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Conservation biology for suites of species: Demographic modeling for Pacific island kingfishers

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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 findings useful to conservation efforts for other species. We presented and explored the concept of conducting conservation-oriented research for suites of geographically separated populations with similar natural histories, resource needs, and extinction threats. An example was provided in the form of an investigation into the population demography of endangered Micronesian kingfishers (*Todiramphus cinnamominus*). We provided the first demographic parameter estimates for any of the 12 endangered Pacific *Todiramphus* species, and used results to develop a population projection matrix model for management throughout the insular Pacific. Further, we used the model for elasticity and simulation analyses with demographic values that randomly varied across ranges that might characterize congener populations. Results from elasticity and simulation analyses indicated that changes in breeding adult survival exerted the greatest magnitude of influence on population dynamics. However, changes in nestling survival were more consistently correlated with population dynamics as demographic rates were randomly altered. We concluded that conservation practitioners working with endangered Pacific kingfishers should primarily focus efforts on factors affecting nestling and breeder survival, and secondarily address fledgling juveniles and helpers. Further, we described how the generalized base model might be changed to focus on individual populations and discussed the potential application of multi-species models to other conservation situations.

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1. 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. Some endangered species have also been so affected that population remnants may not reflect historic behavior as accurately as surrogates. However, few researchers have initiated investigations or presented results with the intent of providing conservation-oriented information useful to the management of similar populations. We emphasize the need for conducting research and structuring results to benefit geographically

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separated populations of related organisms that share similar natural histories, resource needs, and extinction threats.

In many regions there are suites of geographically disparate populations that are phylogenetically related and ecologically similar, but the pattern is especially prevalent among the avifauna of oceanic islands. For example, island groups in Pacific Oceania host resident populations 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 characterized by kingfishers (*Todiramphus* spp.), flightless rails (*Gallirallus* spp.; *Porzana* spp.), megapodes (*Megapodius* spp.), and pigeon species (*Ducula* spp.; Baker, 1951; Pratt et al., 1987; Mayr and 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 and Stattersfield, 1990). Within the aforementioned 11 genera, 76 species in Oceania are listed as vulnerable, threatened, or in danger of extinction (US Fish and Wildlife Service, 1984; International Union for Conservation and Natural Resources, 2004). Despite these dire threats, however, researchers have failed to describe even the most basic natural history characteristics for these species.

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 endangered species (Casswell, 2000; Morris and Doak, 2002; Beissinger et al., 2006), yet many modeling attempts have been hindered by a lack of life history data (Ruggiero et al., 1994; Caughley and Gunn, 1996; Beissinger and McCullough, 2002). We 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.

2. Pacific kingfishers

Twelve Pacific region *Todiramphus* kingfisher species are listed as vulnerable, threatened, or endangered by federal and international conservation authorities (US Fish and Wildlife Service, 1984; International Union for Conservation and Natural Resources, 2004). Life histories of the birds are generally similar across the islands, as they are terrestrial forest birds inhabiting similar vegetation communities and climates (Mueller-Dombois and Fosberg, 1998). The kingfishers 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 and Fry, 1992; Kesler and Haig, 2004, 2005a). 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 (US 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 in perhaps the most perilous predicament, as they are extinct in the wild and only exist in a captive population (Marshall, 1989; Haig and Ballou, 1995; Haig et al., 1995). Plans are now underway to reintroduce the Guam Micronesian kingfisher back to native habitats and demographic data are vital to the effort (US Fish and Wildlife Service, 2004). 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. Herein, we explored the use of foundational demographic data from Pohnpei Micronesian kingfishers (*T. c. reichenbachii*) in the development of a generalized *Todiramphus* kingfisher population model. We then used the model to evaluate the potential importance of demographic parameters to population dynamics in a range of Pacific *Todiramphus* kingfisher species.

3. Methods

3.1. Study area

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). Three sites were selected for this investigation including the Ranch (6°57'N, 158°12'E), College of Micronesia (COM; 6°54'N, 158°9'E), and Palikir (6°55'N, 158°9'E) study areas. The study sites have been described extensively elsewhere (Buden, 2000; Kesler, 2002, 2006; Kesler and Haig, 2004, 2005a,b, 2007a,b).

