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Population Ecology

Survival and Population Persistence in the Critically Endangered Tuamotu Kingfisher

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ABSTRACT A wide range of threats affect populations of Pacific island birds and conservationists have been challenged to identify factors upon which to focus management. The Tuamotu kingfisher (*Todiramphus gambieri*) is one of the most endangered vertebrate species in the world, yet little has been published about basic biology or causes of the population decline. We used 4 years of mark-resight and territory resource information to model survival in juvenile and adult Tuamotu kingfishers. Annual survival of adult males ($\phi = 0.77$) was similar to congeneric species, whereas survival of adult females ($\phi = 0.40$) and juveniles ($\phi = 0.12$) was much lower. The best-supported survival model indicated adult female survival was positively related to territory size, whereas adult male survival was negatively related to atoll forest within territories. We used parameter estimates from survival models in a life-stage simulation analysis to evaluate the relative influence of vital rates and territory habitats on population processes. Results indicated that adult female and juvenile survival had the greatest impact on Tuamotu kingfisher populations, accounting for 58% and 32% of variation in the finite rate of population increase, respectively. Nocturnal predation by rats (*Rattus* spp.) on incubating kingfishers may explain the lower survival of females than males, whereas juvenile birds may be especially vulnerable to predation by cats (*Felis catus*). Thus, conservation management for Tuamotu kingfishers should include use of metal guards on cavity trees to protect nests and incubating females, and control predator access during fledging periods.

KEY WORDS endangered, French Polynesia, island birds, life-stage simulation, population processes, population projection matrix, survival, *Todiramphus gambieri*, Tuamotu kingfisher.

Island birds face a range of threats that contribute to extinction rates 4 times greater than their continental counterparts (Butchart et al. 2006, Whittaker and Fernández-Palacios 2007). Conservation management of island avifauna has been hampered by limited resources, ignorance about natural history, and paucity of management tools for mitigating threats. Determining the cause of population declines through a process of elimination of threats or by monitoring individual causes of mortality can be difficult, expensive, and time consuming. These challenges have led managers and conservationists to embrace broad management programs focused on factors that commonly affect island ecosystems, rather than investigating the cause of the decline and using targeted approaches to address species- and location-specific problems.

Eradication of invasive mammals is a common technique applied to islands threatened by rodents (*Rattus* spp. and *Mus* spp.), cats (*Felis catus*), and other mammals. Introduced mammals often compete for animal and insect forage and prey directly on birds and eggs (O'Donnell 1996, Courchamp et al. 2003, Wiles et al. 2003, Blackburn et al. 2004). Introduced herbivores (e.g., *Capra aegagrus* and *Sus scrofa*) can drastically change island vegetation, thereby decreasing cover, nesting substrate, and food for native wildlife (Coblentz 1978, Vázquez 2002). Similarly, introduced diseases have resulted in insular population changes (van Riper et al. 1986). Anthropogenic habitat destruction is also a substantial threat to island fauna (Steadman 1997, BirdLife International 2000). Although broad-based conservation programs have had some successes, a more efficient approach might include identifying and targeting specific factors driving declines in individual populations of critically threatened species.

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Knowledge about survival and reproduction provides information about the key life stages that affect population dynamics. Comparisons between vital rates in stable and threatened populations can identify the age and sex classes that are most vulnerable. Conservation strategies can then target life-history periods that are likely to influence population dynamics. Similarly, population projection matrix models can be used to identify which sex or age classes are most closely correlated with the finite rate of population

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increase (λ; Heppell et al. 1994, Plissner and Haig 2000, Kaye et al. 2001). Because survival, reproduction, or transition parameters can exert greater or lesser influence on λ, once identified, conservation planning can target those factors that have the greatest influences on population processes (Morris and Doak 2002, Beissinger et al. 2006, Mills 2007).

Population projection matrices are inherently simple, as they are usually deterministic and include rudimentary representations of annual survival and reproduction (Caswell 2000, Morris and Doak 2002, c.f. Morris and Doak 2005). Despite their simplicity, substantial information about the population of interest is required to compose a projection matrix (Beissinger and McCullough 2002). When only scant information exists, many population projection matrices borrow information from the literature, expert opinions, or closely related species (Silvertown et al. 1996, Heppell 1998, Sæther and Bakke 2000). Matrix elements associated with the juvenile life stage are a recurring challenge for avian population models because of difficulties associated with gathering information from mobile fledglings. Nonetheless, without direct demographic measures, population matrices often lack the resolution to identify crucial life stages that influence population processes.

We investigated demography and population processes of a severely endangered bird, the Tuamotu kingfisher (*Todiramphus gambieri*; International Union for the Conservation of Nature [IUCN] 2010). The nominate subspecies (*Todiramphus gambieri gambieri*) was extinct from the Gambier Islands in the 19th century (Holyoak and Thibault 1984) and the only remaining Tuamotu kingfisher (*Todiramphus gambieri gertrudae*) exists in a single population of approximately 125 birds on the small atoll island of Niau (Gouni and Zysman 2007, IUCN 2010). As with many birds on oceanic islands, very little is known about the kingfisher's basic biology, population status, or factors limiting population size. These birds face a host of conservation challenges. The lowland forest in Niau has been almost entirely converted to agriculture for coconut (*Cocos nucifera*) production (Butaud 2007). Although the birds currently use coconut plantations for foraging (Coulombe et al. 2011), the comparative value of coconut plantation versus historic lowland forest is unknown. Additionally, we previously observed substantial variation in home range size, indicating this species may respond to differences in habitat quality and food availability throughout the island (Coulombe 2010). The island of Niau also has 2 invasive rats (*R. exulans* and *R. rattus*), which affect terrestrial island birds throughout the region (O'Donnell 1996, Courchamp et al. 2003). Finally, feral cats and dogs (*Canis domesticus*) roam the island and are prevalent in areas inhabited by the kingfisher (Gouni et al. 2006).

