

## SOURCES OF VARIATION IN SURVIVAL, RECRUITMENT, AND NATAL DISPERSAL OF THE HAWAI'I 'ELEPAIO

ERIC A. VANDERWERF<sup>1</sup>

*Pacific Rim Conservation, 3038 Oahu Avenue, Honolulu, HI 96822*

**Abstract.** I investigated survival, recruitment, and dispersal in the Hawai'i 'Elepaio (*Chasiempis sandwichensis sandwichensis*), a territorial, nonmigratory monarch flycatcher endemic to the island of Hawai'i. I color-banded and resighted 137 individuals from 1991–2000 and collected longevity data until 2008. The oldest known 'Elepaio was at least 17 years and 10 months old. I used multistate models to examine variation in survival and recruitment, with different states for territory holders and floaters. I classified birds into eight age-sex groups, with individual body size and annual reproduction as covariates. Territory holders of all ages had higher survival than floaters. Survival of territory holders was higher in years with low reproduction and was consistently higher in males ( $0.87 \pm 0.02$ ) than in females ( $0.81 \pm 0.03$ ) due to costs of reproduction. Larger body size was associated with higher survival in males but not in females because males engage in more intense physical competition. Survival and recruitment of floaters were influenced by different factors. Survival of floaters was not related to sex or size and may depend on foraging proficiency and avoiding aggression from dominant adults. Older and larger floaters were more likely to recruit. Natal dispersal distances were short but were longer in males ( $539 \pm 68$  m) than in females ( $357 \pm 82$  m), and this difference was due to higher survival of adult males. Accurate estimates of survival and recruitment are crucial for understanding population dynamics and designing effective conservation strategies.

**Key words:** *Chasiempis sandwichensis*, 'Elepaio, longevity, mark-recapture, natal dispersal, recruitment, survival.

### Fuentes de Variación en la Supervivencia, el Reclutamiento y la Dispersión Natal de *Chasiempis sandwichensis sandwichensis*

**Resumen.** Investigué la supervivencia, el reclutamiento y la dispersión en *Chasiempis sandwichensis sandwichensis*, un atrapamoscas monarca territorial y no migratorio que es endémico de la isla de Hawai. Marqué con anillos de colores y observé posteriormente 137 individuos entre 1991 y 2000 y recolecté datos de longevidad hasta 2008. El individuo más viejo conocido tenía por lo menos 17 años y 10 meses de edad. Utilicé modelos multiestado para examinar la variación en la supervivencia y el reclutamiento, con diferentes estados para los individuos con territorio y los individuos flotantes. Clasifiqué las aves en ocho grupos según la edad y el sexo, usando como covariables el tamaño del cuerpo y la reproducción anual. Los individuos con territorio de todas las edades tuvieron una mayor supervivencia que los flotantes. La supervivencia de los individuos con territorio fue mayor en los años con baja reproducción y fue consistentemente mayor en los machos ( $0.87 \pm 0.02$ ) que en las hembras ( $0.81 \pm 0.03$ ) debido al costo reproductivo. El tamaño mayor del cuerpo estuvo asociado con una supervivencia mayor en los machos pero no en las hembras, debido a que los machos participan en competencias físicas más intensas. La supervivencia y el reclutamiento de los flotantes estuvieron influenciados por diferentes factores. La supervivencia de los flotantes no estuvo relacionada con el sexo o el tamaño, y puede depender de la habilidad de forrajeo y de evitar la agresión por parte de los adultos dominantes. Los flotantes más viejos y de mayor tamaño tuvieron mayor probabilidad de reclutamiento. Las distancias de dispersión natal fueron cortas, pero fueron mayores en los machos ( $539 \pm 68$  m) que en las hembras ( $357 \pm 82$  m) debido a una mayor supervivencia de los machos adultos. Las estimaciones precisas de la supervivencia y del reclutamiento son cruciales para entender las dinámicas poblacionales y para diseñar estrategias de conservación efectivas.

## INTRODUCTION

Accurate measures of age-specific survival and recruitment are fundamental to population dynamics, and understanding sources of variation in these parameters can provide insights into the ecology and conservation of a species (Nur and Syde-man 1999, Sandercock et al. 2000, Martin 2002). Depressed

rates of survival or recruitment can indicate suboptimal habitat (Gardali and Nur 2006, Johnson et al. 2006), a threat such as habitat loss (Rappole and McDonald 1994, Sillett and Holmes 2002) or predation (Robertson et al. 1994, VanderWerf and Smith 2002), or unsustainable harvest (González 2003, Arnold et al. 2006). For rare and declining species, such information is crucial to designing effective conservation

Manuscript received 30 August 2007; accepted 14 March 2008.