3.2. Study population and field methods

Pohnpei Micronesian kingfishers breed as pairs and cooperative groups (Kesler, 2002; Kesler and Haig, 2005a,b). For the purposes of this study, we followed the terminology of recent literature by using "dominant" to refer to the putative breeders on a territory and "helper" for offspring that delayed dispersal through subsequent reproductive attempts. Additionally, we used hatch-year (HY) to describe progeny of the most recent breeding season, and after-hatch-year (AHY) to describe all non-juveniles.

We radio-marked and color-banded a population of Micronesian kingfishers on Pohnpei study areas between 1999 and 2004. 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. Micronesian kingfishers were captured in mist nets and the age and sex of each individual was determined using genetic analyses, plumage, and morphological characteristics (Kesler et al., 2006). We captured 39 juveniles (16 male [M], 23 female [F]), 14 helpers (10M, 4F), and 44 dominants (23M, 21F), and fitted each individual with a unique combination of

colored leg-bands and a numbered aluminum US Fish and Wildlife Service band. In 1999, 2000, and 2002, we fitted 1.8 g telemetry packages (Holohil Systems Ltd., Ottawa, Canada) to Micronesian kingfishers using leg-harnesses (Rappole and Tipton, 1991). We radio-marked 16 juveniles (7M, 9F), which were subsequently observed for 130 bird*weeks during the first 10 months post-fledge (839 telemetry locations, 579 bird*days). Additionally, we radio-marked 13 helpers (8M, 5F) and 35 dominants (19M, 16F), which were monitored for 128 helper bird*weeks and 443 dominant bird*weeks. Radio-marked individuals were located using triangulation (Kesler and Haig, 2007a,b), and birds were approached on foot to verify mortality if movement was not detected during three consecutive days.

3.3. Population model

We outlined a conceptual *Todiramphus* kingfisher population model (Fig. 1) to guide the development of a quantitative projection matrix. Briefly, the conceptual model describes a cooperatively breeding population that includes helpers who delay dispersal and independent attempts at reproduction. To translate the conceptual model into a quantitative deterministic population projection matrix we used data from six years of color-band resighting, three years of radio telemetry, and numerous nesting and behavior observations.

3.3.1. Survival

Survival was assessed in two stages. First, we used odds ratio tests and Cormack–Jolly–Seber modeling of color band resight data to determine population model structure. Potential differences in juvenile survival (fledging to first year) on cooperatively breeding ($n = 12$ fledglings) and pair-breeding ($n = 19$ fledglings) territories were assessed by comparing the odds of resighting marked fledglings during subsequent years. To determine whether survival in juveniles, helpers, and dominants should be separated by class, sex, both, or neither in the matrix model, Cormack–Jolly–Seber estimation methods were applied to color band resight data (described above; Pollock et al., 1990; Lebreton et al., 1992). We estimated both apparent survival and the probability of resight because individuals may have been present on study areas but missed when resighting color-bands (Anders and Marshall, 2005). We constructed biologically reasonable survival models with

Table 1 – Models of annual survival (ϕ) and recapture probabilities (p) for color-banded Pohnpei Micronesian Kingfishers between 1999 and 2004

Model	K	AIC _c	Δ_i	w_i
$\phi_{j,AHY};p^\bullet$	3	187.642	0.00	0.37
$\phi_{j,h,d};p^\bullet$	4	189.195	1.57	0.17
$\phi_{j,AHY*sex};p^\bullet$	4	189.687	2.06	0.13
$\phi_{j*sex,h*sex,d*sex};p^\bullet$	7	190.039	2.42	0.11
$\phi_{j,h,d*sex};p^\bullet$	5	190.664	3.04	0.08
$\phi_{j,AHY};p_{j,h,d}$	5	191.204	3.56	0.06
$\phi_{j,h,d};p_{j,h,d}$	6	192.943	5.32	0.02
$\phi_{juv,AHY*sex};p_{j,h,d}$	6	193.339	5.71	0.02
$\phi_{j*sex,h*sex,d*sex};p_{j,h,d}$	9	193.873	6.25	0.01
$\phi_{j,h,d*sex};p_{j,h,d}$	7	194.462	6.84	<0.01
$\phi^\bullet;p^\bullet$	2	196.892	9.27	<0.01
$\phi^\bullet;p_{j,h,d}$	4	199.176	11.55	<0.01

Also noted for each model is the number of parameters (K), second-order Akaike's Information Criterion (AIC_c) values, AIC_c differences (Δ_i), and AIC_c weights (w_i). Subscript indicates model parameterization for juveniles (j), helpers (h), dominants (d), combined estimates for helpers and dominants (AHY), and all classes combined (\bullet). Separate survival estimates were made for males and females when subscripts were modified by 'sex'. For example, $\phi_{j,AHY*sex}$ represents separate survival estimates for juveniles, a combined estimate for male helpers and male dominants, and a combined estimate for female helpers and female dominants.

covariates for sex and life-stage, and combined parameter estimates (Table 1). Models were ranked using Akaike's Information Criteria (AIC_c; see Burnham and Anderson, 2002) in the live recapture module of Program Mark (White, 2005) and the top-ranked model was used to determine whether survival differed among social classes and sexes.