Our study had 3 objectives. The first was to model survival of juvenile and adult Tuamotu kingfishers, as these vital rates are critical to conservation management. Second, we assessed the influence of 4 within-territory habitat covariates on survival. Finally, we integrated results from survival analyses into a population projection matrix model for the suite of Pacific kingfishers (*Todiramphus* spp.; Kesler and Haig 2007*a*). We conducted sensitivity and elasticity analyses with fixed matrix values (de Kroon et al. 2000, Heppell et al. 2000), and then varied matrix elements in a life-stage simulation analysis (Wisdom and Mills 1997, Wisdom et al. 2000) to assess the relative influence of input variables on population processes. Our intent was to identify age and sex classes upon which to focus management actions as a means to increase the population of critically endangered Tuamotu kingfishers.

STUDY AREA

Niau is a small, coral atoll in the Tuamotu Archipelago of French Polynesia (16°10′S, 146°22′W; Fig. 1). The land area is <26 km^2 and encloses a central lagoon (Andréfouët et al. 2005). The inland consisted of dense atoll forest (18 km^2) on jagged fossilized limestone coral, with coconut agricultural plantations (7 km^2) replacing historic lowland forest along the oceanic and lagoon shores (Butaud 2007). At the time of study, lowland broadleaf and palm forests were absent from Niau and much of the Pacific, and almost entirely replaced by coconut agriculture (Mueller-Dombois and Fosberg 1998). A village of approximately 170 people was located on the northeast side of the island. The climate was tropical oceanic without pronounced seasons (Mueller-Dombois and Fosberg 1998). We conducted our research during 2006–2010 on 2 study areas situated on the east side of the island, 1 on the ocean coast and 1 near the lagoon (Coulombe et al. 2011). Coconut plantations on the 2 study areas were managed by farmers using hand tools and prescribed burns to clear understory vegetation. Coconut habitat was narrow (approx. 50–100 m wide) along the coast and wider (approx. 100–150 m wide) on the lagoon side. The lagoon study area also included mixed coconut-atoll forest and wetlands dominated by *Sesuvium portulacastrum* (Butaud 2007). The narrow littoral zone along the coast consisted of coral reef with low strand vegetation and sparse trees.

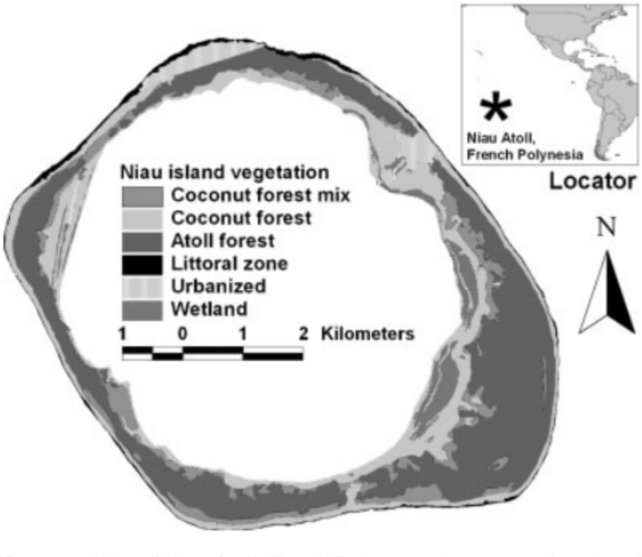

Figure 1. Map of Niau Atoll, French Polynesia, where we used mark and resight techniques to evaluate demography of critically endangered Tuamotu kingfishers from 2006 to 2010 (adapted from Butaud 2007 with permission).

METHODS

Field Methods

We used mist nets to capture Tuamotu kingfishers during February–March 2006, October–November 2006, October–November 2007, September–November 2008, and February–March 2010. During the study, we marked 16 juveniles (HY) and 67 adults (AHY) with unique combinations of colored, plastic leg bands and a numbered aluminum band. We identified juvenile birds by the presence of buffy-tipped primary and secondary flight feathers, which are retained through the first year. We determined sex for all birds using molecular genetic techniques (Kesler et al. 2006). Territory boundaries were generally stable for the duration of our investigation (Coulombe 2010), despite occasional new-occupant individuals. During mist netting visits, and again in November 2010, we searched each territory using broadcasts of Tuamotu kingfisher calls to resight-marked birds. Adult Tuamotu kingfishers remained faithful to their territory year-round and generally throughout their lives (Coulombe 2010). Stable territory boundaries and the kingfishers' propensity to respond to call broadcasts facilitated our ability to detect birds and identify breeding vacancies and social replacements on territories. This study was approved by the Institutional Animal Care and Use Committee of the University of Missouri (reference #4356). The government of French Polynesia granted us authorization to capture and band Tuamotu kingfishers (ordinance #1726).