<sup>1</sup>E-mail: [ewerf@hawaii.rr.com](mailto:ewerf@hawaii.rr.com)

strategies and making informed management decisions (Nur and Sydean 1999, Anders and Marshall 2005).

Investigation of survival and recruitment often is hindered by difficulty in distinguishing mortality from emigration, low or biased recapture probability due to transients, and potentially confounding factors such as sex, age, social status, and reproductive effort (Lebreton et al. 1992, Nichols et al. 1994, Martin et al. 1995, Pradel et al. 1997, Sandercock et al. 2000). In this study, I report on variation in survival, recruitment, and dispersal of the Hawai'i 'Elepaio (*Chasiempis sandwichensis sandwichensis*), a monarch flycatcher endemic to the island of Hawai'i, based on 10 years of encounter data from Hakalau Forest National Wildlife Refuge. Survival, recruitment, and dispersal could be accurately estimated in this case due to the life history of the species and demography of the study population. 'Elepaio are nonmigratory, and pairs defend the same territories all year. Site fidelity was high between years (0.98 in males, 0.93 in females), and rare instances of breeding dispersal were short (238 ± 39 m in males, 170 ± 31 m in females) compared to the size of the study sites, resulting in very high encounter probabilities even for dispersing birds (VanderWerf 2004). Natal dispersal distances were also relatively short, so recruitment could be measured. Floaters were readily recognizable by behavior; thus, analyses could be stratified by social class. 'Elepaio are sexually dichromatic, and both sexes have a two-year delay in plumage maturation (VanderWerf 2001a), allowing comparison of survival among age-groups and between the sexes.

There is an urgent need for accurate demographic information to aid in conservation of 'Elepaio and other Hawaiian forest birds (U.S. Fish and Wildlife Service 2006). 'Elepaio populations on Hawai'i have declined in several areas (Gorreson et al. 2005), and the O'ahu 'Elepaio (*C. s. ibidis*) has declined to fewer than 2000 birds and is listed as endangered under the U.S. Endangered Species Act (VanderWerf et al. 2001, U.S. Fish and Wildlife Service 2006). Status of the species as a whole was recently elevated to endangered by the International Union for the Conservation of Nature (2006). Demographic data from a large, stable 'Elepaio population are needed to help understand normal population dynamics and why other populations are declining.

## METHODS

### STUDY SITE AND SPECIES

This study was conducted at Hakalau Forest National Wildlife Refuge (Hakalau) on the eastern slope of Mauna Kea volcano on the island of Hawai'i (19°47'N, 155°20'W). Hakalau lies within the largest expanse of native forest left in the Hawaiian Islands and supports part of the largest remaining populations of several native forest bird species, including 'Elepaio (Scott et al. 1986, Gorreson et al. 2005). Habitat in the area consists of montane rain forest variably modified by

prior human activities, particularly cattle ranching and timber harvesting. Two study sites were located 10 km apart at 1550–1900 m elevation in the Pua 'Ākala and Maulua tracts of the refuge. These sites were approximately 65 and 55 ha in size and encompassed 40 and 23 'Elepaio territories, respectively. An epizootic of avian pox virus (*Poxvirus avium*) occurred at the Maulua site in 1992, resulting in temporary perturbations of population density and age structure (VanderWerf 2001b), but 'Elepaio inhabiting these sites were not known to differ in other respects (VanderWerf 2004). Data from both sites were combined in this study.

The 'Elepaio is a small (body mass 16.2 ± 1.1 g in males, 14.4 ± 0.8 g in females) monarch flycatcher (Monarchidae) endemic to the Hawaiian Islands (VanderWerf 1998). Different forms currently regarded as subspecies occur on the islands of Kaua'i, O'ahu, and Hawai'i (Pratt et al. 1987, VanderWerf 2007). 'Elepaio have four visibly distinct age-classes: juveniles, first-year subadults, second-year subadults, and adults (three or more years old). In bird banding terminology, these age-classes respectively correspond to hatch year (HY), second year (SY), third year (TY), and after third year (ATY).

