actual extent to which spatial resources are distributed among a

cooperatively breeding group has never been assessed to my knowledge. Although

birds within a territory are generally thought to share resources, some space may

also be reserved for specific social classes, and relationships may differ among

cooperative and pair-held territories.

Here, I investigate territoriality, prospecting movements, and dispersal behaviors in cooperatively breeding Pohnpei Micronesian Kingfishers (*Todiramphus cinnamominus reichenbachii*). I synthesize observations of color-banded and radio-marked birds to assess the distribution and movement of individuals within and among territories. I evaluate home ranges, territories, prospecting distances, timing, and the relationship between dispersal and extraterritorial movements using a geographic information system (GIS) and behavior observations. Additionally, radio telemetry and color-band observations were used to assess within and among year dispersal. Results from this study are intended to lend insight into space use and dispersal, and provide information to recovery efforts for the Guam Micronesian Kingfisher (*T. c. cinnamominus*). The Guam kingfishers were listed as endangered under the U.S. Endangered Species Act following precipitous declines from introduced brown trees snakes (*Boiga irregularis*; U.S. Fish and Wildlife Service 1984, Savidge 1987). They now exist only as a captive population in U.S. zoos (Haig et al. 1995, Haig and Ballou 1995, Bahner et al. 1998, Kesler and Haig 2004). Plans have been announced to reintroduce the birds back into the last native habitats on Guam, but cannot be carried out without information about spatial distribution and dispersal (U.S. Fish and Wildlife Service 2004).

4.3. METHODS

Research was conducted on the island of Pohnpei, Federated States of Micronesia (6°52'N, 158°13'E). Pohnpei is a circular 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 sites were selected for this investigation, including the Ranch (6°57'N, 158°12'E), College of Micronesia (6°54'N, 158°9'E), and Palikir study areas (6°55'N, 158°9'E). Each site included strand vegetation, early succession and mature lowland rainforest, grassland, urban vegetation, and agroforest. Grasslands were comprised of pastures and fallow fields. Early succession rainforest and agroforest vegetation was characterized by lower canopy (2-20 m high) hibiscus (*Hibiscus tiliaceus*), banana (*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 and Fosberg 1998, Buden 2000).

4.3.1. Study Population

I follow the terminology of recent literature (*e.g.,* Haydock and Koenig 2002) by using "dominant" to refer to the putative breeders on a territory and "helper" for offspring that have delayed dispersal through subsequent parental reproductive attempts. Additionally, I use "juvenile" to describe progeny for the most recent breeding season. I radio-marked and color-banded a population of Micronesian Kingfishers on study areas between January 1999 and November 2004. The study populations were intensively observed from January to July 1999, March to September 2000, September 2001, September 2002 to January 2003, October and November 2003, and September 2004. Birds were radio-marked during 1999, 2000, and 2002, and color-banded every year. Because observers were present on study areas daily, I believe that the social class (dominant, helper, juvenile) of all individuals was known. Birds were captured in mist nets and fitted with a 1.8g telemetry package (Holohil Systems, Ltd., Ottawa, Canada) using the leg-harness design (Rappole and Tipton 1991), and a unique combination of colored leg bands. I observed no negative effects from capture, observation, color-bands, or radio-marking. Age and sex of each bird was determined using molecular analyses and plumage characteristics (Kesler et al. *in review*). In Pohnpei Micronesian Kingfishers, adults older than one year have white breast plumage (Pratt et al. 1987, Fry et al. 1992), fledglings and juveniles are characterized by varying degrees of rufous breast plumage. The rufous feathers progressively molts into

white along the ventral feather tract (Kesler et al. *in review*). The

plumage of helpers occasionally shows remnant rufous coloration, but older helpers

are similar to dominants (D. Kesler, personal observation).

4.3.2. Radio telemetry and home range

I used radio-telemetry and GIS analyses to evaluate territoriality and movement in

Micronesian Kingfishers. Hand-held Yagi antennas, compasses, and global

positioning systems (GPS; March III, Corvallis Microtechnologies Inc., Corvallis,

OR) were used to record a bearing group of two to five (mean = 2.98) directional

bearings for each Micronesian Kingfisher ($n = 2,108$ locations). If birds were

visually observed during telemetry sessions, I recorded their actual location using

the offset function of the GPS ($n = 1,942$ locations). Bearing groups were used to

estimate the best maximum likelihood locations for each bird using default settings

in LOAS (Ecological Software Solutions, http://www.ecostats.com/), and they were

excluded if LOAS failed to identify a location or if observers noted that birds

moved during the observation period. Locations with 95% error ellipses (White

and Garrott 1990) > 5,000 m^2 (approximately 10% of the area of a mean

Micronesian Kingfisher home range) were also excluded ($n = 17$). Most birds were

located once daily, and all observations were separated by ≥ 2 h to avoid

autocorrelation (mean temporal separation of subsequent observations = 27 h).

Additionally, kernel density analyses can be biased by clusters of locations during

the breeding season (White and Garrott 1990), so I eliminated 104

locations that were within 15m of nest sites. The process yielded a total of 3,929

locations.

Differential detection probabilities and missing data have the potential to

bias representations of movement and resource use (Porter and Dooley 1993,

Koenig et al. 1996, Koenig et al. 2000). For example, data are biased when

observers fail to identify the presence or location of color-banded or radio-marked

animals that move off study areas or into portions of the landscape that hinder

detection. I avoided biasing results by locating birds every time I attempted to find

them, with the exception of several attempts cut short by factors unrelated to bird

movement such as weather and equipment failures. Several study-specific factors

allowed me to consistently locate birds, including pre-sampling identification of

biasing factors, the 1-2 km detection distance of the Holohil transmitters in the

generally flat landscape, and the short distance movements of Micronesian

Kingfishers. When birds were not immediately identified on their home territory,

observers traversed the surrounding landscape until the location of prospecting

individuals was identified. Radio telemetry results can also be biased if diurnal

movement patterns correlate with telemetry sampling regimes. Thus, I repeatedly

sampled throughout the day and night. I focused most sampling on daylight hours

because sixty sequential telemetry locations recorded during nighttime hours, and

observer comments, indicated that birds do not move substantially between sunset

and sunrise. Additionally, I balanced sampling equally during each 2-

hour time block between 0600 and 1800 hours (approximate sunrise and sunset at

7° N latitude; mean obs. per time block = 649 $\pm$ 69 SD). During telemetry

observation periods, behaviors were also recorded if the observers could visually

identify individuals. Particular emphasis was placed on recording aggressive

interactions, fights, courtship behaviors, and noting behavior during prospecting

movements. I believe this method yielded a data set that was temporally and

spatially representative of Micronesian Kingfisher space use and movement

throughout the annual cycle.

4.3.3. Prospecting, dispersal, and behavior

I employed a combination of empirical and subjective criteria to identify telemetry

locations recorded while birds were prospecting. First, I used the ArcView animal

movement extension (Hooge and Eichenlaub 1997) to conduct kernel density

analyses (White and Garrott 1990) of telemetry locations. Home range was then

considered to be the 95% use contour of each bird within a particular year (White

and Garrott 1990, Roshier 2003, Roshier 2003). The 95% use contours for

dominants on each territory were then amalgamated to delineate the boundaries of

16 focal study territories (see Kesler and Haig 2005b). Kernel polygons were

considered to be outliers and excluded from the territory amalgamations if they

were distinctly separated from the main territory polygon and surrounded only a

single telemetry point. Extraterritorial movements were then defined as locations of birds outside territorial boundaries by > 50 m, a figure selected because it represents approximately half the radius of a mean-sized circular home range. Radio-marked birds were considered to have dispersed if they remained at a prospecting destination for more than 24 hours and after daily movements to home territories ceased. I considered that color-banded individuals dispersed if they moved from one territory to another between years.

4.3.4. Analysis

Statistical analyses were conducted using SAS statistical analysis software package (SAS Institute SAS Institute 1999). Two-sample t-tests were used to make comparisons among sexes, and the linear model analysis of variance (ANOVA; Proc GLM) function of SAS Analyst was used to evaluate social class comparisons. Chi-square analyses were calculated by hand. Statistical tests used for each analysis, adjustment methods for multiple comparisons, 95% confidence intervals (CI), and least squared mean parameter estimates are presented whenever appropriate. Unless otherwise noted, estimates are reported as means with standard deviations (SD) in parentheses and differences are considered statistically significant at $\alpha \leq 0.05$.

4.4. RESULTS

From 1999 to 2004, 57 male and 53 female Micronesian Kingfishers were marked with individual-specific color-band combinations. On 16 focal territories, 43 birds were marked as dominants, 12 were helpers, and 39 were juveniles or nestlings. Fifty-seven were observed during only the year they were marked, 22 were observed during two field seasons, 13 were observed for three seasons, one bird was observed during a fifth, and one during a sixth season. During 1999, 2000, and 2002 breeding seasons, 54 Micronesian Kingfishers were radio-marked and tracked for approximately 16 weeks each. Additionally, one female and two males were radio-marked during consecutive years, yielding a total of 57 kingfisher*radio years.

4.4.1. *Space distribution within and among territories*

Home ranges were evaluated for radio-marked Micronesian Kingfishers (Table 4.1). The mean error ellipse for bearing groups was 409 m^2, and a mean of 64 (22 SD, min 13, max 100) locations were used for each home range estimate. Mean home range size was 7.31 (6.83 SD) ha for all radio-marked birds. The disparate point distributions of three individuals that dispersed during observations yielded estimates that exerted undue leverage on results, so they were excluded and treated in the subsequent section. After disperser data were removed, mean home range size was 6.28 ha (3.33 SD; Table 4.1).

Table 4.1. Estimates of home range size and prospecting distances from home
territories for each sex and social classes of Micronesian Kingfishers during the
1999, 2000, and 2002 using radio telemetry and kernel density analyses. Mean
estimates are presented for each class ($\pm$ SD).

Sex	Class	All Observations			Prospecting		
		Birds*	Mean Obs.	HR Size (ha)[+]	Birds	% Obs.	Mean Dist.
F	Dominant	16	69 (20)	5.7 (2.7)	6	0.7%	77
F	Helper	3	63 (23)	7.8 (4.8)	2	9.0%	399
F	Juvenile	9	56 (13)	5.2 (3.7)	8	9.4%	221
M	Dominant	16	67 (18)	7.1 (2.7)	9	1.2%	114
M	Helper	7	60 (33)	7.9 (4.4)	6	11.0%	429
M	Juvenile	6	51 (27)	4.6 (3.4)	1	2.8%	189

* Sample sizes are presented in bird years
[+] Data for three dispersing individuals are addressed elsewhere because they
   exerted undue leverage on estimates.

There was no difference among the home range sizes of dominants, helpers,

and juveniles (ANOVA with Tukey-Cramer adjustment for multiple comparisons;

$P = 0.09$), nor between males and females (*t*-test; $P = 0.26$). The relationship

between sociality and home range size was evaluated by comparing home ranges of

birds in cooperative group-held territories ($n = 31$) with those on pair-held

territories ($n = 26$). Overall, the home ranges of birds on pair-held territories were

1.8 ha smaller than those on cooperative territories (*t*-test, $F_{1,55}$ 4.45; $P = 0.04$, *95%*

CI 0.1 to 3.5 ha). By social class, dominant home ranges were 2.4 ha larger ($P = $

0.009; CI 0.7 to 4.0 ha), and the home ranges of fledglings were 1.8 ha

larger (P = 0.04; CI 0.1 to 3.5 ha) on cooperative territories.

Groups or pairs of Micronesian Kingfishers share space within each

territory. However, aggressive interactions among co-territorial occupants suggest

that not all space is commonly used by every individual, and that portions of each

territory may be reserved for use by only specific birds. To gain insight into the

sharing of space within territories, I assessed the amount of space used

simultaneously by radio-marked birds, or the amount of home range overlap (Table

4.2). Forty-two birds were radio-marked while a co-territorial occupant was

simultaneously being tracked, and dyad combinations of these individuals yielded

34 pairs of simultaneous co-territorial home ranges. Home ranges of co-territorial

birds overlapped by a mean of 3.97 (2.10) ha. No differences were identified

between the area overlapped by two dominants, dominants and helpers, dominants

and juveniles, helpers and juveniles, or two juveniles (Table 4.2; one-way

ANOVA; $F_{4,33}$=1.78, P = 0.16). Relative to mean home range size, results

illustrate that birds share 63% of their home range with other individuals on the

same territory, but that not all space is commonly used by all territory occupants.

When a comparison was made between mean home range overlap on cooperative

(n = 12 dyads; 2.75 ha., 0.39 SE) and pair-held territories (n = 22 dyads; 4.63 ha;

0.46 SE), results indicated that home ranges on cooperative territories overlapped

by 1.88 ha. more than those on less crowded pair-held territories (two-sample t-test; $P = 0.01$, CI 0.48 to 3.29 ha).

Micronesian Kingfisher occupancy on 16 focal territories was recorded between 1999 and 2003. Territories were defended by single individuals, breeding pairs, a single dominant and a juvenile, breeding pairs and juveniles, and cooperative family groups (respectively, $n = 2, 13, 1, 25,$ and 24 territory*years). Dominant mortalities altered group membership in four territory*years, and social composition could not be determined for 11 territory*years. When home ranges of radio-marked dominants were amalgamated to empirically define each territory, the mean territory size was 8.1 ha. There was no difference between territories that had cooperative groups during at least one field season, and consistently pair-held territories ($n = 12, 4$ respectively; $F_{1,14} = 2.41$; $P = 0.14$).