Survival Analysis

We analyzed survival of Tuamotu kingfishers with Cormack–Jolly–Seber models of color-band mark and resight data (Pollock et al. 1990, Lebreton et al. 1992) in Program MARK (White and Burnham 1999). We assessed survival of juveniles (hatched during the most recent breeding season) and adults (hatched during a previous breeding season) separately. We estimated both apparent survival ($\hat{\phi}$) and the probability of resight ($\hat{p}$) to account for individuals that might have been present on study areas but were missed when resighting color bands (Lebreton et al. 1992, Anders and Marshall 2005).

We incorporated island and territory resource metrics into the analysis of adult survival (ϕ_{AHY}) using previously published results of resource use, wherein we defined home range area (ha) by the 95% isopleth constructed with a kernel density analysis of radio-marked individuals (Coulombe et al. 2011). We intersected home range polygons with vegetation cover maps for Niau (Butaud 2007) to identify the area of each habitat within home ranges, including atoll forest, mixed coconut and atoll forest, agricultural coconut plantation, littoral zone, urbanized, and wetland. We excluded portions of home ranges overlapping with ocean or lagoon because Tuamotu kingfishers are strictly terrestrial. We did not have resource use information for all individuals because some birds were color-banded but not radio-tracked. However, our previous work demonstrated only slight resource use differences between different individuals within a single territory (Coulombe 2010). Therefore, for each territory ($n = 14$ territories) we averaged resource use measures from radio-marked birds and used those mean metrics as individual covariates for all occupants of the same territory. For each territory, we used mean territory size (ha), mean area (ha) of coconut habitat within the territory, and mean atoll forest area (ha) within the territory as individual covariates in the adult survival models.

We evaluated adult survival for 39 known-sex adult (22 female, 17 male) Tuamotu kingfishers from 14 territories with quantified resource metrics. We assessed survival using 22 models that incorporated the potential effects of sex, territory resources, and study site (Table 1). Covariates included the study site (lagoon or coast) and the territory resource metrics described above. We also estimated a single resight probability for males and females and across years because our field methods included revisiting each territory and seeking out the residents. Both nesting and non-nesting birds responded to playback similarly, so season and sex differences in detection seemed unlikely. Additionally, the same 2 technicians made most observations. We fit mark and resight data collected during 6 study periods to survival models using the live recapture module in program MARK (White and Burnham 1999) and ranked them from least to greatest with Akaike's Information Criteria corrected for sample size (AIC_c; Burnham and Anderson 2002). We tested for overdispersion ($\hat{c}$) with a median $\hat{c}$ test of the most saturated model, without covariates (White and Burnham 1999). Estimates for $\hat{c}$ were near 1 for adults ($\hat{c} = 1.01$). Additionally, we incrementally raised $\hat{c}$ values (range: 1.00–1.75; Cooch and White 2011) and found that the top-ranked model remained in the same superior position so no adjustments were made for overdispersion. We considered a single model to be best-approximating if it was $\geq$2.0 AIC_c units from the next-best model (Burnham and Anderson 2002). We model averaged survival metrics if multiple models were competitive.

We did not attempt to include territory, sex, site, or resource covariates in the analysis of survival for juvenile Tuamotu kingfishers (ϕ_{HY}) because of the restricted sample size ($n = 16$). We fit band-resight data to an age-structured survival model, such that first-year survival was estimated separately from survival thereafter. Additionally, we used $\hat{p}$ from the top-ranking model of adult survival (0.926). We found no evidence of overdispersion for juvenile birds using the median $\hat{c}$ method ($\hat{c} = 1.09$). We then used resight data to estimate juvenile survival using the live recapture model in program MARK (White and Burnham 1999).

Projection Matrix Model

We combined results from Tuamotu kingfisher survival analyses with a previously published population projection matrix model for insular Pacific kingfishers (Kesler and Haig 2007*a*) to evaluate the relative influence of vital rates and territory resources on population processes. The matrix was based on females and included an annual time step occurring immediately before nesting. The Pacific kingfisher matrix was structured for cooperatively breeding Micronesian kingfishers (*Todiramphus cinnamominus*; Kesler and Haig 2007*b*, *c*) and it included a cooperative helper life-history stage that

Table 1. Top-ranking ($\Delta_i \leq 4.00$) models of annual survival (ϕ) for adult color-banded Tuamotu kingfishers on Niau Atoll between 2006 and 2010. Noted for each model is the number of parameters (K), second-order Akaike's Information Criteria (AIC_c), AIC_c differences (Δ_i), and Akaike weights (ω_i). Subscript indicates model parameterization for combined sex estimates ($\cdot$), for males (M) or females (F) when survival was estimated separately and resource covariates were included, and for sex (sex) when male and female survival was estimated separately but without a covariate. Survival covariates included study site (site), area of atoll forest within the territory (atoll), area of coconut agriculture within the territory (coconut), and territory size (territory). Note that all models were also fitted with a single resight probability (p) that applied to both males and females.