Pairs of 'Elepaio defend all-purpose territories year round (VanderWerf 1998). Both sexes participate in all aspects of reproduction, including nest construction, incubation, and feeding of nestlings, though the male plays a larger role in territory defense, and the female alone incubates at night (VanderWerf 1998). Juveniles remain with their parents on natal territories until the start of the next breeding season, when they are evicted and begin to act as floaters, moving inconspicuously among territories until vacancies open or they are able to challenge and depose territory owners (VanderWerf and Freed 2003, VanderWerf 2004). An individual 'Elepaio usually does not acquire a territory until it is three years old if competition for space is intense, but in sparse populations or less preferred habitats, it may acquire a territory and breed when one or two years old (VanderWerf 2004).

### DATA COLLECTION

I captured 'Elepaio with mist nets in 1991 and 1994–2000 and marked each bird with an aluminum leg band and a unique combination of three plastic colored leg bands. Marking of 'Elepaio in the area began in 1987 (L. Freed, University of Hawaii, unpubl. data), and some previously marked birds were still present at the time of my study. I systematically resighted marked birds each year by repeatedly revisiting every 'Elepaio territory on the study sites during the breeding season from February–July. I also searched up to one km (less if the forest edge was closer) in all directions from each study site for marked birds that dispersed. I made brief visits in April 2004, March and July 2006, and March 2008 to collect supplemental data on longevity.

I classified 'Elepaio as territory holders or floaters based on their behavior and encounter histories. Territory holders could each be reliably found with a mate in the same area on

repeated visits, frequently vocalized as part of territory defense, and responded aggressively to conspecifics and to playbacks of recorded vocalizations. Floaters were solitary, rarely vocalized, did not respond aggressively to playbacks, and were each seen irregularly over a large area encompassing several territories. Some birds had territories when they were first captured ( $n = 110$ ); others were first captured as floaters ( $n = 27$ ), some of which acquired territories in subsequent years. There were no birds of equivocal status and no evidence that any birds had been misclassified.

STATISTICAL ANALYSES

I created an encounter history for each bird based on the year of initial capture and recaptures and resightings in subsequent years. I used multistate models in program MARK (White and Burnham 1999) to generate maximum-likelihood estimates of survival ( $\phi$ ), recapture probability ( $p$ ), and transition probability ( $\psi$ ) between territorial (T) and floater (F) states. I classified 'Elepaio by sex (male or female) and age (HY, SY, TY, or ATY), for a total of eight groups. Age-specific groupings were achieved in MARK by structuring elements in the first through third diagonals of the parameter index matrix for each age-class. Some groups did not exist in both territorial and floater states—I never observed a juvenile attempt to defend a territory, and I never observed an adult floater. Survival, encounter, and transition probabilities for these non-existent groups were therefore fixed at zero. Similarly, I never

observed a territorial 'Elepaio revert back to the floater state, so this transition probability also was fixed at zero. This study encompassed a period of 10 years (1991–2000), but there were only eight sampling occasions because no fieldwork was conducted in 1992 or 1993. I therefore set the interval between the first and second occasions at three years.

I devised a set of candidate models that examined factors of interest (Table 1). Models attempting to include both age and sex effects contained inestimable parameters because sample sizes of some groups were too small, so those models had to be discarded. Model notation follows Lebreton et al. (1992), in which subscripts indicate whether parameters differed among groups (e.g.,  $\phi_{sex}$ ) or time periods (e.g.,  $\phi_t$ ), or were constant, indicated by a dot (e.g.,  $\phi$ ). Additive effects of more than one factor are indicated by a plus sign (e.g.,  $\phi_{t+sex}$ ), while interactions between factors are indicated with an asterisk (e.g.,  $\phi_{t*sex}$ ). Models in the candidate set were evaluated with Akaike's information criterion corrected for small sample size ( $AIC_c$ ), as calculated by MARK. The model with the lowest  $AIC_c$  value was considered to have the best fit, but models with  $AIC_c$  values that differed ( $\Delta AIC_c$ ) from the lowest value by  $\leq 2$  also were considered to have a reasonable fit (Burnham and Anderson 2002). Normalized  $AIC_c$  weights were used as a measure of each model's relative likelihood.

I investigated whether body size was associated with survival or recruitment by using body size as an individual covariate. A single measure of body size was created for each

TABLE 1. Multistate models used to investigate survival ( $\phi$ ) and encounter probability ( $p$ ) of Hawai'i 'Elepaio at Hakalau Forest National Wildlife Refuge from 1991–2000 in territorial (T) and floater (F) social classes, and the probability of recruitment ( $\psi$ ) from floater to territorial. No territorial 'Elepaio were observed to revert back to the floater class, so that transition probability was fixed at zero. Subscripts indicate whether parameters differed among groups (e.g.,  $\phi_{sex}$ ) or time periods (e.g.,  $\phi_t$ ) or were constant (e.g.,  $\phi$ ). Models were evaluated using Akaike's Information Criterion ( $AIC_c$ ). Log ( $\mathcal{L}$ ) is the log-likelihood,  $K$  is the number of parameters,  $\Delta AIC_c$  is the difference from the best model, and  $w_i$  is the model weight. Arrows indicate the sequence of models followed to arrive at the best model. Dashed arrows indicate models that resulted in worse fit.