Second, radio-telemetry data were grouped in accordance with results from Cormack–Jolly–Seber modeling, and known-fate models (White, 2005; Kaplan and Meier, 1958) were used to estimate survival for simulation matrices. We used known-fate analyses rather than color-band resight results because they are less likely to be biased by birds that were present on study areas, but that went unseen. In accordance with odds ratio tests and model ranking analyses, we made a survival estimate for the period between fledging through the end of the first year ($\phi_{juvenile}$), and a combined

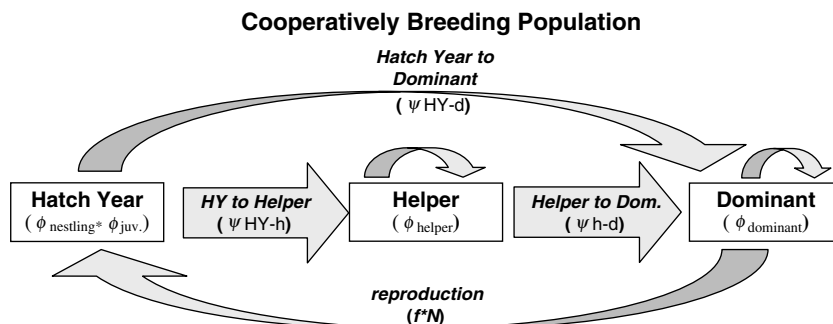


Fig. 1 – Conceptual population model for Pacific *Todiramphus* kingfishers, and associated model parameters. Parameters include survival (ϕ) and transition (ψ) variables.

estimate of after-hatch-year survival for helpers and dominants of both sexes (ϕ_{AHY}). To estimate survival for an individual from the time that it was an egg through the first year of life, we combined juvenile survival estimates from the known fate analyses with previously published nestling survival estimates for Micronesian kingfishers ($\phi_{\text{nestling}} = 0.534$, Kesler, 2006). Previously published nestling survival was based on a study of both cooperative and pair-breeding nests, which were proportionally represented. Thus, survival for the first year of life, or hatch-year survival (ϕ_{HY}) from both nestling and juvenile stages was:

$$\phi_{\text{HY}} = \phi_{\text{nestling}} * \phi_{\text{juvenile}}$$

3.4. Reproduction

Survival estimates (described above) included the period between laying and fledging, so parameters associated with reproduction were limited to the number of nest attempts by those that bred (f), the number of eggs laid during each attempt, the potential for age structuring in reproductive success, and the proportion of the population that attempted to breed (N). We used direct observations of 10 territories to determine the mean number of breeding attempts made by Micronesian kingfishers during 2000 fieldwork, when observers were present on study areas throughout the breeding season. Breeding attempts were directly observed as nests with eggs. Previously published findings indicated that Micronesian kingfishers were characterized by two-egg clutches (Kesler, 2002, 2006), and we assumed a 1:1 sex ratio for eggs.

To determine whether reproduction was age-structured and whether all pairs attempted to breed, we compared the odds of nesting in newly settled dominants ($n = 15$ male*years; 18 female*years) with dominants observed on territories during the previous years ($n = 15$ male*years; 14 female*years). We further compared the number of young at the end of each field season on newly settled territories with those on previously settled territories ($n = 30$ male and 32 female*years) to evaluate breeder experience.

3.5. Social class transition

We estimated the proportion of individuals transitioning among life history stages (ψ) using resight observations of the 39 color-banded juvenile and 13 helper Micronesian kingfishers. Transitions were directly observed when in subsequent years juveniles became helpers or dominants, and when helpers became dominants (respectively, ψ_{j-h} , $1 - \psi_{j-h}$, ψ_{h-d}).

3.6. Population model structure

Following assessment of Pohnpei Micronesian kingfisher demographic parameters, a deterministic prospective population projection matrix model was structured to reflect a cooperatively breeding population of *Todiramphus* kingfishers. The model included a pulse-breeding population with a time step occurring immediately after laying, and with demographic parameters that were consistent across time. Both sexes have been observed as helpers and territory holders (Kesler and Haig, 2007a,b), so the model was based on females.