Micronesian Kingfishers excluded conspecifics from entering territories through aggressive interactions. Chases and bill-swooping posture displays were observed 99 times during the course of fieldwork. Among the aggressive displays observed on the study areas, 29 were located along territorial boundaries and 13 were inside territories. All age and sex classes participated in the behaviors, which usually terminated when one or more territory occupants chased intruders from confrontation areas. I evaluated the effects of spatial exclusion by assessing home range overlap among 83 dyad pairs of radio-marked birds on neighboring territories. The home ranges of neighboring birds overlapped less than birds on the

same territory (0.21 vs. 3.97 ha; two sample *t*-test, $P < 0.001$), a pattern

that applied to all combinations of social classes (Table 4.2). The home ranges of

the six neighboring pairs of helpers overlapped more than other combinations of

neighboring dominants, helpers, or juveniles (ANOVA; $F_{5,77}$ 12.96, $P < 0.0001$),

indicating that helpers invaded the space of extraterritorial conspecifics more than

other social classes.

Table 4.2. Home range overlap within and among Micronesian Kingfisher territories on Pohnpei during 1999, 2000, and 2002. Results are presented as area in hectares, with sample sizes in parentheses. P-values are reported for two sample *t*-tests for equal means.

Overlap Type	Overlapping Home Range Area (ha.)		
	Neighbors	Within Territories	P-value
Dominant-Dominant	0.14 (22)	4.39 (8)	<0.0001
Dominant-Helper	0.34 (12)	4.78 (10)	<0.0001
Dominant-Fledgling	0.11 (21)	3.29 (9)	<0.0001
Fledgling-Helper	0.04 (2)	4.74 (3)	0.017
Helper-Helper	1.18 (6)	--	--
Fledgling-Fledgling	0.01 (20)	2.05 (4)	<0.0001

* Home ranges of neighboring helpers overlapped significantly more than home ranges of all other neighboring social classes.

4.4.2. Prospecting movements

Prospecting was observed in 31 individuals of all age and sex classes (Table 4.1).

Of 3,929 telemetry locations recorded during my investigation, 170 were observed

during 152 prospecting movements (multiple locations were recorded during long

forays). Observer remarks about behavior accompanied 113 of the prospecting

movements, and the GIS verified that all locations were > 50M from home-territory

boundaries. All prospecting movements terminated with birds returning to home

territories prior to sunset. I used two methods to evaluate mean departure time,

mean foray duration, and mean return time. On 59 occasions, I observed birds on

their home territories and prospecting during the same day. I estimated a mean

departure time of 10:25 hours (1.7 h SE; $n = 27$) and a mean return time of 12:21

hours (2.4 h SE; $n = 27$) by averaging the times birds were observed on their home

territories with the times they were observed prospecting. The difference in means

yields an estimated foray duration of 1.9 *h*. (*t*-test; *P* = 0.0012; *95% CI* 0.7 to 3.1).

I also observed round-trips on four occasions, when birds were detected on their

home territory, while prospecting, and then back on their home territory again on

the same day. The mean estimated departure time, prospecting duration, and return

times for round trips were similar to those identified above (09:35 hours, 3.0 *h*, and

12:37 hours respectively).

Prospecting frequency differed among social classes (ANOVA; arcsine square root transformed proportion observations prospecting; $F_{2,61}$ 4.32, P = 0.018), with prospecting making up 2.4% more of the helper telemetry observations than dominants (P = 0.03; Bonferroni correction and back transformed *95% CI* from 0.01% to 8.5%). Similarly, helpers prospected 161 m farther from home territory boundaries than dominants (ANOVA; $F_{2,29}$ 4.95, P = 0.014; *95% CI* from 31 to 292 m). No differences were identified between juveniles and dominants, or juveniles and helpers (P > 0.05). Sexes did not differ (*t*-test; P > 0.05), and no difference was identified among cooperative and pair-held territories (*t*-test of arcsine square root transformed proportion observations prospecting; P > 0.05; mixed models ANOVA; P > 0.05).

I evaluated the temporal distribution of prospecting by comparing the number of observed monthly prospecting movements with the number expected if they were proportional to all telemetry observations. Prospecting movements were temporally disproportionate to predictions for all three social classes (for dominants, helpers, and juveniles respectively; χ^2 = 16, 54, 21; DF = 2, 7, 4; P < 0.001 for all; cells with predicted occurrence < 5 were excluded). Additionally, the monthly proportion of prospecting observations differed among dominants, helpers, and juveniles (Kruskal-Wallis Test; χ^2 = 6.86, DF= 2; P = 0.029). The timing of dominant prospecting corresponded with reproduction because the proportion that
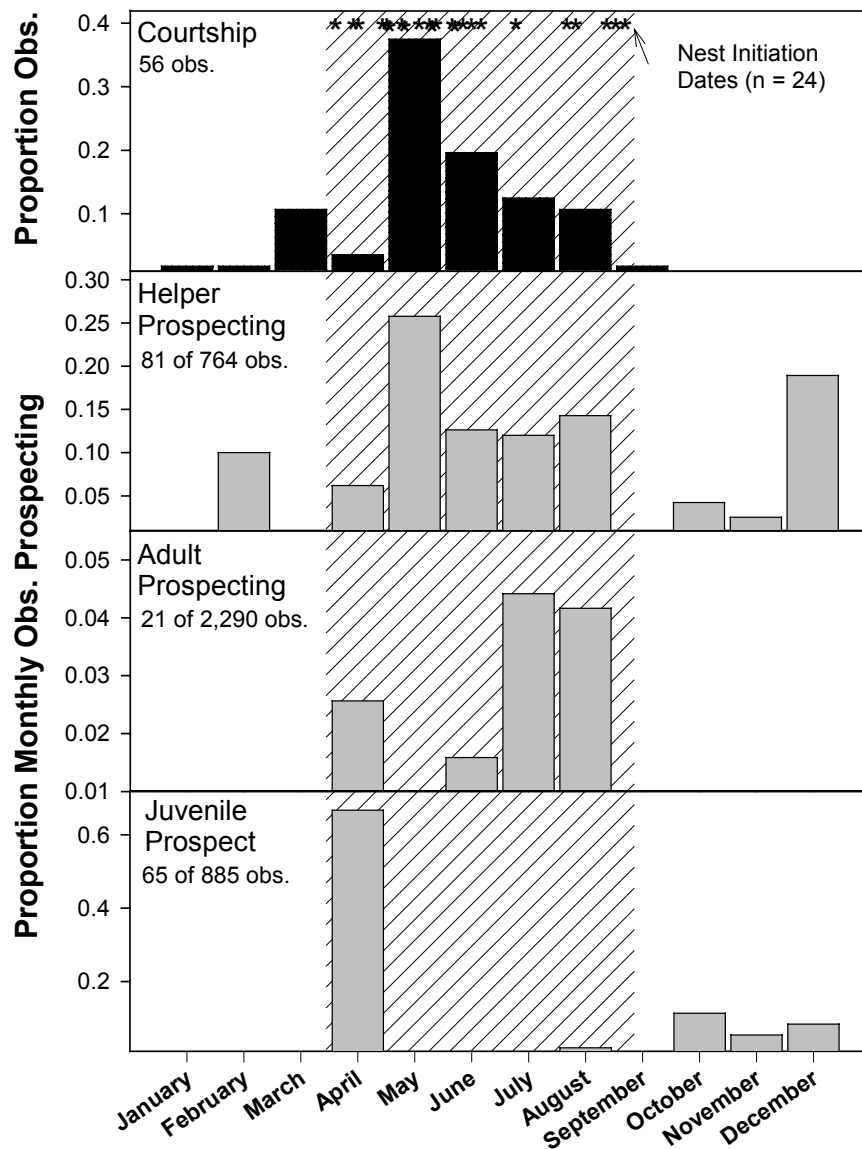
Figure 4.1. Temporal distribution of observed courtship behaviors and prospecting movements among social classes of Pohnpei Micronesian Kingfishers. Crosshatching denotes period of nest initiations on focal territories between 1999 and 2004. Courtship observations included copulations, courtship feedings, and nest excavations (*n* = 7, 6, and 43 respectively) recorded between 1999 and 2004. Histograms illustrate the monthly proportion of courtship behaviors among all behaviors, and monthly proportion extraterritorial observations for radio-marked Micronesian Kingfishers in each social class during 1999, 2000, and 2001.

occurred during breeding months (April-August) differed from non-breeding months (Fig. 1; t-test, $F_{1,9} = 10.2$; $P = 0.010$; estimated 2.3% more off-territory obs. during breeding season; *95% CI* 0.7 to 3.9%). Neither helpers nor juveniles showed differences between the proportion of prospecting movements that occurred during breeding and non-breeding months (t-test, $P > 0.05$ for both).

Behavioral observations support assertions that extraterritorial movements may be motivated by searches for searching for extra-pair mating opportunities. Courtship behaviors were observed in association with eight forays. Male helpers were observed at the nests of neighboring birds three times, and telemetry showed that the neighboring female was present on at least one of those occasions while her mate was elsewhere. Furthermore, estimates based on hatch dates for the nests visited by prospecting males ($n = 3$) indicated that visits occurred within three days of respective laying dates, when females were presumably available for fertilization. The prospecting birds then went on to nest with their mates on home territories. Courtship calling with non-mates was observed during four extraterritorial movements. Aggressive territorial head-dipping displays, aerial pursuit chases, and territory calling also characterized prospecting observations (n = 2, 5, 9 respectively).

4.4.3. *Philopatry and dispersal*

Five birds color-banded as juveniles (1M:4F) and five banded as helpers (4M:1F) were observed on natal territories during subsequent years. However, none remained to obtain new mates and breed on natal areas, which suggests that territory inheritance by helpers or offspring is rare or does not occur in Micronesian Kingfishers. Three males and five females dispersed from natal territories during my investigation. Two (1M:1F) dispersed as juveniles, four (1M:3F) remained as helpers for one breeding season prior to dispersal , and two (1M:1F) were not observed between fledging and filling a vacancy on neighboring territories two years later. Three birds dispersed while being radio-tracked (mean dispersal distance 849±57 SE m), and the remaining five color-banded birds dispersed between field seasons (mean dispersal distance 535±214 SE m). No differences were found in dispersal distances detected by radio-marked and color-banded birds (n=8; *t*-test, $P = 0.31$), nor between males and females (*t*-test, $P = 0.14$). Dispersal has been previously evaluated in terms of the number of territories between natal areas and breeding locations, and my observations show a 2.05 territory-width separation between natal and breeding territories in radio-marked Micronesian Kingfishers (assuming diameter of 320 m from circular territory with mean territory area). Prior to dispersal, three radio-marked individuals made repeated prospecting visits (mean = 13) to the locations where they eventually dispersed.

The fate of 31 color-banded juveniles and 10 helpers that disappeared from study areas remains unknown.

Insight into territory ownership and inheritance comes from the behavior of territory-holding dominants following death of their mates. Territory ownership is not reserved for either sex. A dominant male was left as the single territory holder when a hunter shot his radio-marked mate, and he remained on the territory with the previous year's offspring. On two other territories, dominant females retained ownership after the death of radio-marked mates. One of these females was observed courtship calling with an unmarked male 17 days after her mate died, and the other bred with a new mate the following year. Inferences about territory ownership can also be drawn from changes in territory occupancy across years. New mates on two territories replaced dominant males, while the dominant females remained across breeding seasons. On six territories, dominant males remained while female mates were replaced.

4.5. DISCUSSION

Pohnpei Micronesian Kingfishers hold all-purpose territories throughout the year. Their high degree of territoriality was illustrated by results showing that the home ranges of co-territorial occupants overlapped by 63%, while the home ranges of birds on neighboring territories overlapped by only 3%. Brown (1964) suggested that territoriality would evolve if resources were distributed so that an individual

could satisfy its nesting requirements, food supply, and attraction of a

mate in a relatively fixed area, and if individuals could balance the costs of

defensive aggression with the benefits of defended resources. Accordingly,

Micronesian Kingfishers are terrestrial generalists that primarily subsist on the

abundant invertebrate and lizard prey items (orders Isoptera, Lepidoptera, and

Othoptera; *Emoia* spp; Family Gekkonidae; D. Kesler, unpublished obs.). The

birds nest in arboreal termitaria that are apparently not limited in abundance

(McClean et al. 1998, Kesler 2002, Kesler and Haig 2005a, Kesler and Haig

2005b), and they do not require specialized cover resources in the amiable

climactic conditions on Pohnpei (Kesler and Haig 2005a). Additionally, less than

1% of my telemetry locations from dominant kingfishers were prospecting

movements, which further suggests that Pohnpei Micronesian Kingfisher territories

contained all the resources necessary for survival and reproduction.

On cooperative territories, home ranges of dominants were larger than those

on pair-held territories. Resource availability has been shown to cause sociality in

Seychelles Warblers (Komdeur 1991, Komdeur 1992, Komdeur 1994) and Red-

cockaded Woodpeckers (*Picoides borealis*; Walters et al. 1992), and larger

territories and greater resources have been correlated with sociality in other

cooperative species such as Splendid Fairy-wrens (*Malurus splendens*; Brooker

and Rowley 1995). Greater or higher quality resources can also influence

reproductive success (Forbes et al. 2002, Luck 2003, Löhmus and Väli 2004) and

breeding behavior (Emlen and Oring 1977, Walters et al. 1992, Byrkjedal

et al. 1997, Pribil and Searcy 2001), which may induce potential dispersers to

delay. Thus, additional insight into space use, dispersal, and territory quality might

be gained from an evaluation of the interaction between specific foraging and

nesting resources, reproductive success, and cooperative breeding in Micronesian

Kingfishers.