Model	K	AIC_c	Δ_i	ω_i
$\phi_{\text{M + atoll}}$, $\phi_{\text{F + territory}}$	5	107.2	0.00	0.40
$\phi_{\text{M + atoll}}$, $\phi_{\text{F + coconut}}$	5	109.5	2.21	0.13
$\phi_{\text{M + atoll}}$, $\phi_{\text{F + site}}$	5	110.6	3.39	0.07
ϕ_{sex}	3	111.2	4.00	0.05
$\phi_{\text{sex + coconut}}$	4	111.9	4.70	0.04
$\phi_{\text{M + coconut}}$ $\phi_{\text{F + territory,}}$	5	111.9	4.71	0.04
$\phi_{\text{sex + territory}}$	4	112.0	4.74	0.04
$\phi_{\text{M + site,}}$ $\phi_{\text{F + territory,}}$	5	112.3	5.07	0.03
$\phi_{\text{M + coconut,}}$ $\phi_{\text{F + atoll,}}$	5	112.3	5.08	0.03
$\phi_{\text{M + territory,}}$ $\phi_{\text{F + atoll}}$	5	112.5	5.03	0.03
$\phi_{\text{M + site,}}$ $\phi_{\text{F + atoll}}$	5	112.7	5.44	0.03
$\phi_{\text{sex + site}}$	4	113.5	6.21	0.02
$\phi_{\text{sex + atoll}}$	4	113.5	6.23	0.02
$\phi_{\cdot}$	2	113.8	6.55	0.02
$\phi_{\text{M + territory,}}$ $\phi_{\text{F + coconut}}$	5	114.4	7.16	0.01
$\phi_{\text{M + site,}}$ $\phi_{\text{F + coconut}}$	5	114.5	7.31	0.01
$\phi_{\cdot\ \text{+ coconut}}$	3	114.7	7.50	0.01
$\phi_{\cdot\ \text{+ territory}}$	3	115.1	7.84	0.01
$\phi_{\text{M + coconut,}}$ $\phi_{\text{F + site}}$	5	115.4	8.15	0.01
$\phi_{\text{M + territory,}}$ $\phi_{\text{F + site}}$	5	115.6	8.33	0.01
$\phi_{\cdot\ \text{+ atoll}}$	3	116.0	8.71	0.01
$\phi_{\cdot\ \text{+ site}}$	3	116.0	8.73	0.01

is not present in Tuamotu kingfishers. In accordance with recommendations published with the original model, we removed elements that were associated with non-breeding helpers (center row and column) so that the remaining model was structured for kingfisher species that breed as pairs. The structure of the resulting population projection matrix model (A) was

$$\begin{array}{c} \mathrm{HY} \rightarrow \mathrm{AHY} \\ A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \end{array}$$

$$= \begin{bmatrix} (\phi_{\text{Nestling}} \times \phi_{\text{HY}} \times f \times N) & (\phi_{\text{AHY Female}} \times f \times N) \\ (\phi_{\text{Nestling}} \times \phi_{\text{HY}}) & (\phi_{\text{AHY Female}}) \end{bmatrix}$$

where ϕ_{HY} represents apparent survival from fledge to the next breeding season, f represents the proportion of the population breeding, and N is the number of nests attempted by each breeding adult (Fig. 2).

We then populated the projection matrix model using parameter estimates from our analysis of marked Tuamotu kingfishers, and parameter estimates published with the first generalized model (Table 2). Apparent survival for juvenile Tuamotu kingfishers (ϕ_{HY}) was drawn directly from the results of our color-band resight evaluation described above and we used the apparent survival estimate from the best model for adult females ($\phi_{\text{AHY Female}}$). The best-approximating survival model also included the effect of territory size on adult female survival, so we also included this as a covariate in the population projection matrix.

We used reproduction parameters provided with the generalized matrix model for insular Pacific kingfishers (Table 2). Our observations of Tuamotu kingfishers suggested that reproduction was similar to rates previously

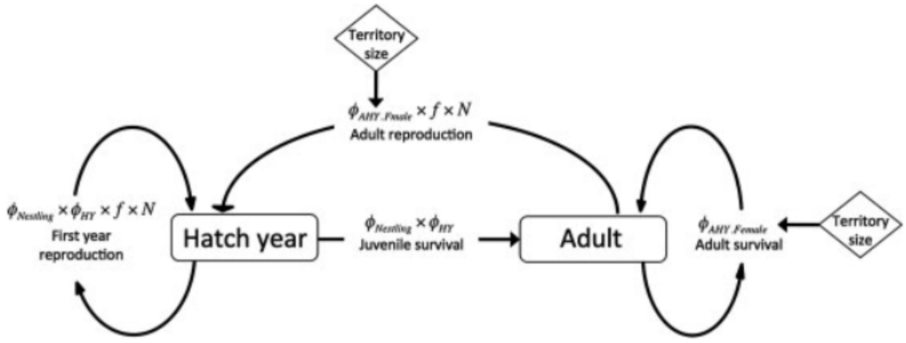

Figure 2. Conceptual population model for Tuamotu kingfishers illustrating influence of nestling, juvenile (HY), and adult (AHY) female survival (ϕ), proportion of population breeding (f), annual number of nests (N), and the influence of territory size on female survival.

Table 2. Input values and ranges of parameters used in simulation analysis ($n = 1{,}000$) of Tuamotu kingfisher population processes and resultant slope and r^2 relating parameters to rate of population change (λ) as well as elasticity (E_θ) and sensitivity (S_θ) of point-estimate models from evaluating change in demographic parameters.