3.7. Sensitivity, elasticity, and simulation analyses

The prospective population projection matrix was employed in sensitivity and elasticity analyses, and in a simulation analysis to identify demographic parameters key to population dynamics and conservation (Caswell, 2001; Wisdom et al., 2000; Williams et al., 2001; Morris and Doak, 2002). We estimated the dominant eigenvalue (λ), which represents the asymptotic rate of population change and provides a general measure of whether a population was projected to increase or decrease in size. Sensitivity (S) and elasticity (E) statistics were estimated by altering each parameter by 0.01 and using a “brute force” method to assess change in λ (Heppell et al., 2000; Morris and Doak, 2002, p. 330). Sensitivity for each demographic parameter represents the amount of change in λ associated with small changes in θ , where θ was the demographic parameter of interest, or

$$S_{\theta} = \partial\lambda/\partial\theta$$

(Williams et al., 2001, p. 151). Elasticity is a metric scaled to reflect the proportional change in λ that was brought about by a similarly proportioned change in θ , which facilitates comparisons among θ (Williams et al., 2001, p. 152):

$$E_{\theta} = \frac{\partial\lambda/\partial\theta}{\lambda/\theta}$$

To provide insight into how demographic parameters influenced model behavior across populations of *Todiramphus* kingfishers that were characterized by demographic rates different from those on Pohnpei, we simulated 10,000 combinations of randomly varied parameters. As a guideline for survival variation we used an interval that was equal in width to the 95% confidence intervals from the Cormack–Jolly–Seber estimates (Morris and Doak, 2002, p. 348), which were centered on mean survival estimates derived from the known fate analyses. 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 we observed in Pohnpei. Nestling survival ranged from 0.24 to 0.74, which were previously published estimates for nestlings on pair-breeding and cooperatively breeding territories (Kesler, 2006). Annual nest attempts were varied from 1.4 to 2.0, and the proportion of the population that bred ranged from 0.75 to 1.00. Rates varied independently and they were randomly selected from a uniform distribution (Wisdom and Mills, 1997) generated by SAS (SAS Institute, 1999). We then recalculated λ , S , and E for each simulated set of values. Microsoft Excel (Microsoft Corporation, Seattle) and Matrix and Linear Algebra adding for Excel (Fox’s Team, 2005) were used to simulate value combinations, calculate and rank sensitivity and elasticity values for each, and summarize results.

As a second method of evaluating the influence of demographic parameters on λ across combinations of demographic rates likely to characterize multiple *Todiramphus* kingfisher species, we used SAS (PROC REG). For simulated values, λ was regressed against each parameter using linear regression. The resulting regression slopes (m) reflected the predicted magnitude of each parameter’s influence on λ and the coefficient of determination (r^2) values indicated the amount of

variation in λ accounted for by each parameter (Wisdom and Mills, 1997). Thus, m represented the magnitude of each parameter's influence on λ , while r^2 provided insight into the stability of a parameter's effect within the range of demographic values likely to characterize multiple Pacific *Todiramphus* kingfishers. Unless otherwise noted, estimates were reported as means with 95% confidence intervals (95% CI) in parentheses and differences were considered statistically significant at $\alpha < 0.05$.

4. Results

4.1. Demographic parameter estimation

4.1.1. Survival

We used color-band resight data, odds ratio tests, and Cormack–Jolly–Seber methods to determine the population projection matrix model structure. Odds ratio tests indicated that separate parameters were not warranted for juvenile survival on cooperative and pair-breeding territories because there was no difference in the odds of resighting individuals fledged from cooperative (three resighted) and pair-breeding territories during subsequent years (two resighted; $P > 0.05$; log odds ratio = 0.87; 95% CI 2.80 to -1.06). The top-ranked model in the Cormack–Jolly–Seber analysis of color band resight data indicated that the population projection matrix should include separate survival estimates for juveniles and after-hatch-year individuals, but that further structuring was not necessary (Table 1). Thus, radio telemetry data for dominant and helper birds were pooled in accordance with results from the model ranking procedure, and known-fate analyses indicated an estimated $\hat{\phi}_{\text{AHY}}$ of 0.577 (95%CI = 0.326–0.794). Known-fate analysis of juvenile radio telemetry data yielded an estimated weekly survival rate of 0.977 (95% CI 0.931–0.993) and $\hat{\phi}_{\text{juvenile}}$ estimate of 0.366 (95% CI 0.088–0.777). When estimated juvenile survival was combined with previously published survival rates from laying to hatch (0.534; Kesler, 2006), the estimated probability that an individual survives from the time of laying through the next breeding season was 0.195 ($\hat{\phi}_{\text{HY}} = 0.534 \cdot 0.366$).