4.5.1. Prospecting

Juvenile and helper Micronesian Kingfishers may prospect to gather information

about potential dispersal destinations. In the cooperatively breeding Red-cockaded

Woodpecker, there is evidence that reduced familiarity with the environment

decreases disperser fitness (Pasinelli et al. 2004). Previous investigations have also

shown that knowledge of localized resources can affect foraging efficiency,

territoriality, predator detection, and mate attraction (Greenwood 1980, Part 1994,

Smith and Metcalfe 1997, Bensch et al. 1998). For Micronesian Kingfishers,

nesting and foraging resources are vital to daily survival and reproduction, and

experiences with these resources during prospecting may educate birds about

availability. I observed birds foraging, excavating nest cavities, and in close

proximity to the nests of neighboring birds while prospecting. A similar nest

resource assessment behavior has been observed in other cooperative species (*e.g.,*

Green Woodhoopoes, *Phoeniculus purpureus*; Ligon and Ligon 1990), and many

pair-breeding species (see Reed et al. 1999). While prospecting,

Micronesian Kingfishers may have also been assessing the ability of conspecifics

to defend territories through direct interactions like territorial head-dipping

displays, aerial pursuit chases, and territory calling, or through indirect indicators

like plumage (*e.g., Euplectes axillaris*; Pryke and Anderson 2003).

Investigators have previously suggested that in cooperative species,

potential dispersers choose to either remain on a natal territory as a helper and

"stay and foray" or depart from natal territories and search as a "floater" until they

find a territory vacancy to fill (Brown 1987, Walters et al. 1992). Stay and foray

models have been envisaged for cooperative breeders (Reed et al. 1999) and

simulations have shown the benefits of such a "foray search" strategy over the

random strategies (Boulinier and Danchin 1997, Conradt et al. 2003). None of the

radio-marked Micronesian Kingfishers employed a floater dispersal strategy during

3,929 telemetry*bird*days. Rather, birds made movements that resemble a stay

and foray strategy because prospecting was directed, repeated, short in duration,

and birds returned to their home territories prior to sunset. This may reflect

attempts to retain social status and nepotistic benefits on a natal territory (Ekman et

al. 2001) while simultaneously gathering contemporary information about extrinsic

conditions with which to make informed decisions about the costs and benefits of

dispersal.

Our results suggest that prospecting may provide an opportunity to solicit reproduction (*e.g.,* Pitcher and Stutchbury 2000). Although parentage has not been investigated in Micronesian Kingfishers, previous studies of other cooperatively breeding species show high levels of promiscuity and extra pair paternity (Mulder et al. 1994, *but see* Haig et al. 1994Delay et al. 1996, Li and Brown 2000, Richardson et al. 2001). Prospecting movements of dominants were temporally aligned with courtship observations and nest initiations (Fig. 1), and I observed prospecting individuals rendezvousing at the nest sites of neighboring females several days prior to laying. Unlike previous descriptions from other species (Reed et al. 1999), some prospecting kingfishers were not failed breeders merely gathering information about resources because they went on to breed with mates on home territories shortly thereafter.

Reproduction obtained during extraterritorial movements has the potential to greatly enhance the fitness of prospecting birds, while simultaneously reducing that of cuckolded males. Additionally, costs to prospectors may be small because I observed no mortality during extraterritorial movements. Covert reproduction by delayed dispersers during forays would evidence previously undocumented pathways to fitness, and suggest that delaying and foraying may be more of an alternate life history strategy than simply "making the best of a bad situation," as some have suggested (*e.g.,* Emlen 1997). Further, if covert extraterritorial helper reproduction is common in many species, the behavior even has the potential to

alter perceptions about the costs and benefits of cooperative breeding and delayed dispersal, which have been debated for more than three decades (Skutch 1935, Vehrencamp 1980, Kokko and Lindstrom 1997, Clutton-Brock 1998, Cant and Johnstone 1999). A molecular genetic investigation of parentage in Micronesian Kingfishers has the potential to lend insight into this phenomenon.

4.5.2. Dispersal

Although rare, long distance dispersal has been observed in other cooperatively breeding species (Bowen et al. 1989, Koenig et al. 1996). During my study, Micronesian Kingfishers neither prospected nor dispersed great distances from home territories. The island of Pohnpei is limited in size (approximately 20 km in diameter), so dispersal distances may be restricted by behavior and geography.

An increased probability of obtaining a high quality breeding territory by delaying dispersal is fundamental to the benefits of philopatry hypothesis (Stacey and Ligon 1991). By delaying, individuals can inherit natal areas or occupy neighboring territories when vacancies occur. Thus, inheritance is characteristic of many cooperatively breeding species (Hale et al. 2003), and some investigators have even suggested that long-term data sets might yield evidence of dynasties (Emlen 1997). However, my five-year investigation of Micronesian Kingfishers provides no evidence of helpers queuing for breeding vacancies because none of

the delayed dispersers bred on natal territories. However, some did

disperse to nearby neighboring territories where they bred in subsequent years.

In summary, Micronesian Kingfishers are a highly territorial species that

maintains all-purpose, year-round territories as pairs and cooperative groups. No

kingfishers became floaters during my investigation, but all age and sex classes

made short duration prospecting movements to neighboring territories. Because

juveniles and helpers made repeated and extended homesteading movements to

settlement areas before dispersal, prospecting may allow birds to gather

information about localized resources and conspecifics before making dispersal

decisions. Prospecting movements of dominant birds were temporally associated

with courtship and nesting activities and birds were observed in close proximity to

opposite-sex neighbors, which suggests that prospecting may also be used to solicit

reproduction.

Results from this investigation suggest that a reintroduced population of

Micronesian Kingfishers on Guam would require at least enough space for birds to

maintain territories approximately 8.1 ha in size. The limited prospecting and

dispersal distances detected here also suggest that a recovering population of Guam

kingfishers should not be expected to disperse across the landscape quickly.

Additional investigation into parentage, and the interaction between specific

resources, dispersal decisions, and population demography, would lend further

insight into the costs and benefits of cooperative breeding in Micronesian Kingfishers.

4.6. ACKNOWLEDGEMENTS

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5. NESTLING SURVIVAL AND SIBLICIDE IN COOPERATIVE MICRONESIAN KINGFISHERS

5.1. ABSTRACT

I estimated nestling survival and provided evidence of siblicide in cooperatively breeding Pohnpei Micronesian Kingfishers (*Todiramphus cinnamominus reichenbachii*). A single egg or nestling disappeared from 11 of 32 nests and Pohnpein residents smashed two nests. Mean daily survival of 53 individual nestlings was estimated to be 0.989. Data from 29 nestlings on territories of known social structure were fitted to four models to evaluate the relationship between daily survival, cooperative breeding, and nesting phase. The top-ranked model in an AICc model selection was congruent with siblicidal mortality patterns in other Coraciiformes. It indicated high nestling mortality around the time of hatching and suggested differences between nestling survival on cooperative and pair-breeding territories. Additionally, I provide photographs of a morphologically modified upper mandible on Pohnpei and Guam Micronesian Kingfisher (*T. c. cinnamominus*) nestlings that is similar to the bill used for nestling attacks in other siblicidal species. I concluded that siblicide was a reasonable explanation for the nestling mortality patterns observed in Micronesian Kingfishers.

5.2. INTRODUCTION

I evaluated nestling survival in cooperatively breeding Micronesian Kingfishers (*Todiramphus cinnamominus*) on the island of Pohnpei, Federated States of Micronesia. On cooperative territories, young delay dispersal and remain with parents through subsequent breeding attempts while adults nest unassisted on pair territories (Kesler 2002, Kesler and Haig 2005a). In many cooperatively breeding species, some individuals delay dispersal when extra-territorial resources are not available or when substantially higher quality resources can be gained by delaying (Emlen 1982, Stacey and Ligon 1991; e.g., Walters et al. 1992, Komdeur 1992, Komdeur 1994).

Asynchronous hatching and partial brood losses also characterize species in environments with ephemeral resource limitations (Mock 2004). Size differences occur between earlier and later hatching individuals in asynchronously hatching clutches, and larger nestlings are stronger and better able to survive food shortages. Thus, brood reduction is thought to be an adaptive mechanism that enhances parental fitness with high fledging rates during good years while simultaneously ensuring that resources are invested in only those young that can survive during poor years (*see* Drummond and Garcia Chagelas 1989, Mock and Parker 1997, Mock 2004). Broods that can be optimally sized to current environmental conditions may provide fitness benefits to parents but they also set up a competitive environment for nestlings that vie for limited resources. In some species, parents

may even encourage competition to facilitate brood reduction, and

chicks are thought to have evolved specialized behaviors and morphological

characters for the competition that sometimes results in siblicide (Mock 1984,

Mock and Parker 1997, Mock 2004).

To assess whether nestling aggression might have caused partial brood

losses in Micronesian Kingfishers, I compared mortality patterns and

morphological characteristics to other cooperatively breeding and siblicidal

Coraciiformes. Nestling aggression and siblicide have been observed in Blue-

throated Bee-eaters (*Merops viridis*, Bryant and Tatner 1990) and Laughing

Kookaburras (*Dacelo novaeguineae*; Legge and Cockburn 2000, Legge 2000b,

Nathan et al. 2001). Nestling mortality occurs shortly after hatching in Laughing

Kookaburras (Nathan et al. 2001) and modified bills with sharp-hooked tips were

observed during early stages of development in both the kookaburras and bee-

eaters (Bryant and Tatner 1990, Legge 2000b). The hooks apparently facilitated

sibling aggression by enabling nestlings to wound and kill nest mates.

Micronesian Kingfishers are among the most endangered species in the

world. The Guam subspecies of Micronesian Kingfisher (*T. c. cinnamominus*) is

listed as endangered, and only exists as a captive population of fewer than 100

individuals (U.S. Fish and Wildlife Service 1984, U.S. Fish and Wildlife Service

2004). The Pohnpei Micronesian Kingfishers (*T. c. reichenbachii*) have declined

by 63% (Buden 2000). In addition to the implications of these data to

understanding behavior in cooperative Micronesian Kingfishers, I hope results will provide guidance to those attempting to recover the endangered Guam kingfishers through captive breeding and provide information to conservation practitioners in Pohnpei.

5.3. METHODS

Research was conducted on the island of Pohnpei, Federated States of Micronesia (6º 52' N, 158º 13' E). Pohnpei is a circular island with an approximate diameter of 20 km circumscribing the highest peak in the Micronesian chain (nearly 800 m, Engbring et al. 1990). Lowland coastal plateau and mangrove swamps surround the inner mountain range, which is characterized by dense tropical rainforests. Three sites were selected for this investigation, including the Ranch (6º 57' N, 158º 12' E), College of Micronesia (COM; 6º 54' N, 158º 9' E), and Palikir (6º 55' N, 158º 9' E) study areas, which have been described extensively elsewhere (Buden 2000, Kesler 2002, Kesler and Haig 2004, Kesler and Haig 2005a, Kesler and Haig 2005b). Fieldwork was conducted from January to July 1999, March to September 2000, and September 2001.

Nests were located using radio telemetry and by searching forested areas (*see* Kesler and Haig 2004, Kesler and Haig 2005a). Upon discovery of a nest, I estimated development stage by immersing eggs in water (Hays and LeCroy 1971) or visually inspecting chicks. Observers checked nests approximately every two

weeks using a harness and gaff pole-climbers. During each visit,

photographs or video recordings documented nestling condition and developmental

characteristics. Additionally, nest exteriors were visually inspected weekly for

signs of intrusion by macro-predators (e.g. *Felis catus* and *Homo sapiens*).

Estimates of daily and nest period survival were made using Program

Mark's nest survival module (White 2005). A nest schedule was needed to

structure Mark models, so I used observations of a 23 day incubation period from

captive Micronesian Kingfishers (Bahner et al. 1998), and my fledging

observations for a 34 day nestling rearing phase. Nest losses caused by

anthropogenic causes were excluded ($n = 2$) and visit records were scaled to nest

stage and structured to reflect nestling survival for each egg or nestling (*e.g.,*

Anders et al. 1997). Four models were developed to evaluate the relationship

between nestling survival, sociality, and nest phase. The full model included a

covariate for cooperation or pair breeding, and variables for differential survival

during each nest phase. Phases included incubation (days 1-16), hatch and post

hatch (days 17-33), and nestling rearing (days 34-57). Length of the hatch phase

was determined using observations from captive kingfishers, which indicated that

hatching occurred from day 17 through 28 (Bahner et al. 1998). Reduced models

excluded one variable and the null was parameterized for uniform daily survival

from laying to hatching (Table 5.1). The models were fitted to nestling

observations from territories with known social systems, and ranked using second-

order Akaike's Information Criterion (AICc; Burnham and Anderson

2002) in Program Mark (White 2005). I also averaged the nesting cycle days when

birds or eggs were last observed with the first noted date of absence to provide a

second estimate of the timing of nestling disappearances. Unless otherwise noted,

estimates are reported as means with standard deviations (SD) and differences were

considered statistically significant at $\alpha \leq 0.05$.

5.4. RESULTS

I tracked survivorship for 32 nests located on the study areas between March and

October. Generally, Micronesian Kingfishers laid two-egg clutches; only one of 19

nests located during the incubation stage contained a single egg. Observations

from two nests observed during hatching suggested that eggs hatch one to two days

apart. Asynchronous hatching was further confirmed by direct observations of

nests simultaneously containing one egg and a single chick.

The only complete nest failures included two that were smashed by humans.