	Input		Regression		Elasticity	
Parameter	**Base value**	**Range SD**	**Slope**[a]	r^{2}[b]	S_θ	E_θ
Reproduction						
Nests (N)	1.7	0.15	0.11	0.02	0.12	0.20
Breeding adults (f)	0.95	0.02	<0.01	<0.01	0.21	0.20
Survival (ϕ)[c]						
ϕ Nestling	0.534	0.105	0.27	0.05	0.37	0.20
ϕ Juvenile	0.115	0.099	0.85	0.32	1.72	0.20
ϕ Adult females	0.402	0.091	0.99	0.58	2.00	0.80
Survival covariate[c]						
Territory size (T)	4.22	1.49	0.02	0.06	0.04	0.18

[a] Slope represents the association between change in a variable and the response in λ.

[b] The r^2 value represents the amount of variation in λ accounted for by each demographic parameter.

[c] The simulation model is based on females Tuamotu kingfishers so the survival parameter and covariate are not shown for males.

published for the congener Micronesian kingfisher, which reported a mean of 1.7 nests each year, each with 2 eggs (Kesler and Haig 2007*a*). Our field seasons did not encompass the 2 nesting periods (nearly 60 days each), but observations of staggered-age chicks during post-breeding visits to Niau in February 2006 and 2010 indicated that nestlings were indeed produced during 2 different nesting attempts. Nestling survival (ϕ_{Nestling}), which encompassed laying to fledge, was estimated at 0.54 for Micronesian kingfishers (Kesler 2005) and we used this rate in our model for the Tuamotu kingfisher, because no formal measure was available, and because nestling survival appeared similar to that of Micronesian kingfishers (D. C. Kesler, University of Missouri, unpublished data).

Factors Influencing Population Processes

To calculate a general estimate of whether the model Tuamotu kingfisher population was projected to increase or decrease in size we used MATRIX 2.3 (Foxes Team, Rome, Italy) to estimate the dominant eigenvalue (λ). The λ value represented the asymptotic finite rate of population change. The prospective population projection matrix was used in sensitivity (S) and elasticity (E) analyses to identify parameters key to population dynamics and conservation (Caswell 2001, de Kroon et al. 2000, Wisdom et al. 2000, Williams et al. 2001, Morris and Doak 2002). Sensitivity for each parameter represented the change in λ associated with small changes in θ, where θ was the demographic parameter of interest, or

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

(Williams et al. 2001:151). Elasticity was a metric scaled to reflect the proportional change in λ realized by a similarly proportioned change in θ, thereby facilitating comparisons among θ (Williams et al. 2001:152):

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

We estimated sensitivity and elasticity statistics by altering each parameter by 0.01 and assessing resultant change in λ (Heppell et al. 2000, Morris and Doak 2002:330). However, sensitivity and elasticity do not incorporate effects of simultaneous changes in variables. Thus, we also used a life-stage simulation approach to evaluate the relative influence of each metric on λ under a range of altered matrix element values (Wisdom et al. 2000). We randomly selected simulation input values for the population projection matrices from a range of values expected on Niau. We generated random seeds using SAS software (Version 8.2; SAS Institute Inc., Cary, NC) and for each metric, we sampled from a distribution of values normally distributed about the mean (Table 2). We used the sample standard error from survival models as guidance for the spread of juvenile and adult survival values that might be expected on Niau. We randomly sampled parameter values associated with reproduction from a normally distributed set with 95% of the values drawn from a range approximating the bounds previously published (Kesler and Haig 2007*a*). We used a mean of 0.95 (SD 0.02) for f, a mean of 1.7 (SD 0.15) for N, and a mean of 0.534 (SD 0.105) for ϕ_{Nestling}. We selected simulation input values for effects of territory size on adult female survival from a normally distributed set of values centered on the mean home range size of birds used in our survival analysis (4.2 ha, SD 0.1; Coulombe et al. 2011).

We simulated 1,000 value combinations for matrix variables and derived λ_i for each. To eliminate extreme variable combinations drawn from the tails of the distributions, we excluded and re-ran simulations when randomly selected survival values were <0 or >1, or when the resulting set of λ_i was >2 or <0. We then regressed the effects of each parameter on the resulting λ_i using SAS software (PROC REG). The estimated slope (m) predicted the magnitude of parameter influence on λ, and the coefficient of determination (r^2) assessed the strength of each variable's association with the projected rate of population change (Wisdom and Mills 1997, Wisdom et al. 2000, Beissinger et al. 2006). We reported estimates as means with 95% confidence intervals.

RESULTS

Survival

The best-approximating model of survival in adult Tuamotu kingfishers was 2.2 AIC$_c$ units from the second best model and accounted for 40% of Akaike weight (ω_i). The model estimated male and female survival separately and included a covariate for males that represented area of atoll forest within male territories and a covariate for females representing territory size (Table 1). Models with combined parameter estimates for males and females and those with single covariates applied to both sexes ranked substantially lower, indicating strong support for differential survival among sexes (Table 1).