4.1.2. Reproduction

Nest observations and plumage characteristics suggested that breeding pairs initiated multiple nests each year. Renesting occurred on 70% of territories in 2000, so we used 1.7 nesting attempts per year (N) in the matrix model. When territories with newly settled dominants were compared to territories with dominants that had previously been observed, results showed no differences in either the odds of nesting ($P > 0.05$; 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-tests; for males $P = 0.452$, mean offspring = 1.20 on newly settled territories and 1.53 on previously settled territories; for females $P = 0.948$, mean offspring = 1.33 on newly settled territories and 1.36 on previously settled territories). Thus, results did not indicate strong age structuring in Micronesian kingfisher reproduction and suggested that an age-structured matrix model was not necessary. Failure to breed was primarily linked to anthropogenic

activities (e.g. deforestation and fires), so we assumed that all birds attempted to breed for the point estimate model and that attempts ranged from 0.75 to 1 for simulation models.

4.1.3. Social classes transition

Observations of transitions among social classes were rare. One female 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.

4.1.4. Model structure

Using information from the survival, reproduction, and transition analyses, we developed the following cooperative breeding population projection matrix model:

$$\begin{aligned}
 A &= \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \\
 &= \begin{bmatrix} (\hat{\phi}_{\text{HY}} * f * N * [1 - \hat{\psi}_{j-h}]) & (\hat{\phi}_{\text{AHY}} * \psi_{h-d} * f * B) & (\hat{\phi}_{\text{AHY}} * f * B) \\ (\hat{\phi}_{\text{HY}} * \hat{\psi}_{j-h}) & (\hat{\phi}_{\text{AHY}} * [1 - \hat{\psi}_{h-d}]) & 0 \\ (\hat{\phi}_{\text{HY}} * [1 - \hat{\psi}_{j-h}]) & (\hat{\phi}_{\text{AHY}} * \hat{\psi}_{h-d}) & (\hat{\phi}_{\text{AHY}}) \end{bmatrix} \\
 &= \begin{bmatrix} 0.2658 & 0.549 & 0.9809 \\ 0.0391 & 0.2564 & 0 \\ 0.1564 & 0.3206 & 0.5770 \end{bmatrix}
 \end{aligned} \tag{1}$$

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 (Caswell, 2001; Morris and Doak, 2002). From left to right, columns represent hatch year, helper, and dominant classes. Elements in the top row were functions of survival and fecundity whereas those below were elements of survival and transition. The second matrix illustrates how elements were calculated from demographic parameter data presented above, and the third includes base-value point estimates. The λ value for the cooperative breeding population projection matrix was 0.877, which represents a declining population.

4.1.5. Sensitivity, elasticity, and simulation analyses

We evaluated the influence of demographic parameters on population dynamics using sensitivity and elasticity analyses (Table 2). Results from the point-estimate model indicated that survival of dominant breeders had the strongest influence on population dynamics ($E = 0.623$). 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 was likely a result of their minor contribution to reproduction within the model. 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 demographic parameters.

Simulations were used to gain insight into the population dynamics of *Todiramphus* kingfisher populations with demographic parameters different from those identified on the

Table 2 – Elasticity (E) and sensitivity (S) results from the point-estimate model, and r^2 values for demographic parameter regressions with λ in the simulation of randomly varied demographic parameters for *Todiramphus* kingfishers

Parameter	Point estimate		Simulation		
	Base value	S/E	Range	90% E interval ^c	r^{2d}
Reproduction					
Nests (N)	1.7	0.191/0.325	1.4–2.0	0.184–0.359	0.05
Breeding adults (f)	1	0.321/0.321	0.75–1.00	0.184–0.359	0.03
Survival (ϕ)^a					
ϕ_{nestling}	0.534	0.607/0.325	0.240–0.740	0.184–0.359	0.40
ϕ_{juvenile}	0.366	0.887/0.325	0.232–0.500	0.184–0.359	0.21
ϕ_{helper}	0.577	0.091/0.052	0.479–0.675	0.019–0.120	<0.01
ϕ_{dominant}	0.577	1.080/0.623	0.479–0.675	0.573–0.762	0.26
Transitions (ψ)^b					
$\psi_{\text{hatch-year to helper}}$	1/5 = 0.2	–0.174/–0.035	0.000–0.500	–0.070 to –0.009	0.02
$\psi_{\text{helper to dominant}}$	5/9 = 0.6	0.032/0.018	0.250–0.750	–0.005–0.033	<0.01

a Base value estimates for ϕ_i resulted in known-fate analyses of radio telemetry data, and were structured in accordance with the top-ranked model from color-band resight 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 demographic parameter.