One of two eggs or nestlings also disappeared from 11 nests. Observations of 53

eggs and nestlings, excluding those killed by humans, were used to estimate a mean

daily nestling survival of 0.989 (*95% CI* 0.980 to 0.994). When extrapolated to the

57-day nesting period, results yielded an estimated nestling survival from laying to

fledging of 0.534 (*95% CI* 0.32 to 0.71). I averaged the nesting cycle days when

birds or eggs were last observed with the first noted date of absence to estimate

Table 5.1. Models of nestling survival (*S*) from laying to hatching for Pohnpei Micronesian Kingfishers during the 1999, 2000, and 2001 breeding seasons. Also noted for each model is the number of parameters (*K*), second-order Akaike's information criterion (AICc) values, AICc differences (Δ_i), and AICc weights (w_i). Subscript indicates model parameterization, with 'social' representing individual estimates for cooperative and pair-breeding territories, "phase" representing different parameter estimates for incubation, hatching, and nestling stages; and (.) representing a pooled estimate.

Model	K	AICc	Δ_i	w_i
$S_{social + phase}$ (full model)	3	60.21	0.00	0.65
S_{social}	2	62.10	1.98	0.25
S_{phase}	2	64.20	4.00	0.09
$S_.$ (null model)	1	68.10	7.89	0.02

timing of nestling disappearances. This yielded nesting day 27.4 (2.7 SE) as the estimated mortality day, which falls shortly after the estimated hatch date. Furthermore pipped shells from two eggs were found below nests containing only a single chick shortly after hatching.

Data from 29 nestlings located on study territories with known social systems (*n* = 15 cooperative, 14 pair-breeders) were used to evaluate the relationship between nestling mortality, nest phase, and sociality. Eight nestlings disappeared from nests on pair territories, while three disappeared from nests on cooperative territories. The top-ranked model from the AICc model ranking process included covariates for both nest phase and social system, indicating a relationship between nestling survival, sociality, and nest phase. Although the top-

ranked model captured 65% of the AICc weight, the second and third-

ranked models also fell within the top 90% of the cumulative weights, suggesting

that they too might be reasonable models (e.g., Burnham and Andersen 2002, p169;

Table 5.1). However, the close rankings probably occurred because the top-ranked

model incorporated parameters from models in the second and third-ranks.

Parameter estimates from the top-ranked model indicated that daily survival

on both pair-breeding and cooperative territories was 1.0 for eggs during the

incubation stage. On pair-breeding territories, parameter estimates suggested a

daily survival 0.937 (0.023 SE; *95% CI* 0.873 to 0.970) during hatching, and 0.986

(0.014 SE; *95% CI* 0.908 to 0.998) during the nestling phase. On cooperative

territories, daily survival estimates were 0.986 (0.001 SE; *95% CI* 0.956 to 0.996)

during hatching, and 0.997 (0.003 SE; *95% CI* 0.979 to 0.999) during the nestling

phase. Together, results reflect no mortality during incubation, the highest rate of

mortality around the time of hatching, and lower rates during nestling rearing

phases. Further, results indicated that nestlings on pair territories have a

probability of survival from laying to fledging of 0.239 (*95% CI* 0.01 to 0.57) and

those on cooperative territories had a probability of 0.741 (*95% CI* 0.28 to 0.93).

Photographs of nestling Pohnpei Micronesian Kingfishers and Guam

Micronesian Kingfishers illustrate that they have hook-tipped bills (Figure 5.1).

The distal end of the upper mandible clearly turns down in a raptor-like curve.

Figure 5.1. Photographs of hooked upper mandible on nestling Micronesian Kingfishers. Series on the left depicts Pohnpei nestlings approximately 10, 14, and 22 days post-hatch, and an adult kingfisher in the last frame for reference. Note that the tips of the bills on Pohnpei Micronesian Kingfishers appeared to have broken off during the nestling phase. The series on the right depicts captive hand-reared Guam Micronesian Kingfisher nestlings on hatch day, and 4, 10, and 18 days post-hatch. Pohnpei photographs by D. Kesler and Guam Micronesian Kingfisher photographs courtesy of H. Bailey, Houston Zoo.

The hook is also differentiated from the eggtooth, which is used to assist

hatching (Gill 1995). Pigmentation differences in the bill brightly offset the sharp

hook from the midsection. Hooks on Pohnpei Kingfisher bills appear to have

broken off prior to fledging, while the tips of the captive Guam Kingfisher bills did

not.

5.5. DISCUSSION

Theory and results from previous investigations suggest that limited resource

availability affects nestling survival and rates of cooperative breeding (*see*

Komdeur 1991, Komdeur 1994, Ligon 1999, Mock 2004). Similar to Legge

(2000), the top-ranked model estimated higher nestling survival on cooperative

territories than on non-cooperative territories. Micronesian Kingfishers on

cooperative territories have access to more resources (Kesler and Haig *in review a*,

which may result in higher nestling survival as well as encourage more delayed

dispersers. Alternatively, the higher nestling survival observed on cooperative

kingfisher territories might be the result of increased feeding rates from helpers.

Although helpers have never been observed delivering food items to nests, results

from radio telemetry suggested that they occasionally travel from foraging areas to

nests and that helpers remain for extended periods in nesting areas (Kesler,

unpublished data).

Numerous investigations of nesting success have been
conducted for a range of continental species, but few have addressed the
demographic characteristics of forest birds on oceanic islands. Predators have
profound influence on nesting and the evolution of life history characteristics in
continental systems (Martin 1988, Martin 1995), but oceanic islands often lack
predators (Savidge 1984, Brockie et al. 1988, Loope et al. 1988, Milberg and
Tyrberg 1993). While typical predators are generally absent from Pohnpei, the
island does host introduced rats (*Rattus* sp.). However, if predators were
responsible for the mortalities reported here, it seems that two nestlings would have
been lost from at least some of the nests and that the timing of nestling mortality
would have been variable. Contrarily, I observed only single nestling
disappearances that occurred almost entirely during the hatching phase. Eggshell
evidence further suggested that nestlings hatched and then disappeared shortly
thereafter. My observations are similar to those of Laughing Kookaburras, in
which one third of the nestlings were lost to siblicide within a few days of hatching
(Legge 2000b). Hatching asynchronously, phylogenetic relatedness, and being
cooperative breeders in low-predation environments are also characteristic of other
siblicidal species (Mock and Parker 1997).

Hooked bills identified on both Guam and Pohnpei nestling Micronesian
Kingfishers are similar to those present in other siblicidal Coraciiformes during
early stages of development. The hooks may facilitate sibling aggression, as they

do in Laughing Kookaburras and Blue-Throated Bee-eaters (Bryant and

Tatner 1990, Legge 2000b, Nathan et al. 2001). Alternatively, the hooked bills

may be used to scrape nests for sanitation purposes, a behavior previously reported

in Belted Kingfishers (*Ceryle alcyon*; Cornwell 1963). However, evidence of

scraping was never observed during work with Pohnpei Micronesian Kingfishers.

The hooks may also be used to manipulate or tear apart food, but forage items are

consumed whole by captive Guam Micronesian Kingfisher nestlings (S. Median,

Guam Department of Wildlife and Aquatic Resources, personal communication)

and Pohnpei Micronesian Kingfisher adults (D. Kesler, personal observation).

Further, the hooks are offset in appearance from the rest of the bill by a lack of

pigmentation, which may serve as a warning to nest mates in the darkened nest

cavities. Thus, I concluded that siblicide is a reasonable explanation for nestling

morality in the Pohnpei Micronesian Kingfishers.

Previous work evaluating kin aggression has outlined several pathways to

increased fitness for both parents and nestlings (O'Connor 1978, Mock and Forbes

1994, Mock and Parker 1997). Individuals in smaller broods may be better able to

survive than those in larger broods when food resource are limited, so brood

reduction can ultimately increase parents' fitness. Similarly, nestlings may gain

increased fitness by killing brood mates who compete for food resources. Because

those brood mates are likely to be kin, they also suffer some loss of inclusive

fitness. The fitness benefits associated with the death of nestlings differs between

parents and siblings, however, so there is also the potential for parent-offspring conflict over siblicide (Trivers 1974, O'Connor 1978, Mock, 1987). The conflict can be especially intense when nestlings possess "weaponry", like the hook-tipped bills of Micronesian Kingfishers, to resolve the issue in their favor (OConnor 1978, Mock 1984, Mock 1987). Thus, documenting the timing and occurrence of siblicide, the parents' involvement in encouraging or discouraging the behavior, and impacts on individual fitness are worthy of additional investigation in Micronesian Kingfishers. Furthermore, there is suggestive evidence that some Micronesian Kingfisher brood mates may not be full siblings (Kesler and Haig *in review b*), which would alter inclusive fitness costs associated with killing brood mates and broaden the gap between fitness benefits for nestlings and parents. Thus, a study of parentage would provide insight into motivation for sibling aggression and the distribution of fitness in Micronesian Kingfishers.

Results provide insight into the conservation management of Micronesian Kingfishers. Survival estimates may be used for population demographic analyses and projection models for Pohnpei birds or a reintroduced population of Guam kingfishers (U.S. Fish and Wildlife Service 2004). However, survival may be localized and the reliability of the laying to fledging values is related to the estimated nesting schedule, so estimates should be employed with caution. Guam kingfishers only exist as a captive breeding population in U.S. zoos. Although many of the captive nestlings are hand-reared, some are left under parental care (B.

Bahner, Philadelphia Zoo, personal communication). Institutions propagating the birds should consider hand-rearing one of two nestlings from all clutches to prevent the potential for nestling losses to siblicide. Additionally, the population of Micronesian Kingfishers has declined by 63% in Pohnpei (Buden 2000). Investigation into the importance of resources and supplemental feeding by helpers, which may underlie siblicidal behaviors, could provide direction to management agencies about actions that may increase Micronesian Kingfisher reproductive success.

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6. CONSERVATION BIOLOGY FOR SUITES OF SPECIES: DEMOGRAPHIC MODELING FOR PACIFIC ISLAND KINGFISHERS

6.1. ABSTRACT

Conservation practitioners frequently extrapolate data from single-species investigations when managing critically endangered populations. However, few researchers initiate work with the intent of making their findings useful to conservation efforts for other species. I emphasize the need for research and results structured for suites of geographically separated populations with similar natural histories, resource needs, and extinction threats. An example is provided in the form of an investigation into the population demography of endangered Micronesian Kingfishers (*Todiramphus cinnamominus*). I assessed vital rates in a study population on the island of Pohnpei, and used results to develop a population projection matrix model that could serve as base model for the 12 endangered Pacific *Todiramphus* species. Elasticity analyses were used to assess the importance of vital rates and life history stages to population dynamics. A simulation of matrices with randomly varied rates was also employed to gain insight into the model's robustness to vital rate differences and assess its applicability as a generalized representation of kingfisher population dynamics. Results from elasticity analyses suggested that even as rates changed, adult survival

exerted greater influence on population dynamics than other vital rates.

To the contrary, a regression of simulated vital rates against the lambda parameter suggested that all life history stages similarly influenced population behavior. I concluded that conservation practitioners addressing endangered Pacific kingfishers should broadly focus efforts on survival during all life history stages. I further discuss how the generalized base model might be enhanced with additional information or altered to focus on individual populations.

6.2. INTRODUCTION

Conservation biologists have long embraced the use of information from surrogate populations for managing endangered species (Bednarz 1987; Sydeman 1989; Legge 2000; Linacre et al. 2004; Bar-David et al. 2005; Doak et al. 2005). Surrogates can be necessitated by a lack of knowledge about the particular population of interest, combined with time and resource constraints that prevent thorough investigations. Additionally, some endangered populations have been so affected by their situation, that the natural history of remnant individuals may not reflect historic behavior as accurately as surrogates.

Many researchers have used meta-analyses to provide information about biological patterns that are characteristic of groups of species (e.g., Sæther 1988; Heppell et al. 2000; Sæther & Bakke 2000). However, the data needed for meta-analyses are not always available, so conservation practitioners frequently

extrapolate or transfer information laterally one species to another for

conservation purposes. Despite the common transference of information for

management, few researchers have initiated investigations with the *a priori* intent

of providing conservation-oriented results that can be used for similar populations.

Here, I emphasize the need for identifying research and structuring results to

benefit geographically separated populations of related organisms that share similar

natural histories, resource needs, and extinction threats.

Suites of geographically disparate populations that are phylogenetically

related and ecologically similar characterize many regions. The pattern is most

prevalent in isolated island populations and numerous examples are found among

the avifauna of oceanic islands in the tropical Pacific. For example, most islands in

Pacific Oceania host a resident population of doves (*Ptilinopus* spp., *Gallicolumba*

spp.), fantails (*Rhipidura* spp.), white-eyes (*Zosterops* spp.), reed-warblers

(*Acrocephalus* spp.), and honeyeaters (*Myzomela* spp.). Similarly, larger islands

are also characterized by kingfishers (*Todirhamphus* spp.), flightless rails

(*Gallirallus* spp.; *Porzana* spp.), megapodes (*Megapodius* spp.), and pigeon species

(*Ducula* spp.; Baker 1951; Pratt et al. 1987; Mayr & Diamond 2001). These small

pockets of endemism are also subject to extreme extinction rates, as over 90% of

the world's recent bird extinctions have occurred on islands (Johnson &

Stattersfield 1990). Within the aforementioned 11 genera, 76 species in Oceania

are listed as vulnerable, threatened, or in danger of extinction (U.S. Fish and

Wildlife Service 1984; IUCN 2004). However, few researchers have addressed even the most basic morphological and natural history characteristics for many of these species despite the dire situation. Clearly, there is not enough time or resources to thoroughly investigate the biology of each before conservation practitioners must act.