Parameter estimates from the best model indicated that survival of adult males ($\hat{\phi}_{\text{Male}} = 0.765$; 95% CI = 0.558–0.894 at mean forest area within territories) was higher than females ($\phi_{\text{Female}} = 0.402$; 95% CI = 0.128–0.723 at mean territory size). Adult male survival included a covariate for area of atoll forest inside the territory, so the resulting equation for apparent adult male survival was

$$\hat{\phi}_{\text{AHY Male}} = \frac{e^{(F\beta_1+\beta_2)}}{1+e^{(F\beta_1+\beta_2)}}$$

where F is the area (ha) of atoll forest within the territory, β_1 is the associated parameter estimate (−0.898, 95% CI = −1.864–0.068), and β_2 is the survival parameter (1.728, 95% CI = 0.579–2.878). The parameter estimate for atoll forest indicated lower survival with more forest within the territory (Fig. 3).

The model for adult survival in female Tuamotu kingfishers provided suggestive support for a positive relationship between survival and territory size (Fig. 3). The equation for adult female survival was

$$\hat{\phi}_{\text{AHY Female}} = \frac{e^{(T\beta_1+\beta_2)}}{1+e^{(T\beta_1+\beta_2)}}$$

where T is the territory area (ha) and β_1 is the associated parameter estimate (0.091, 95% CI = −0.013 to 0.195), and β_2 is the survival parameter (−0.780, 95% CI = −1.918 to 0.358). The combined resight probability, estimated for both males and females, was 0.926 (95% CI = 0.684 to 0.986). The model parameterized to estimate survival of juvenile kingfishers yielded an estimate that was substantially lower than adult male or female survival ($\hat{\phi}_{\text{HY}} = 0.115$, 95% CI = 0.019 to 0.468).

Factors Influencing Survival

We adjusted the population projection matrix for Tuamotu kingfishers to incorporate results from survival analyses. We substituted the equation presented above for $\hat{\phi}_{\text{Female}}$ so that the population projection matrix was:

$$\begin{aligned} B &= \begin{bmatrix} \left(\phi_{\text{Nestling}} \times \phi_{\text{HY}} \times f \times N\left(\frac{e^{(T\beta_1+\beta_2)}}{1+e^{(T\beta_1+\beta_2)}} \times f \times N\right)\right. \\ \left(\phi_{\text{Nestling}} \times \phi_{\text{HY}}\right)\left(\frac{e^{(T\beta_1+\beta_2)}}{1+e^{(T\beta_1+\beta_2)}}\right) \end{bmatrix} \\ &= \begin{bmatrix} 0.0990.649 \\ 0.0610.402 \end{bmatrix} \end{aligned}$$

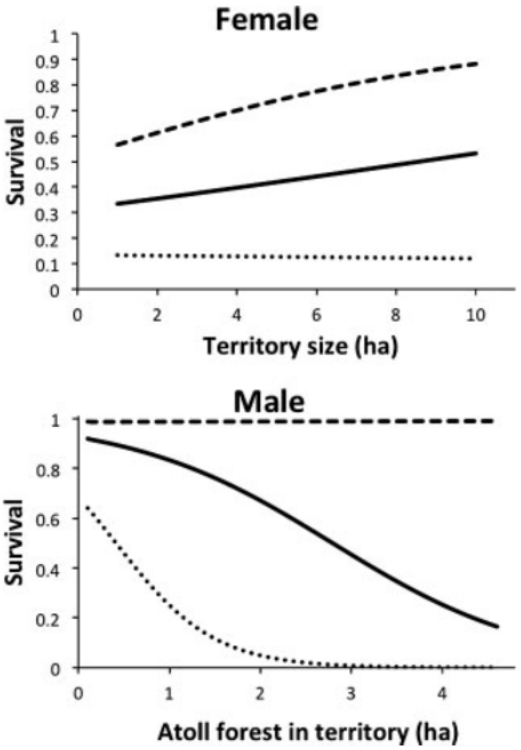

Figure 3. Predicted relationship between territory size and female survival (top; ±95% CI), and between the amount of atoll forest in a territory and male survival (bottom; ±95% CI) in Tuamotu kingfishers on Niau, French Polynesia, 2006–2010.

The dominant eigenvalue for the matrix evidenced a severely declining population of Tuamotu kingfishers ($\lambda = 0.50$).

Results from the evaluation of S_θ and E_θ indicated that $\phi_{\text{AHY Females}}$ had the greatest influence on Tuamotu kingfisher population change (Table 2). Sensitivity results further suggested that ϕ_{HY} also has substantial influence. However, the E_θ parameter for ϕ_{HY} indicated nearly equal per-unit effect on λ as N, f, ϕ_{Nestling}, and territory size (Table 2). Results of the simulation analysis illustrated similar patterns across a range of parameter values. Adult female survival had the strongest magnitude of influence ($m = 0.99$) and explained the most variation in λ ($r^2 = 0.58$; Fig. 4). Parameterizing the regression equation indicated that a 5% increase in adult female survival would yield a corresponding 5% increase in λ. Simulation results also indicated a strong relationship between ϕ_{HY} and λ ($m = 0.85$, $r^2 = 0.32$). When considered together, S, E, and simulation results indicated that λ could be most influenced by conservation actions that improve adult female survival and hatch-year survival.