Pohnpei study areas (Table 2). Results for λ ranged from values indicating severe population declines to values associated with growing populations (Fig. 2). Results further suggested that the overall ranking of elasticities did not differ from the point-estimate model, because adult survival had the highest proportional influence on population dynamics. Simulated demographic parameters were regressed against resulting λ estimates to assess the potential importance of each parameter to multiple Pacific *Todiramphus* kingfisher populations (Table 2; Fig. 3). Adult survival rates had the highest slope ($m = 0.94$), indicating that changes in annual adult survival have greater proportional influence on λ than other

demographic parameters. However, the correlation coefficient for nestling survival was substantially higher than adult survival ($r^2 = 0.40$ vs. 0.26), which indicated that the parameter’s influence on λ was more predictable across the simulated combinations of varied demographic parameters. Regression results further indicated that juvenile survival had substantial influence on population dynamics ($m = 0.62$), whereas the number of nesting attempts, social class transitions and the breeding proportion of the population did not (Fig. 3).

5. Discussion

5.1. Demographic parameter estimates

We 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. To our knowledge no other investigations of demography have been reported for any Pacific *Todiramphus* kingfisher. When compared to a range of bird species presented by Sæther and Bakke (2000), our estimated survival rate in juvenile Micronesian kingfishers (0.37) was similar to a mean rate in 39 other species (0.40), and survival in after-hatch-year kingfishers (0.58) was lower than the mean reported for 49 adult species (0.72). However, most previous demographic studies focused on species that differ drastically from the year-round resident, territorial, and forest kingfishers of tropical Pacific islands (Oring et al., 1983; Reed and Oring, 1993; Heppell et al., 1994; Anders et al., 1997; Porneluzi and Faaborg, 1999; Daniels and Walters, 2000).

Demographic parameters are often similar among species with like phylogenies, ecologies, and life history patterns. 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,

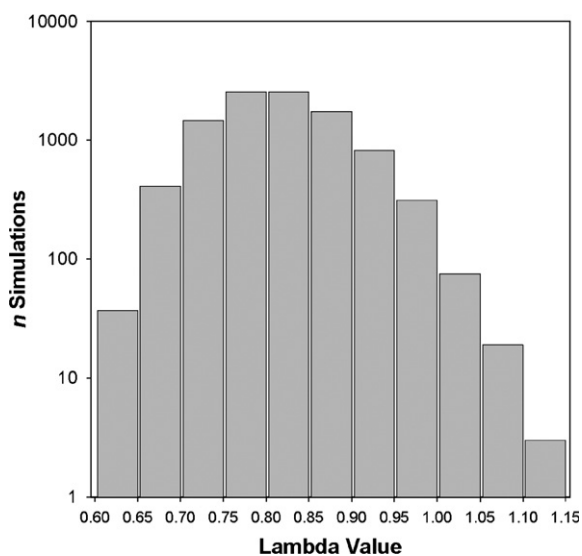


Fig. 2 – Distribution of λ values from 10,000 population projection matrix model simulations with varying demographic parameters for cooperatively breeding Micronesian kingfishers.