One option for addressing the immediate need for information is to use surrogate populations and plan research so that results are useful to conservation efforts for suites of ecologically similar and related taxa. Population biology is an especially appealing arena for generalized research because population models are some of the most fundamental tools used by those managing severely declining and critically endangered populations (Morris & Doak 2002; Beissinger & McCullough 2002). Population models range in scope and complexity from qualitative conceptual models to individualized and spatially explicit models that are used to predict extinction probabilities in population viability analyses (PVA; Caswell 2001; Morris & Doak 2002; Beissinger & McCullough 2002; Beissinger et al. *in press*). Quantitative models are all driven by demographic information and many modeling attempts have been hindered by a lack of data about survival, reproduction, and movement (Ruggiero et al. 1994; Caughley & Gunn 1996; Morris & Doak 2002; Beissinger & McCullough 2002). Thus, population demography is an appropriate place to explore the benefits of investigations intended to provide information useful to conservation efforts for suites of species.

I present an example of a demographic investigation of the Pohnpei

Micronesian Kingfisher (*Todiramphus cinnamominus reichenbachii*) that was

initiated with the intent of benefiting both the Pohnpei population of kingfishers

and related endangered Pacific island congeners.

6.2.1. Pacific Kingfishers

Micronesian Kingfishers (*T. cinnamominus*) are one of 12 Pacific region

Todiramphus species listed as vulnerable, threatened, or endangered by federal and

international conservation authorities (U.S. Fish and Wildlife Service 1984; IUCN

2004). Life histories of the birds are generally similar across the islands, as they

are all terrestrial forest birds inhabiting similar vegetation communities and

climates. They are also nutritional generalists that nest in cavities excavated from

the soft wood of decaying trees or the soft material of arboreal termite nests

(Marshall 1989; Fry et al. 1992; Kesler & Haig 2004, 2005b). Nonetheless, there

are critically few data available for conservation practitioners to use in managing

these endangered birds.

Demographic data are of particular interest to those involved with

conservation efforts for the Micronesian Kingfisher (U.S. Fish and Wildlife Service

2004), Marquesas Kingfisher (*T. godeffroyi*), Niau Kingfisher (*T. gambieri*), and

the Pacific Kingfisher (*T. tuta*; A. Gouni, Société d'Ornithologie de Polynésie,

personal communication). Of these, the Guam subspecies of Micronesian

Kingfisher (*T. c. cinnamominus*) is perhaps in the most perilous

predicament, as they are extinct in the wild and only exist in a captive population.

Few studies were made of the Guam kingfishers before the last wild individuals

were captured and placed in captivity in 1985 (Marshall 1989; Haig & Ballou

1995; Haig et al. 1995). However, plans are now under way to reintroduce the

Guam Micronesian Kingfisher back to native habitats (U.S. Fish and Wildlife

Service 2004), and demographic data are vital to the effort. Similarly, conservation

practitioners responsible for *T. c. reichenbachii, T. c. pelewensis, T. godeffroyi, T.*

gambieri, and *T. tuta* are faced with the likely possibility that needed demographic

information cannot be obtained from each respective population in time to prevent

extinction (A. Gouni, Société d'Ornithologie de Polynésie, personal

communication).

I evaluated survival and reproduction in a resident population of Pohnpei

Micronesian Kingfishers (*T. c. reichenbachii*) to provide foundational demographic

information for a generalized *Todiramphus* kingfisher population model. As has

been suggested for other congeners (Beckon 1987), the Pohnpei Micronesian

Kingfishers breed as pairs or cooperative groups of three (Kesler 2002; Kesler &

Haig 2005a, 2005b). Cooperative groups are comprised of a pair of dominant

putative breeders, and a delayed disperser from a previous reproductive attempt, or

helper. I used multiple techniques to validate survival estimates, and attempted to

broadly address vital rate parameters. Then, I developed a prospective population

projection matrix that was used in sensitivity and elasticity analyses

(Caswell 2000; Williams et al. 2001; Morris & Doak 2002). Vital rates were

randomly varied across a range of potential values that might characterize multiple

Todiramphus species across the insular Pacific in a life-stage simulation analysis

(Wisdom et al. 2000) of 10,000 matrices. I estimated elasticities and regressed

vital rates against λ to identify demographic parameters key to population

dynamics and conservation.

6.3. METHODS

6.3.1. Study area

Research was conducted on the island of Pohnpei, Federated States of Micronesia

(6º52' N, 158º13' E). Pohnpei is a circular 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 sites were selected for this investigation including the Ranch

(6º57' N, 158º12' E), College of Micronesia (COM; 6º54' N, 158º9' E), and Palikir

(6º55' N, 158º9' E) study areas. The study sites have been described extensively

elsewhere (Buden 2000; Kesler 2002; Kesler & Haig 2004; Kesler & Haig 2005a,

2005b). Each area included strand vegetation, early succession and mature lowland

rainforest, grassland, urban vegetation, and agroforest (Mueller-

Dombois & Fosberg 1998; Buden 2000).

6.3.2. Study population

I radio-marked and color-banded a population of Micronesian Kingfishers on

Pohnpei study areas between 1999 and 2004. Birds were captured by mist net and

fitted with a 1.8g telemetry package (Holohil Systems, Ltd., Ottawa, Canada) using

a leg-harness design (Rappole & Tipton 1991), and a unique combination of

colored leg-bands and a numbered aluminum U.S. Fish and Wildlife Service band.

The age and sex of each bird was determined using genetic analyses, plumage, and

morphological characteristics (Kesler et al. *in review*). The study population was

intensively observed from January to July 1999, March to August 2000, September

2001, September 2002 to January 2003, and October and November 2004. Birds

were radio-marked during 1999, 2000, and 2002 fieldwork and color-banded every

year.

Pohnpei Micronesian Kingfishers breed as pairs and cooperative groups

(Kesler 2002; Kesler & Haig 2005a, 2005b).   For the purposes of this study, I

follow the terminology of recent literature (e.g., Haydock & Koenig 2002) by using

"dominant" to refer to the putative breeders on a territory and "helper" for

offspring that delayed dispersal through subsequent reproductive attempts.

Additionally, I use hatch-year (HY) to describe progeny of the most

recent breeding season, and after hatch year (AHY) to describe all non-juveniles.

6.3.3. Population model

The conceptual *Todiramphus* kingfisher population model and its associated

parameters are illustrated in Figure 6.1. Briefly, it describes a cooperatively

breeding population that includes helpers who delay dispersal and independent

attempts at reproduction. I used data from six years of color-band resighting, three

years of radio telemetry, and numerous nesting and behavior observations to

translate the conceptual model into a quantitative deterministic population

projection matrix. To determine whether vital rates should be separated by social

class, sex, or both in the model, color-band resight data were analyzed using

Cormack-Jolly-Seber (CJS) estimation methods (Pollock et al. 1990; Lebreton et al.

1992). Individuals may be present on study areas but missed when resighting

color-bands (Anders & Marshall 2005), so I estimated both apparent survival and

the probability of resight ($\hat{p}$ juvenile, $\hat{p}$ helper, $\hat{p}$ dominant). I constructed biologically

reasonable survival models with covariates for sex and life-stage, and combined

parameter estimates for survival (ϕ) and p (Table 6.1). Models were then ranked

using Akaike's Information Criteria (AICc; see Burnham & Anderson 2002) in the

live recapture module of Program Mark. The top-ranked model was then used to

structure the population projection matrix.

I also evaluated whether cooperation influenced apparent

survival by comparing the probabilities of resighting birds following a year of

occupancy on cooperative and pair territories. Further, I compared the odds of

reproduction among newly settled dominants with dominants that had been

observed for multiple years to determine whether the population projection matrix
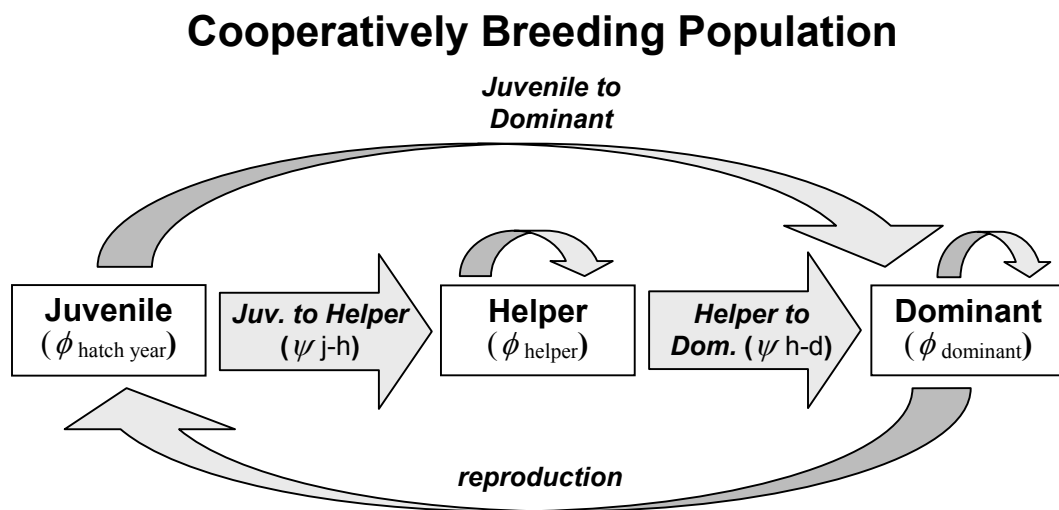
model should include age structuring.

Cooperatively Breeding Population

Figure 6.1. Conceptual population model for Pacific *Todiramphus* kingfishes, and associated model parameters (in parentheses).

6.3.4. *Model parameterization*

Once a matrix model structure had been determined, I used observations from

kingfishers on the Pohnpei study areas to derive estimates for the vital rates needed

to populate the model. Nestling survival estimates were previously published for

Micronesian Kingfishers from laying to fledging ($\phi_{nestling}$; Kesler & Haig *in review*

a). I used radio-telemetry observations to estimate mean survival from fledging

through the first year ($\phi_{juvenile}$), and for after hatch year survival (ϕ_{AHY}). Radio-

marked individuals were located using triangulation (see Kesler & Haig *in review*

b), and birds were approached on foot to verify mortality if movement was not

detected during three consecutive days. Annual survival estimates were made with

the known fate model in Program Mark (White 2005) using Kaplan-Meier

estimation methods (Kaplan & Meier 1958). Together, survival estimates for

nestling and juvenile stages yielded a survival estimate for the first year of life, or

hatch year survival (ϕ_{HY}), such that:

$$\phi_{HY} = \phi_{nestling} * \phi_{juvenile}$$

Additionally, the population matrix model required estimates of the proportion of

individuals transitioning among life history stages (ψ). Transitions included

juveniles that became helpers or dominants, and helpers that became dominants

(respectively, ψ_{j-h}, $1-\psi_{j-h}$, ψ_{h-d}). I used the observed proportion of color-banded

individuals that made each transition to populate the model.

6.3.4.1. Population model structure

Following assessment of Pohnpei Micronesian Kingfishers, a deterministic

population projection matrix model was structured to reflect a cooperatively

breeding population of *Todiramphus* kingfishers. I assumed a 1:1 sex ratio for eggs

and constancy in rate parameters across time. Both sexes have been observed as

helpers and territory holders, so the model was based on females (Kesler & Haig *in*

review b). I structured the model to reflect a pulse-breeding population with a time

step occurring immediately after laying, so that nestling and juvenile mortality

could be included separately. I then estimated the dominant eigenvalue (λ), which

represents the asymptotic rate of population change and provides a general measure

of whether a population is projected to increase or decrease in size. Sensitivity (*S*)

and elasticity (*E*) statistics were estimated by altering each rate by 0.01 and using a

"brute force" method to assess change in λ (e.g., Heppell et al. 2000; Morris &

Doak 2002 p. 330). Sensitivity for each vital rate represents the amount of change

in λ associated with small changes in θ, where θ is the demographic parameter of

interest, or

$$S_\theta = \partial\lambda/\partial\theta$$

(from Williams et al. 2001; p151). Elasticity is a metric scaled to reflect the

proportional change in λ that is brought about by a similarly proportioned change

in θ, which facilitates comparisons among θ:

$$E_\theta = \frac{\partial\lambda/\partial\theta}{\lambda/\theta}$$

(from Williams et al. 2001; p152).

To provide insight into how different vital rates across populations of *Todiramphus* kingfishers might influence model behavior, I varied each vital rate and recalculated λ, S and E to evaluate response to changes. As a guideline for survival variation, I used an interval that was equal in width to the 95% confidence intervals from the CJS estimates (*e.g*, Morris & Doak 2002, p348). The CJS interval-widths were selected over known fate intervals because they were collected over a longer period (six vs. three years), and were therefore more likely representative of actual variance in vital rates. Intervals were centered on mean survival estimates derived from the known fate analysis because the point-estimates were less likely to be biased by resight probabilities. Annual breeding attempts ranged from 1.5 to 2.5. The proportion of helpers transitioning to dominants varied between 0.25 and 0.75, and juvenile to helper transition rates varied between 0 and 0.5 to represent a pair-breeding population of kingfishers and a population with a higher proportion of helpers than I observed in Pohnpei. Rates varied independently and they were selected from a uniform distribution (e.g., Wisdom & Mills 1997) generated by SAS (SAS Institute 1999). Microsoft Excel (Microsoft Corporation 2000) and Matrix and Linear Algebra addin for Excel (Volpi 2005) were used to simulate 10,000 models, calculate and rank sensitivity and elasticity values for each, and summarize results.