DISCUSSION

Results from our analyses revealed age- and sex-specific differences in survival of the critically endangered Tuamotu kingfisher. Estimated survival in adult males ($\hat{\phi}_{\text{AHY Male}} = 0.77$) was within a range presented for other forest birds (Sæther and Bakke 2000), although it was greater than that for a congeneric species (Micronesian kingfisher; $\hat{\phi}_{\text{AHY Male}} = 0.57$; Kesler and Haig 2007*a*) or for the

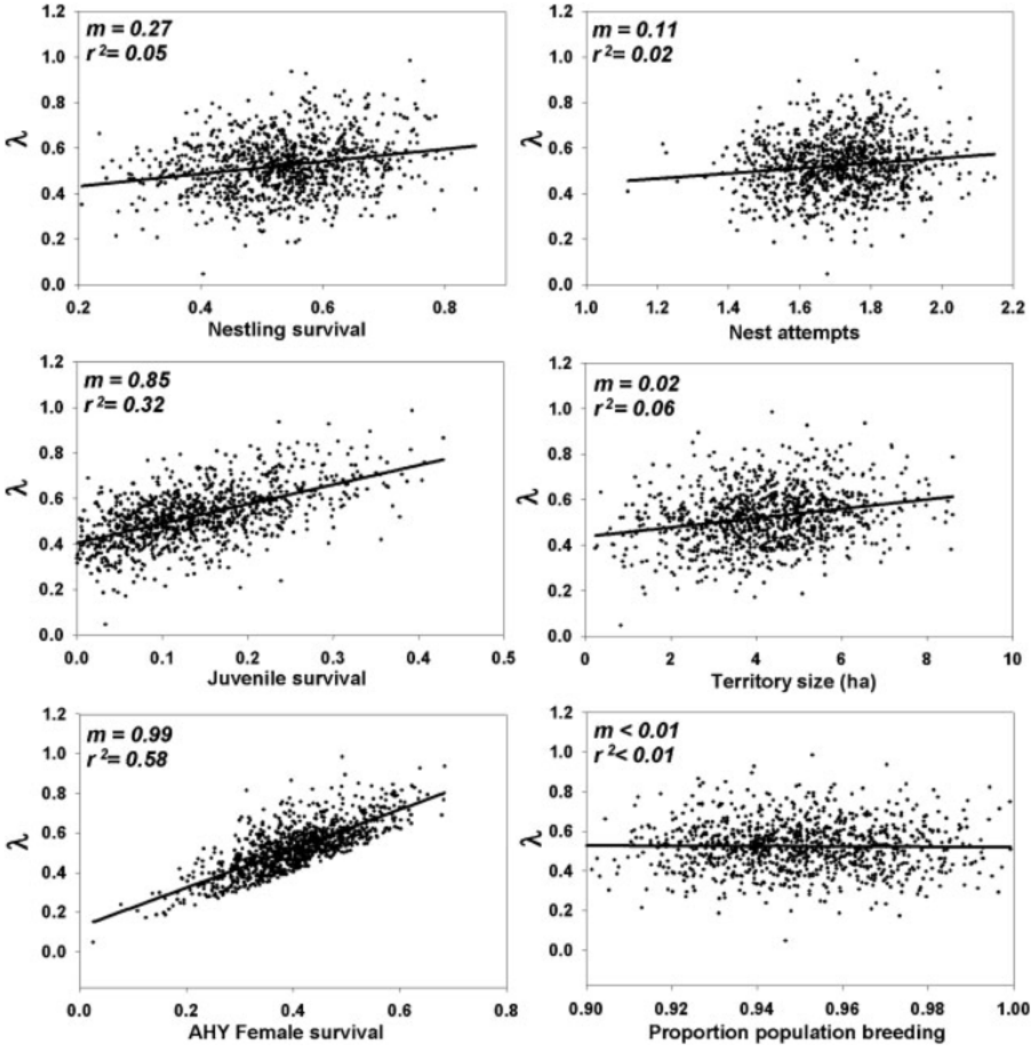

Figure 4. Finite rate of population change (λ) of nestling, juvenile, and female adult (AHY) Tuamotu kingfishers on Niau, French Polynesia associated with change in demographic parameters based on 1,000 population projection matrix model simulations with varying parameter values. Regression slopes (m) indicate magnitude of effects, and r^2 represents the concordance between demographic parameters and λ. Note that r^2 values do not sum to 1 because of the nested position of territory size.

European kingfisher (*Alcedo atthis*; $\hat{\phi} = 0.28$, Bunzel and Drüke 1989 in Sæther and Bakke 2000). Survival of adult female Tuamotu kingfishers, however, was uncharacteristically low ($\hat{\phi}_{\text{AHY Female}} = 0.40$) considering the life-history of this species. Because of a lack of predators and year-round favorable weather conditions, many island birds of the Tropical Pacific fit into the "slow" end of a previously described continuum of life-history strategies (Sæther 1988, Sæther and Bakke 2000). Slow species are characterized by long-lives, small clutches, long maturation periods, and high contributions from adult survival to population change. Our results for adult male Tuamotu kingfishers fit well within what would be expected for a Pacific kingfisher (Kesler and Haig 2007*a*), but estimates for Tuamotu kingfisher adult females and juveniles were closer to the range characterizing "fast" species.