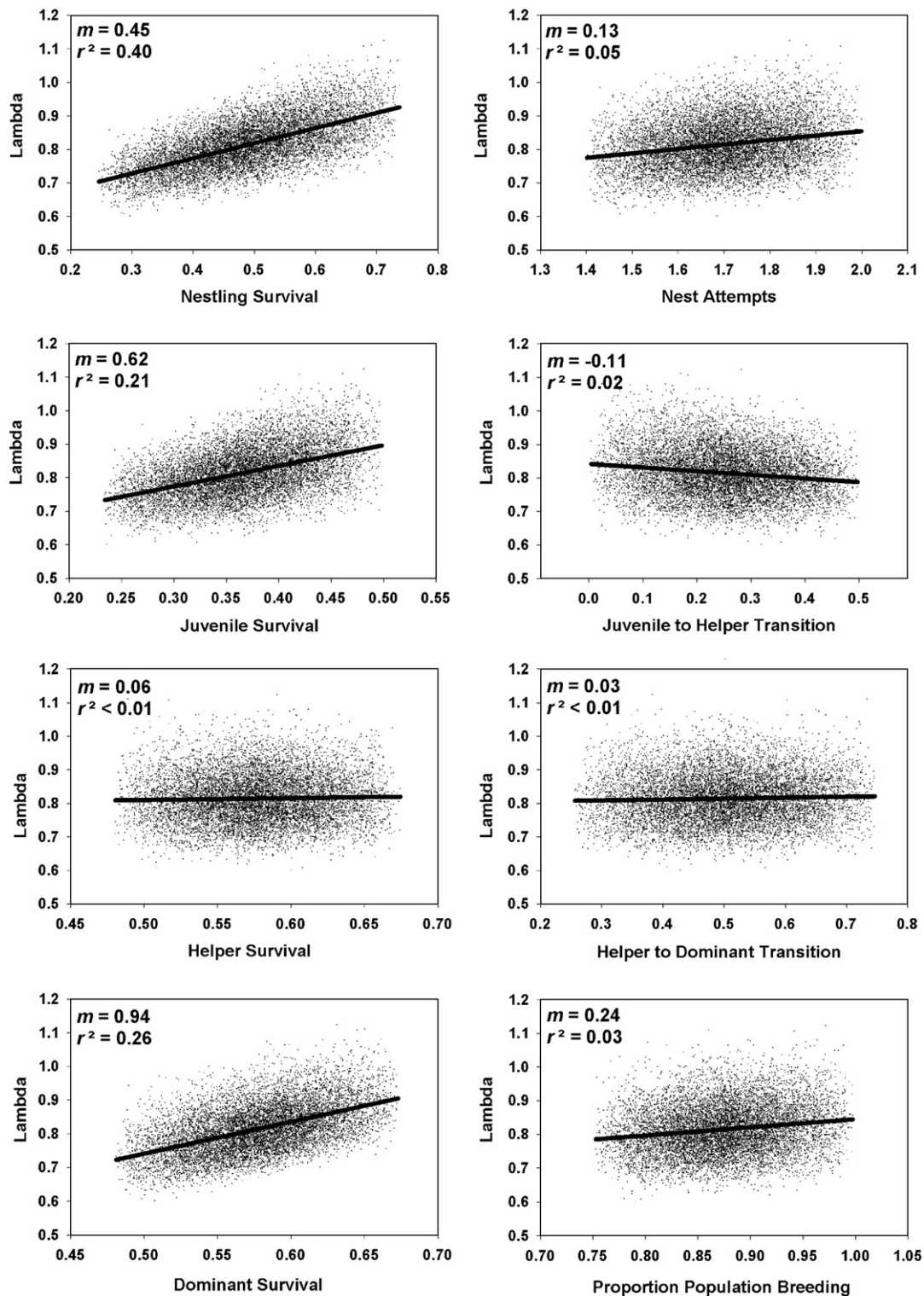


Fig. 3 – Regression of demographic parameters against λ values resulting from 10,000 population projection matrix model simulations with varying parameter values. Regression slope values (m) indicate magnitude effects and r^2 values represent the concordance between demographic parameters and λ .

1989 in Sæther and Bakke (2000)). Among cooperatively breeding species, survival estimates for Micronesian kingfishers were 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)).

Juvenile survival in the cooperative Florida Scrub Jay (*Aphelocoma coerulescens*) was also similar to Micronesian kingfishers (0.35), but woodpecker adult survival was higher (0.83; Woolfenden and Fitzpatrick, 1984 in Sæther and Bakke (2000)). Micronesian kingfisher survival was lower than cooperatively

breeding Red-cockaded woodpeckers (*Picoides borealis*), at both the juvenile (0.50M, 0.42F) and breeder stages (0.77M, 0.71F; Walters et al., 1988; Letcher et al., 1998).