As a second method of evaluating the influence of vital rates on population change across multiple combinations of randomly varied rates, I used SAS (PROC REG, SAS Institute 1999). For each simulated model, λ was regressed against each vital rate using linear regression and coefficients of determination (r^2) were estimated for each (see Wisdom & Mills 1997). Unless otherwise noted, estimates are reported as means with standard deviations (SD) in parentheses and differences are considered statistically significant at $\alpha \leq 0.05$.

6.4. RESULTS

Pohnpei Micronesian Kingfishers bred both as cooperative groups and pairs on the three study areas. I color-banded 39 juveniles (16M; 23F), 14 helpers (10M; 4F), and 44 dominants (21F; 23M), which were observed during 153 bird*years. Sixteen juvenile Micronesian Kingfishers (7M:9F) were radio-marked and observed daily for a mean of 37 (15 SD) days each, during the first 10 months post-fledge ($n = 839$ telemetry locations; 579 telemetry*bird*days). Additionally, 13 radio-marked helpers (8M:5F) and 35 dominants (19M:16F) were monitored for a total of 571 bird*weeks (128 helper*bird*weeks, 443 dominant*bird*weeks).

6.4.1. Model structure

I compared the reproduction in newly settled dominants ($n = 15$ male*territory*years; 18 female*territory*years) with dominants observed on

territories during the previous years ($n = 15$ male*territory*years; 14 female*territory*years). Results showed no differences in either the odds of reproducing ($P > 0.05$; log odds ratio = 0.38, 0.87 SE for males; 0.18, 0.99 SE for females) or in the number of offspring on territories at the end of each breeding season (t-test; $P > 0.05$; $n = 30$ male and 32 female*territory*years; mean offspring = 1.20 and 1.53, 1.33 and 1.36 for males and females respectively). Thus, results did not indicate strong age structuring in Micronesian Kingfisher reproduction and suggested that an age structured model was not necessary.

I used color-band resight data and CJS methods to determine the population projection matrix model structure and estimate apparent survival confidence intervals. Results indicated that the population projection matrix model should include separate survival estimates for HY and AHY individuals, but that further structuring of survival rates for sex, age, or social class was not necessary. The top-ranked model included apparent survival estimates for juveniles (0.220 ± 0.069 SE; *95% CI* = 0.114 to 0.382), and a combined parameter estimate for helpers and dominants (Table 6.1; 0.540 ± 0.051 SE; *95% CI* = 0.440 to 0.636). The model also included a combined resight probability estimate ($\hat{p}$.) for all three

Table 6.1. Models of annual survival (ϕ) and recapture probabilities (p) for color-banded Pohnpei Micronesian Kingfishers between 1999 and 2004. Also noted for each model is the number of parameters (K), second-order Akaike's Information Criterion (AICc) values, AICc differences (Δ_i), and AICc weights (w_i). Subscript indicates model parameterization, with 'social' representing individual estimates for juvenile, helper, and dominant; and 'AHY' representing combined estimates for helpers and dominants. Separate survival estimates are made for males and females when subscripts are modified by '* sex'. No subscript represents estimates for combined classes.

Model	K	AICc	Δ_i	w_i
$\phi_{\text{juvenile., AHY}}\; p_{.}$	**3**	**187.642**	**0.00**	**0.37**
$\phi_{\text{social}}\; p_{.}$	4	189.195	1.57	0.17
$\phi_{\text{juvenile., AHY * sex}}\; p_{.}$	4	189.687	2.06	0.13
$\phi_{\text{social * sex}}\; p_{.}$	7	190.039	2.42	0.11
$\phi_{\text{juvenile., help., dom * sex}}\; p_{.}$	5	190.664	3.04	0.08
$\phi_{\text{juvenile., AHY}}\; p_{\text{social}}$	5	191.204	3.56	0.06
$\phi_{\text{social}}\; p_{\text{social}}$	6	192.943	5.32	0.02
$\phi_{\text{juvenile, AHY * sex}}\; p_{\text{social}}$	6	193.339	5.71	0.02
$\phi_{\text{social * sex}}\; p_{\text{social}}$ *(Full Model)*	9	193.873	6.25	0.01
$\phi_{\text{juvenile., help., dom.* sex}}\; p_{\text{social}}$	7	194.462	6.84	< 0.01
$\phi_{.}\; p_{.}$ *(Null Model)*	2	196.892	9.27	< 0.01
$\phi_{.}\; p_{\text{social}}$	4	199.176	11.55	< 0.01

social classes of 0.968 $\pm$ 0.031 SE (*95% CI* = 0.802 to 0.996). Models

with covariates for sex ranked lower, indicating no strong differences in survival

among males and females.

Odds ratio tests further indicated that separate parameters were not

warranted for cooperative and pair-breeding territories, or for males and females in

the population projection matrix model. During subsequent years, there was no

statistical difference in the odds of resighting individuals fledged from cooperative

(n = 12 fledged, 3 resighted) and non-cooperative territories (n = 19 fledged, 2

resighted; *P* > 0.05; *log odds ratio* = 0.87; *95% CI* 2.80 to –1.06). Similarly, there

was no difference in the odds of resighting fledgling males (n = 15 fledged, 1

resight) or females (n = 16 fledged, 4 resight) the subsequent year (*P* > 0.05; *log*

odds ratio = -1.32; *95% CI* 0.98 to -3.62).

6.4.2. Vital rate estimation

6.4.2.1. Annual breeding attempts

Nest observations and plumage characteristics suggested that breeding pairs initiate

multiple nests each year. During 2000 fieldwork, when observers were present on

study areas throughout the breeding season, I observed renesting after the first

clutch on 70% (7/10) of territories where breeding occurred, with a mean inter-

clutch interval or 45 days (21 SD, 16 min, 61 max; n = 4 territories with known

resenting dates). Subsequent observations following breeding in 2001-

2004 showed staggered plumage coloration in co-territorial juveniles, which further

suggested that renesting was common. Additionally, during three territory*years,

three stages of staggered juvenile plumages suggested that they were the result of

three separate nesting attempts in one year.

6.4.2.2. Survival

Survival from laying to fledging, including clutch size, nest failure rates, and

partial brood losses have been previously elsewhere (Kesler & Haig *in review a*).

Telemetry data from juvenile Micronesian Kingfishers were summarized into

weekly observations ($n = 130$ bird*weeks) and known fate analysis yielded an

estimated weekly survival rate of 0.977 (*95% CI* 0.931 to 0.993) and $\hat{\phi}_{juvenile}$ of

0.366 (*95% CI* 0.088 to 0.777). When estimated juvenile survival is combined with

previously published estimates of survival for nestlings from laying to hatch

(Kesler & Haig *in review a*), the probability that an individual survives from the

time of laying through the next breeding season ($\hat{\phi}_{HY}$) is 0.195 ($\hat{\phi}_{HY} = 0.534$ *

0.366). Known fate analyses of helper and dominant survival were conducted

using radio-telemetry data from 13 radio-marked helpers (8M:5F) and 35

dominants (19M:16F), which were monitored for a total of 571 bird*weeks (128

helper*bird*weeks, 443 dominant*bird*weeks). Known-fate data for helpers and

dominants were pooled in accordance with results from the CJS model ranking

procedure, and the analysis yielded an estimated $\hat{\phi}_{AHY}$ of 0.577 ± 0.130

SE (*95% CI* = 0.326 to 0.794).

6.4.2.3. *Transitions among social classes*

Observations of transitions among social classes were rare. One female first

marked as a juvenile was subsequently observed as a helper and four females were

later observed as breeders. Additionally, four helpers (3M:1F) remained as such

during subsequent observations and five (2M:3F) transitioned to dominant status.

Estimated transition rates were therefore 0.2, 0.8, and 0.6 for $\hat{\psi}_{j-h}$, $1-\hat{\psi}_{j-h}$, and $\hat{\psi}_{h-d}$, respectively.

6.4.3. **Population matrix analysis**

I developed a deterministic population projection matrix model using results from

analyses of survival and reproductive success in Pohnpei Micronesian Kingfishers.

In accordance with the top-ranked CJS model, no differentiation was made between

survival estimates for males and females, or between birds on cooperative and pair-

breeding territories, and the $\hat{\phi}_{AHY}$ estimate was used for both helpers and

dominants. Based on results from the odds-ratio test, I included no age structuring

in reproductive success. Transition rates ($\hat{\psi}$) were set at observed proportions, the

number of nest attempts for each individual (*f*) was set at two, and I assumed that

all dominant individuals attempted to breed (B). The structure of the

cooperative breeding population matrix model follows:

$$
\begin{array}{ccc}
HY & Helper & Dominant
\end{array}
$$

$$
A = \begin{bmatrix}
a_{11} & a_{12} & a_{13} \\
a_{21} & a_{22} & a_{23} \\
a_{31} & a_{32} & a_{33}
\end{bmatrix}
$$

$$
= \begin{bmatrix}
(\hat{\phi}_{HY} * f * B) & (\hat{\phi}_{AHY} * \psi_{h-d} * f * B) & (\hat{\phi}_{AHY} * f * B) \\
(\hat{\phi}_{HY} * \hat{\psi}_{j-h}) & (\hat{\phi}_{AHY} * [1 - \hat{\psi}_{h-d}]) & 0 \\
(\hat{\phi}_{HY} * [1 - \hat{\psi}_{j-h}]) & (\hat{\phi}_{AHY} * \hat{\psi}_{h-d}) & (\hat{\phi}_{AHY})
\end{bmatrix}
$$

$$
= \begin{bmatrix}
0.3127 & 0.6411 & 1.1540 \\
0.0391 & 0.2564 & 0 \\
0.1564 & 0.3206 & 0.5770
\end{bmatrix}
$$

The matrix element a_{ij} represents the number of individuals in class i at the next

time step that will arise from those currently in class j (see Caswell 2001; Morris &

Doak 2002). Elements in the top row are functions of survival and fecundity while

those below are elements of survival and transition. The second matrix illustrates

how elements were calculated from vital rate data presented above, and the third

includes base-value point estimates. The λ value for the cooperative breeding

population projection matrix is 0.927, which represents a declining population.

I evaluated the influence of demographic parameters on population

dynamics using sensitivity and elasticity analyses (Table 6.2). Results from the

point-estimate model indicated survival of dominant breeders had the strongest

influence on population dynamics ($E = 0.590$). Changes in the number

of nests attempted per year, nestling and juvenile survival, and the proportion of the

population breeding also substantially influenced λ. Changes in helper-associated

parameters had relatively little influence on λ, which is likely a result of their

minor contribution to reproduction. The model also included transition parameters

for the proportion of birds moving between social classes, but transitions did not

remove individuals from the population entirely, so it follows that their elasticities

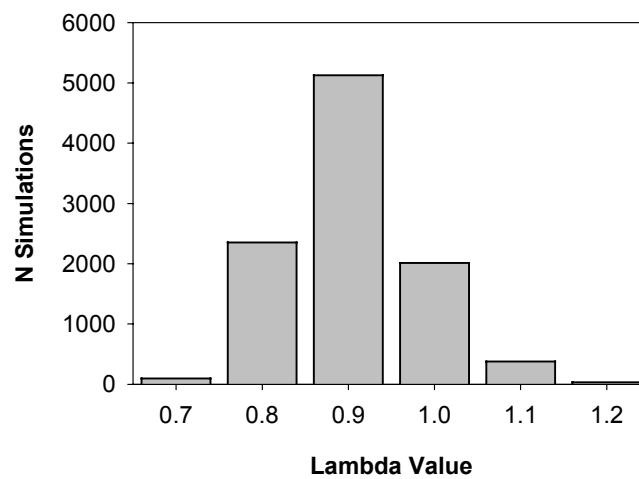were lower than other vital rate estimates.

Figure 6.2. Distribution of λ values from 10,000 population projection matrix model simulations with varying vital rates for cooperatively breeding Micronesian Kingfishers.

Simulations were used to gain insight into possible characteristics of population dynamics of *Todiramphus* kingfisher populations with vital rates different from those identified on the Pohnpei study areas (Table 6.2). The distribution of λ values resulting from the 10,000 simulated matrices is presented in Figure 6.2. Results of the simulation exercise suggested that the overall ranking of vital rate elasticities did not differ from the point-estimate model. Changes in adult survival had the highest proportional influence on population dynamics, as adult survival ranked with the highest elasticity in all simulations (Figure 6.3.).