The cause of elevated mortality in the adult female Tuamotu kingfisher is not clear. Behaviors and activities of adult male and female kingfishers are similar, so the risks of mortality should also be similar. Both sexes excavate nest cavities, defend territorial boundaries, incubate eggs, feed nestlings, and care for fledglings. However, females likely incubate at night like other kingfishers (Woodall 2001), and consequently suffer increased predation from nocturnal rats. Having evolved in the absence of mammalian nest predators, incubating Tuamotu kingfishers may lack effective escape or defense behaviors. Indeed, we found 1 radio-marked female in our study dead in a nest cavity with a wound consistent of a rat bite. Female kingfishers also invest energy and nutrients in egg production, so food limitations might cause differences in male and female survival. However, the birds are terrestrial generalists and a qualitative assessment suggests their primary food source (lizard, *Emoia* spp.) is abundant on Niau (Coulombe et al. 2011).

Low female survival might also be the cause of an apparently skewed sex ratio in the Tuamotu kingfisher population. We observed several territories that were occupied by single adult males, but we never observed single females holding territories, except after we artificially removed males from 3 territories for an experimental translocation (D. C. Kesler, unpublished data). When we removed these birds, we observed new male occupants courting females within 10 days.

Field observations also supported results indicating that survival was low in juvenile Tuamotu kingfishers. We easily identified newly fledged juveniles by plumage and they were common on many territories late in the breeding season. However, we rarely observed first year birds during the following season, despite extensive surveys. Predation is a likely cause of low juvenile survival in Tuamotu kingfishers. Juvenile birds often perch near the ground (<1 m), which may make them more vulnerable to domestic cats than adults. Domestic cats are widely documented to prey on birds, particularly juveniles (Lever 1994, Nogales et al. 2004, Whittaker and Fernández-Palacios 2007, Balogh et al. 2011), and we commonly observed cats on the Niau study areas. Additional investigation regarding interactions among cats, rats, and Tuamotu kingfishers would provide insights into the causes and influence of predation and reveal potential management strategies to increase survival.

Results of survival models supported a positive relationship between adult female survival and territory size. Tuamotu kingfishers primarily use territories for foraging, and larger territories almost certainly provided greater foraging opportunities (Coulombe et al. 2011). Our best-approximating model also indicated a negative relationship between the amount of atoll forest in a territory and adult male survival. A previous study also showed kingfisher avoidance of atoll forest (Coulombe et al. 2011). The birds may avoid atoll forest because the dense understory structure provides hunting cover for cats and rats.

We estimated apparent survival, which has the potential to be biased low when individuals were not resighted (Koenig et al. 1996, Cooper et al. 2008). However, estimated resight probability was high ($\hat{p} = 0.93$), which indicated that emigration from our study areas was infrequent. Additionally, the natural history characteristics of Tuamotu kingfishers and the small size of Niau reduced the chances that dispersal biased our results. Our observations of territory occupancy across years indicated that Tuamotu kingfishers rarely move from 1 breeding territory to another (Coulombe 2010). Juvenile birds are more likely to leave study areas during natal dispersal, but we observed no color-banded juveniles during island-wide surveys. Further, juvenile Tuamotu kingfishers were tracked during the 2006 natal-dispersal phase using radiotelemetry, and daily foray movements were usually well within the study areas (D. C. Kesler, unpublished data).

Sensitivity and elasticity measures and life stage simulations suggested that increased survival of adult females and juveniles has the potential to positively affect population processes. Further, comparisons to other, similar kingfisher populations suggest that sufficient variability exists in both vital rates for management to influence Tuamotu kingfisher population dynamics. Indeed, a matrix model parameterized with increased but plausible variable values projected a growing population of Tuamotu kingfishes. For example, λ reflects a population with strong positive growth ($\lambda = 1.08$) if juvenile survival is set to the level previously reported for the Micronesian kingfisher ($\phi_{HY} = 0.37$; Kesler and Haig 2007*a*), and if adult female survival is elevated to the level observed in adult male Tuamotu kingfishers ($\phi = 0.765$). Together, these results indicated that targeted conservation efforts aimed specifically at elevating female survival and increasing juvenile survival would help stabilize the population of critically endangered Tuamotu kingfishers.

MANAGEMENT IMPLICATIONS

Island-wide attempts at rodent and cat eradication are costly, time-consuming, and often unsuccessful (Thorsen et al. 2000, Nogales et al. 2004); however, this study reveals that focusing conservation efforts on specific life stages could dramatically increase the population of Tuamotu kingfishers. Metal predator guard bands have already been installed around some of the trees used by nesting Tuamotu kingfishers. If the metal bands prove effective in reducing nest predation and female mortality, managers should expand the tree-banding program island wide. With a total population of approximately 125 birds, protection could be garnered for every nesting kingfisher with reasonable effort. In addition, many coconut farmers on the island currently use metal bands to protect live coconut trees from loss of crops to rodents. Therefore, sufficient infrastructure and materials are already available on the island to expand metal banding to dead nest trees. Focusing cat trapping in areas where Tuamotu kingfishers are nesting and during fledge-rearing periods (Oct–Feb) may bolster juvenile survival and help protect the last remaining individuals of this species. Substantial effort should be invested in establishing a robust and ongoing monitoring program with the ability to evaluate Tuamotu kingfisher vital rates, track population changes, and assess effectiveness of predator control and conservation management.

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