Some have characterized demography through meta analyses of 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 (Sæther, 1988; Silvertown et al., 1993; Heppell et al., 2000; Sæther and Bakke, 2000). Avian species on the “slow” end of the continuum were 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 exhibited a high contribution of fecundity to λ , low adult survival, and large clutch sizes (Sæther, 1988; Sæther and Bakke, 2000). Micronesian kingfishers fell toward the slow end of this fast-slow spectrum because they were characterized by higher adult survival contribution to λ , which were illustrated herein by elevated elasticity estimates. However, the kingfishers were also toward the middle of the spectrum because they matured quickly, as they bred during the first year after hatching, they laid two eggs in each of two clutches, and overall survival estimates were neither extremely high nor low. Accordingly, elasticity estimates from the matrix population models also fell toward the middle of the fast-slow spectrum of elasticities presented by Sæther and Bakke (2000).

5.2. Population model and analyses

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 indicated an island-wide decline of as much as 63% during the last two decades (Buden, 2000; Kesler and Haig, 2007a). Together, these suggested that study areas may have been localized population sinks, and that immigration of individuals from other areas of the island may have been subsidizing study area kingfisher populations.

Elasticity rankings and demographic parameter correlations with λ were made to assess the relative influence of demographic parameters on population dynamics across a range of values that might characterize multiple Pacific *Todiramphus* kingfishers. Parameters with higher elasticity estimates and regression slopes had comparatively greater magnitudinal effects on λ , whereas the effects of parameters with higher correlation coefficients were more predictable across the range of simulated populations. Both metrics are thought to be of conservation importance (Wisdom and Mills, 1997; Wisdom et al., 2000; Beissinger et al., 2006). Elasticity rankings and regression slopes indicated that changes in adult breeder survival had greater magnitudinal influence on λ , but correlation coefficient values from simulation analyses indicated that nestling survival was most closely correlated with λ across the range of randomly altered parameter estimates. The λ estimates presented in Fig. 2 also indicated that there was potential for population growth within the range of parameters used in our simulation. Therefore, results suggested that conservation management for multiple Pacific kingfisher populations has the potential to increase

population sizes, and that strategies aimed at increasing both nestling survival and adult survival are most likely to be effective. Furthermore, we believe that these results broadly extend to other Pacific *Todiramphus* populations because similar results were identified in the point-estimate model and throughout simulation analyses.

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), 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, such as reintroduced or translocated populations (i.e. reducing juvenile to helper transition rate).

The observed effect of helper-associated parameters on population dynamics in Micronesian kingfishers was 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, however, previous investigations of behavior suggested that helpers are individuals prevented from breeding and that they would likely transition to a dominant status if opportunities arose (Emlen, 1982; Brown, 1987; Ligon, 1999; Koenig and 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.

In some cooperatively breeding species, helpers enhance reproductive success (Innes and Johnson, 1994; Langen and Vehrencamp, 1999), whereas they apparently have little or no effect in other species (Bednarz, 1987; Sydeman, 1989; Legge, 2000). Previous investigations of Micronesian kingfishers suggested that there were differences in nestling survival on cooperative and pair-breeding territories (Kesler, 2006), so we used nestling survival rates that spanned the gap for simulations. Coupled with results illustrating that the changes in nestling survival were strongly correlated with λ , the broad difference between nestling survival on cooperative and pair breeding territories (Kesler, 2006) indicated that there were likely substantial benefits to sociality among *Todiramphus* kingfishers.

6. Conclusion

The goal of this investigation was to provide population evaluation tools for multiple *Todiramphus* kingfisher populations. These were the first estimates of demographic parameters 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, which might incorporate collateral data, local environmental variation, stochastic environmental events (Lande, 1993), and population-specific demographic parameters (Dugger et al., 2004; LaHaye et al., 2004; Mazerolle et al., 2005). Similarly, the demographic parameters and error estimates presented above might be used singularly or in sets to enhance single species vital-rate based simulation models or population viability analyses.

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 enhance preexisting models by honing parameter precision and variance estimates, recognizing and correcting biases, and including stochastic and density dependent algorithms. Our model might be employed in exactly such a way during the reintroduction of *T. c. cinnamominus* to its native habitats on Guam (US Fish and Wildlife Service, 2004), or during the translocation of *T. gambieri* from Niau to another island in the Tuamotu archipelago, and similar approaches could be used for many other groups (Thibault et al., 2002; Tweed et al., 2003).

Despite their utility, surrogate species data should be used with caution. 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 directly related to both taxonomic and ecological distance from the source population.

Future conservation efforts will benefit from research aimed at suites of species. In addition to the 11 genera of birds mentioned above, suites of insular birds in other regions (Grant et al., 2000; Thibault et al., 2002), and anadromous fishes that spawn in similar but disparate watersheds 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.

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