Elasticity results further suggest that nestling and juvenile survival, and the proportion of the population breeding also substantially influence λ. Vital rate importance was also evaluated by regressing each simulated rate analysis against resulting λ values (Table 6.2; Figure 6.4). Rates with higher r^2 values explained more variation in λ, and are therefore thought to be of conservation importance (Wisdom & Mills 1997; Wisdom et al. 2000; Beissinger et al. *in press*). Unlike the elasticity rankings, results from the regression analysis yielded similar values for nestling survival, juvenile survival, and dominant survival ($r^2 = 0.27, 0.26, 0.23$, respectively). Thus indicating that while nestling and juvenile survival were most closely correlated with changes in lambda, all three survival rates have similar importance to conservation practitioners when considering a broad range of *Todiramphus* populations.
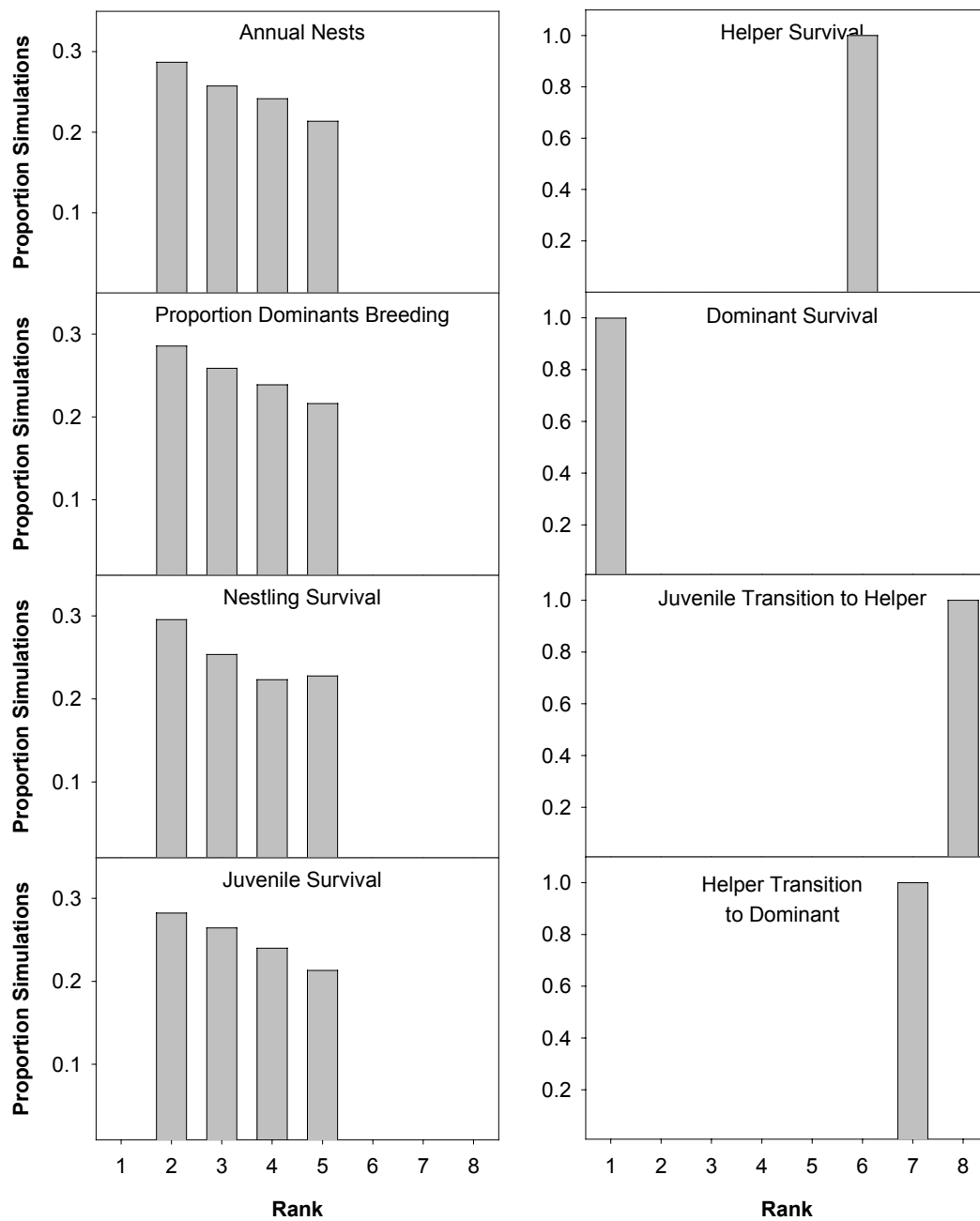
Figure 6.3. Proportional rankings of elasticity values for vital rates from 10,000 simulations of randomly varied population projection matrix for cooperatively breeding Micronesian Kingfishers. Ties received the same rank, so some columns may add to a total value of > 1.
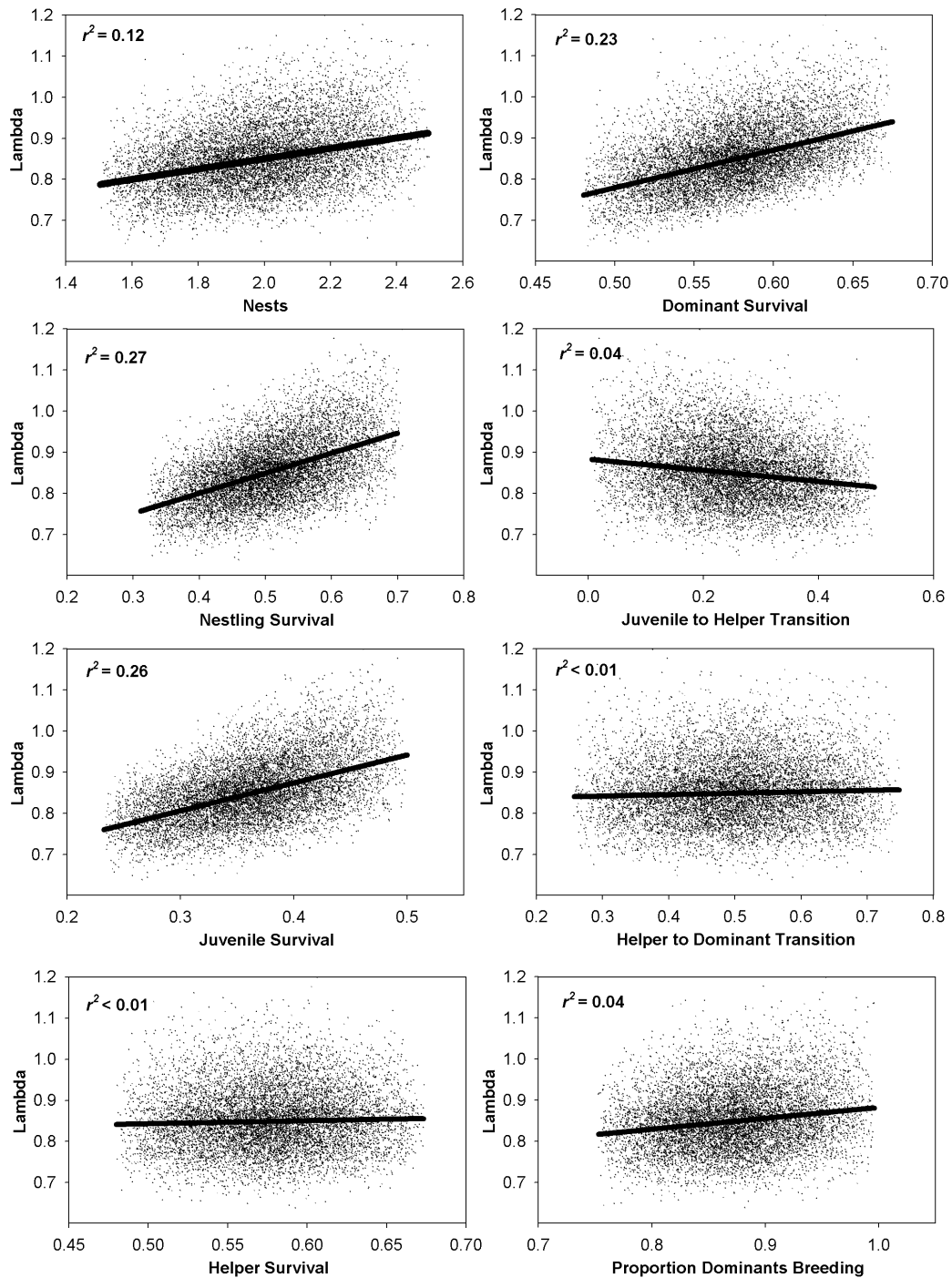
Figure 6.4. Regression of vital rates against λ values resulting from 10,000 population projection matrix model simulations with varying vital rates. Values for r^2 represent the concordance between vital rates and λ

Table 6.2. Elasticity (E), sensitivity (S), and r^2 values for vital rate regressions with λ for results from the point-estimate model and the simulation of randomly varied vital rates for *Todiramphus* kingfishers.

Parameter	Point Estimate		Simulation		r^2 [d]
	Base Value	S/E	Range	90% E Interval[c]	
Reproduction					
Nests (N)	2	0.179 / 0.358	1.5 – 2.5	0.220 – 0.390	0.12
Breeding adults (P)	1	0.358 / 0.358	0.75 – 1.00	0.220 – 0.390	0.03
Survival (ϕ)[a]					
$\phi_{nestling}$	0.534	0.670 / 0.358	0.320 – 0.710	0.220 – 0.390	0.27
$\phi_{juvenile}$	0.366	0.977 / 0.358	0.088 – 0.777	0.220 – 0.390	0.26
ϕ_{helper}	0.577	0.092 / 0.053	0.326 – 0.794	0.020 – 0.123	0.01
$\phi_{dominant}$	0.577	1.022 / 0.590	0.326 – 0.794	0.542 – 0.720	0.23
Transitions (ψ)[b]					
$\psi_{juvenile\ to\ helper}$	1/5 = 0.2	-0.209 / -0.042	0.000 – 1.000	-0.082 – -0.012	0.04
$\psi_{helper\ to\ dominant}$	5/9 = 0.6	0.036 / 0.020	0.250 – 0.750	0.007 – 0.037	<0.01

[a] base value estimates for ϕ_i resulted known-fate analyses of radio telemetry data, and were structured in accordance with the top-ranked model from color-band recaptures only analyses.

[b] base values for ψ_i were derived from observations of color-banded Pohnpei Micronesian Kingfishers that moved among social classes on the study areas.

[c] The 90% E interval represents the observed range of elasticity values with the most extreme 10% removed.

[d] The r^2 value represents the amount of variation in λ accounted for by each vital rate.

6.5. DISCUSSION

I assessed population demographic characteristics in Pohnpei Micronesian

Kingfishers and used those data to develop a population projection matrix model

that could be generalized to other Pacific island *Todiramphus* kingfishers. During

the nestling stage, siblicide apparently causes a major portion of the mortality in

Micronesian Kingfishers (Kesler & Haig *in review a*). After fledging, the observed

survival rate of 0.37 in juvenile Micronesian Kingfishers was similar to a mean rate

of 0.40 in 39 species reviewed by Sæther and Bakke (2000). However, survival in

AHY kingfishers was lower than the mean reported for 49 adult species examined

by Sæther and Bakke (2000; 0.58 in kingfishers vs. 0.72 for other species).

Estimated survival for juvenile and adult Micronesian Kingfishers was higher than

rates for European Kingfishers (*Alcedo atthis*; 0.22 and 0.28 for juvenile and adult;

Bunzel and Drüke 1989 *in* Sæther and Bakke 2000). Survival in Micronesian

Kingfisher juveniles is similar to estimates for cooperatively breeding Florida

Scrub Jay (*Aphelocoma coerulescen*) juveniles (0.35), but below adult survival

(0.83; Woolfenden and Fitzpatrick 1984 *in* Sæther and Bakke 2000). Interestingly,

survival estimates for Micronesian Kingfishers are nearly identical to those for

juvenile (0.39) and adult (0.58) Acorn Woodpeckers (*Melanerpes formicivorus*;

Stacey and Taper 1992; Kendall 1998 *in* Sæther and Bakke 2000), which are also

cooperative breeders.

Vital rates are similar among species with like phylogenies, ecologies, and life history patterns (Sæther & Bakke 2000), but to my knowledge little information is available to reference my results because no other investigations of demography have been reported for any Micronesian Kingfisher congener. Most previous demographic studies have focused on species that differ drastically from the year-round resident, territorial, and forest kingfishers of tropical Pacific islands (e.g., Oring et al. 1983; Reed 1993; Heppell et al. 1994; Anders et al. 1997; Porneluzi & Faaborg 1999; Daniels & Walters 2000). Some have compared demography among vastly different taxa through meta analyses that evaluate patterns characterizing broad ranges of species (Sæther 1988; Heppell et al. 2000). For example, population models have classified organisms along a "slow-fast" continuum used to describe life history patterns (e.g., Sæther 1988; Silvertown et al. 1993; Heppell et al. 2000; Sæther & Bakke 2000). Avian species on the "slow" end of the continuum are long-lived, with small clutches, long maturation periods, and high contributions from adult survival to λ (i.e., high elasticity values). Those on the "fast" end exhibit high contribution of fecundity to λ, low adult survival, and large clutch sizes (Sæther 1988, 2000). Micronesian Kingfishers fall in the middle of this fast-slow spectrum because they are characterized by similar survival and fecundity contributions to λ, which are illustrated by the close elasticity estimates and r^2 values for rate parameters. Additionally, Micronesian Kingfishers mature quickly, as they can breed during the

first year after hatching, they lay two eggs in each of two clutches, and

survival is neither extremely high nor low. Accordingly, elasticity estimates from

the matrix population models also fell in the middle of the fast-slow spectrum

elasticities presented by Sæther & Bakke (2000).

In some cooperatively breeding species, helpers enhance reproductive

success (Walters 1990; Innes & Johnson 1994; Langen & Vehrencamp 1999),

while they apparently have little or no effect in other species (Bednarz 1987;

Sydeman 1989; Legge 2000). I did not detect differences in survival on

cooperative and pair-held territories so no such effects were included in this

population projection matrix. Thus, diversion of some juveniles to a non-breeding

helper life history stage reduced the proportion of the population that reproduced

and caused λ values to be lower than if a helper class were not included. This was

illustrated by the negative sensitivity point-estimate of -0.21 for the transition rate.

The observed effect of helper-associated parameters on population dynamics in

Micronesian Kingfishers is congruent with observations of other cooperative

breeders. Heppell et al. (1994) suggested that changes in the proportion of the

population serving as helpers in Red-cockaded Woodpeckers (*Picoides borealis*)

had the potential to cause lower λ estimates, even if there were no changes in

fecundity or survival among dominants. To the contrary, previous investigations of

behavior suggest that helpers are individuals that are prevented from breeding, and

that they would likely transition to a dominant status if opportunities arose (Emlen

1982; Brown 1987; Ligon 1999; Koenig & Dickinson 2004). Such an interaction would result in a positive influence of helpers on population dynamics, and it could potentially be incorporated into future modeling efforts.

Estimates for λ indicated a declining population of Micronesian Kingfishers on Pohnpei. While kingfisher densities remained relatively stable on the study areas throughout the duration of this project (Kesler, personal observation), results from surveys indicate an island-wide decline of as much as 63% during the last two decades (Buden 2000; Kesler & Haig *in review c*). Together, these suggest that study areas may be localized population sinks, and that immigration of individuals from other areas of the island may be subsidizing the study area kingfisher populations. Reduced λ also has the potential to influence model behavior. While the models and results presented here would likely be appropriate for use with other declining populations, stable or increasing populations might be better described by models with adjusted parameters.

Elasticity rankings and vital rate correlations with λ were made to assess the relative influence of demographic parameters on population dynamics across a range of vital rate values that might characterize multiple Pacific *Todiramphus* kingfishers. Rankings from the point-estimate model and simulation analyses indicated that changes in survival of adult breeders influenced λ more than changes in other vital rates. Elasticity results therefore suggested that conservation-oriented population management for multiple Pacific kingfishers

might be most effective if it first addressed factors influencing adult

survival. Contrarily, results from the regression analyses indicated that

conservation managers should focus on nestling and juvenile survival, but also that

similar correlations were found between nestling, juvenile, and dominant survival

and λ. Thus, regression results suggested that survival across all life stages should

be the focus of conservation practitioners addressing multiple *Todiramphus*

kingfishers.

The population projection matrix model presented here can be altered to

more accurately reflect localized conditions for other congeners. For example,

cooperation may not characterize all Pacific *Todiramphus* species or it may

characterize some species but only during times with specific resource conditions.

Cooperation is commonly thought to be a response to limited resources (Emlen

1982; Brown 1987; Stacey & Koenig 1990; Ligon 1999), so the occurrence of

cooperative behaviors can be influenced by population densities and resource

characteristics (Walters et al. 1992; Komdeur 1994). Thus, conservation

practitioners attempting to generalize the projection matrix model to other

populations would be best served by adjusting transition parameters toward a pair-

breeding model for populations with ample resources (*i.e.* reducing juvenile to

helper transition rate). Ample resources might characterize reintroduced or

translocated populations that are placed in environments devoid of conspecifics

(e.g., in planning translocation of *T. gambieri* within Tuamotus and reintroduction

of *T. c. cinnamominus* to Guam). Further, cooperation can be

influenced by localized factors (Walters et al. 1992), so variations of the same

model might be useful within different portions of a single species' range or the

same population as resources change across time.

Limited data, poor sample representation, sampling error, and missing data

are among the factors that can cause biased parameter estimates (Doak et al. 2005).

I attempted to mitigate biases through the use of multiple rate-estimate techniques,

but there is still potential for inaccuracies in the projection matrix models.

Parameter correlations (Doak et al 2005) can also influence matrix model behavior.

Although correlations are especially problematic in direct evaluations of model

elements, even assessments based on individual vital rates and transition

parameters can be skewed because these too are often correlated within a single

population and at a given time (Morris and Doak 2002). For example, it seems

unrealistic to have an extremely high dominant survival while simultaneously using

an extremely low helper survival. Similarly, in a cooperatively breeding

population, the transition of helpers to dominants is probably correlated with

dominant survival, because helpers fill breeding vacancies as dominants die. I

made no corrections for correlations in these analyses, so the resulting dispersion of

point estimates is likely to be broad.

6.6. CONCLUSIONS

The goal of this investigation was to provide population evaluation tools for multiple *Todiramphus* kingfisher populations. These are the first estimates of vital rates for any of the 12 endangered Pacific *Todiramphus* kingfishers and this is one of the first attempts to summarize information into a population demographic model for application to a suite of endangered species. The deterministic model presented here should be viewed as a plastic and foundational model that can be enhanced as additional data become available. Enhancements to the generalized model might be implemented within an adaptive management framework, through a flexible Bayesian approach (Frigessi et al. 2005) or through other methods of incorporating data from multiple sources and of varying reliability (Linacre et al. 2004). The generalized population matrix also provides a foundation for localized models directed toward managing single species in specific situations. Localized and species-specific models might incorporate collateral data, local environmental variation, stochastic environmental events, and population-specific vital rates (e.g., Dugger et al. 2004; LaHaye et al. 2004; Mazerolle et al. 2005). Similarly, the vital rates and error estimates presented above might be used singularly or in sets to enhance single species vital-rate based simulation models or PVAs. Vital rate estimates and variances are also applicable for use in pre-packaged PVA software programs (e.g., Vortex; Lacy 2003).

Population models based on surrogates may provide an

appropriate and accurate means of managing translocated and reintroduced

populations. Some have suggested that useful population models can be developed

after studying a reintroduced population for five years (Armstrong et al. 2002).

However, model accuracy and utility might be improved even more rapidly if

managers were armed with generalized population models based on surrogates

prior to release. Then, post-release monitoring could be used to enhance

preexisting models by honing parameter precision and variance estimates,

recognizing and correcting biases, and including stochastic and density dependent

algorithms to account for changes in population dynamics with growth. This model

might be employed in exactly such a way during the reintroduction of *T. c.*

cinnamominus to its native habitats on Guam (U.S. Fish and Wildlife Service

2004), or during the translocation of *T. gambieri* from Niau to another island in the

Tuamotu archipelago (A. Gouni, Société d'Ornithologie de Polynésie, personal

communication).

Despite their utility, caution should be used when employing surrogate

species data. The problem of bias takes on a new dimension when information

from one population is generalized to other populations in regions with different

resource and environmental conditions. Although demographic patterns are not

always closely correlated with taxonomic distance (Heppell et al. 2000),

demography is likely similar among congeners with similar ecologies and that

diverged primarily because of isolation by distance.   Perhaps one way

to mitigate effects of bias is to use a level of caution that is positively and directly

related to both the taxonomic and ecological distance from the source population.

Models should also be used conservatively and most frequently for evaluating the

potential relative effects of different management options rather than as pure

predictors of population behavior (Beissinger et al. *in press*).

Conservation efforts will benefit from research aimed at suites of species.

In addition to the 11 genera of insular birds mentioned above, suites of insular birds

in other regions, and anadromous fishes that spawn in disparate locations might

make good candidates for generalized investigations. Finally, conservation

biologists should make a concerted effort to present the potential applications of

their data to other populations when publishing.

6.7. ACKNOWLEDGEMENTS

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7. CONCLUSIONS

7.1. SUMMARY

The investigations presented in this dissertation addressed population demography, resource use, and movement in cooperatively breeding Micronesian Kingfishers (*Todiramphus cinnamominus*). This study was carried out over a seven-year period, on a remote Micronesian island where little avian research has taken place, and it addresses a severely endangered subspecies that had not previously been studied in the wild. Results provide multi-temporal and multi-scale insights into factors influencing social behavior and continue to supply information valuable to conservation efforts for endangered Pacific kingfishers. Methodology provided in chapter two for determining the sex of study individuals facilitated investigations that followed. Chapter three addressed the interaction between Micronesian Kingfishers and resources at both the landscape and home range scale, while chapter four presented analyses of movement and space use. Siblicidal behaviors and population demography were addressed in chapters five and six, which concluded with the development of a population projection model that can be used in conservation efforts throughout the Pacific.

7.2. POPULATION DEMOGRAPHY, RESOURCE USE, MOVEMENT AND COOPERATIVE BREEDING

Micronesian Kingfishers are a cooperatively breeding species, meaning that non-parent individuals assist with the reproductive attempts of others. Many researchers have asked why cooperative behaviors occur, and in at least some situations they appear to be an evolutionary adaptation to limitations in resources necessary for reproduction (Emlen 1982, Brown 1987, Stacey and Koenig 1990, Stacey and Ligon 1991, Ligon 1999, Hatchwell and Komdeur 2000, Koenig and Dickinson 2004). Chapters three and four indicated that Micronesian Kingfishers were more abundant in some vegetation cover types than in others. Even though habitat diversity is generally limited on islands with small land areas, results showing significant among-habitat differences in kingfisher abundance suggested that open areas and lowland forests vegetation cover types were extremely important to the birds (but see van Horn 1983), and that they do indeed select resources from the landscape.

At the home range scale, results presented in chapter three indicated that some Micronesian Kingfisher territories had higher quality resources than others and that space-associated resources were limited. Results further illustrated that Micronesian Kingfishers used combinations of forested and open habitat resources at the home range scale, and that the home ranges of birds on cooperative territories had more forest resources than those on pair territories.

Observations presented in this dissertation exemplify the

ecological situation predicted by theory to cause sociality, and therefore support

resource-based hypotheses about the evolutionary underpinnings of cooperative

breeding for Micronesian Kingfishers. Cooperative breeding theory suggests that

potential dispersers might be prevented from leaving natal territories by

environmental limitations in resources necessary for survival and reproduction (see

Emlen 1982, Brown 1987, Stacey and Koenig 1990, Koenig and Dickinson 2004).

Further, these delayed dispersers may be more successful than immediate

dispersing siblings if they remain and wait to inherit territory resources from

parents or neighbors (Stacey and Ligon 1991, Koenig et al. 1992). Observations in

chapter four indicate that potential dispersers evaluate landscape resources and

disperse only after many days of "homesteading movements". Theory and

empirical evidence also suggest that delayed dispersers may find alternative routes

to fitness through reproduction yielded by group members (Vehrencamp 1993), and

the pattern of extraterritorial movements made by Micronesian Kingfisher

dominants and potential breeders suggested that some individuals may also

purposefully make extraterritorial movements in an attempt to obtain extra-pair

opportunities for reproduction.

Chapter five presented evidence of siblicide among nestling Micronesian

Kingfishers. Like cooperative breeding, siblicidal behaviors are thought to be an

evolutionary response to limited resources (Mock and Parker 1997, Mock 2004).

Thus, observations of siblicide in the kingfishers further suggested that
they are a resource-limited species. Facets of Micronesian Kingfisher population
dynamics were presented in chapter six, including sensitivity and elasticity
analyses on Micronesian Kingfisher population projection matrix models. Results
suggested that even as vital rates changed, adult survival exerted greater influence
on population dynamics. However, a regression of simulated vital rates against
lambda suggested that survival at all life history stages was important.

7.3. CONSERVATION IMPLICATIONS

Micronesian Kingfishers are at risk of extinction on the three islands they inhabit.
The Guam Micronesian Kingfisher (*T. c. cinnamominus*) was extirpated from its
historic range (Haig and Ballou 1995, Bahner et al. 1998, Wiles et al. 2003).
Although plans are underway to reintroduce the bird to its native island, habitats
are severely threatened by development and continued presence of the Brown Tree
Snake (U.S. Fish and Wildlife Service 2004). Results presented in this dissertation
indicated that Micronesian Kingfishers selectively used and/or avoided landscape
features, and that a combination of open areas and forest resources were
fundamental to the birds. Additionally, short prospecting and dispersal distances
suggested that a reintroduced population might remain near hack sites. Potential
dispersers spent a great deal of time investigating dispersal destinations so

conservation practitioners may also be able to detect and influence

dispersal decisions during homesteading movements.

Investigation into siblicide and population demography have implications

for both wild Micronesian Kingfishers and captive breeding efforts. High nestling

mortality has long plagued the captive population of Micronesian Kingfishers

(Bahner et al. 1998). Results presented here suggested that nestling mortality

might be associated with resource availability in the wild. Because captive

breeding institutions are unlikely to provide resources exactly like those in native

ranges, they should consider hand-rearing at least one of two nestlings from each

clutch to prevent the potential for nestling losses. Results further suggested that

populations have great potential to increase in situations lacking resource

restrictions, so a reintroduced population of Micronesian Kingfishers in habitats

with abundant resources on Guam may grow rapidly.

Micronesian Kingfishers are one of twelve Pacific region *Todiramphus*

species listed as vulnerable, threatened, or endangered by federal and international

conservation authorities (U.S. Fish and Wildlife Service 1984, IUCN 2004). Life

histories of the birds are generally similar across the islands in which they occur,

but there are critically few data available for conservation practitioners to use for

management. Thus, chapter six assessed population demographic characteristics of

Pohnpei Micronesian Kingfishers and described a population projection matrix

model that could be generalized to other Pacific island *Todiramphus* kingfishers.

7.3. CONCLUSIONS

Theory about the factors underlying cooperative breeding suggests that potential dispersers in resource-limited situations may be better off remaining on natal areas and waiting for dispersal opportunities to arise, rather than dispersing into a resource-poor environment (Emlen 1982, Brown 1987, Stacey and Koenig 1990, Stacey and Ligon 1991, Ligon 1999, Koenig and Dickinson 2004). Results in chapters three, four, and five suggested that forest-associated resources may indeed be limited for Micronesian Kingfisher populations on Pohnpei, and that these limitations may underlie the evolution of sociality in this species. Results further indicated that conservation efforts for endangered Guam Micronesian Kingfishers and other Pacific *Todiramphus* species should consider the potential importance of landscape resources to the birds. Further, demographic analyses suggested that a population released from resource constraints may have the potential to grow rapidly. Added insight might be gained through future research addressing the particular resources of importance and population responses to temporal and spatial variation in those resources. Furthermore, information about the distribution of reproduction among group members and comparative analyses of spatio-temporal differences in demography among many *Todiramphus* species would provide data to broaden the applicability of models presented here.

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