Model <sup>a</sup>	Log ( $\mathcal{L}$ )	$K$	$\Delta AIC_c$	$w_i$
(1) $\phi_{T_{t+sex*size}} \phi_F p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_F$	1.00	15	0	0.32
(2) $\phi_{T_{t+sex*size}} \phi_F p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_{F_{age}}$	0.83	17	0.36	0.26
(3) $\phi_{T_{t+sex*size}} \phi_F p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_{F_{size}}$	0.49	16	1.43	0.16
(4) $\phi_{T_{t+sex*size+repro}} \phi_F p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_F$	0.40	16	1.64	0.14
(5) $\phi_{T_{t+sex*size}} \phi_{F_{age}} p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_F$	0.13	17	4.01	0.04
(6) $\phi_{T_{t+sex+size}} \phi_F p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_F$	0.11	14	4.43	0.03
(7) $\phi_{T_{t+sex}} \phi_F p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_F$	0.04	13	6.32	0.01
(8) $\phi_{T_{t+sex+size}} \phi_{F_{size}} p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_F$	0.04	15	6.44	0.01
(9) $\phi_{T_{t+sex}} \phi_F p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_{F_{sex}}$	0.02	14	7.83	0.01
(10) $\phi_{T_{t+sex}} \phi_{F_{sex}} p_{T_{sex}} p_F \psi_{T_{fix0}} \psi_F$	0.01	14	8.43	<0.01
(11) $\phi_{T_{t+sex}} \phi_F p_T p_F \psi_{T_{fix0}} \psi_F$	0.01	12	8.68	<0.01
(12) $\phi_{T_t} \phi_F p_T p_F \psi_{T_{fix0}} \psi_F$	0.01	11	9.40	<0.01
(13) $\phi_{T_{t+age}} \phi_F p_T p_F \psi_{T_{fix0}} \psi_F$	<0.01	13	10.69	<<0.01
(14) $\phi_{T_{t*sex}} \phi_F p_T p_F \psi_{T_{fix0}} \psi_F$	<0.01	19	13.95	<<0.01
(15) $\phi_T \phi_F p_T p_F \psi_{T_{fix0}} \psi_F$	<0.01	5	15.71	<<0.01

<sup>a</sup> $AIC_c$  of best model = 515.87.

bird with a principal components analysis of tarsus length and body mass, for males and females separately. The first principal component accounted for 61% and 66% of the total variance in males and females, respectively, and all component loadings were positive, indicating that higher scores represented larger body size. Wing chord and tail length were not suitable metrics for this purpose because the remiges and rectrices are shorter in juvenile 'Elepaio than in older birds (VanderWerf 1998), and these feathers are retained in the first prebasic (postjuvinal) molt (VanderWerf 2001a). Tarsus length or body mass data were missing for six birds. In these cases, the dataset of all birds was sorted by the other metric, and the missing value was assigned a value equal to the average of the next five larger and next five smaller birds.

I investigated whether survival was related to reproduction by using annual productivity as a covariate, measured as the average number of fledglings produced per pair each year. I also examined individual reproductive effort by using chi-squared analysis to compare the number of birds resighted vs. not, depending on whether they made some or no nesting attempt (e.g., built a nest, laid eggs, or fledged offspring).

I conducted a goodness-of-fit test on a global model using the median  $\hat{c}$  approach of MARK to determine if the model adequately fit the data and assumptions underlying this and subsequent analyses were reasonable (Cooch and White 2005). The global model included all factors used in any of the models except body size, because MARK does not allow the median  $\hat{c}$  approach to be used with individual covariates (Cooch and White 2005). The overdispersion or variance inflation factor,  $c$ , was found to be  $0.998 \pm 0.004$  for the global model. This was not different from 1.0, so no adjustment of  $c$  was necessary, and the  $AIC_c$  was used to evaluate models instead of the quasi Akaike Information Criterion (QAIC<sub>c</sub>; Cooch and White 2005).

I measured natal dispersal in two ways: (1) distance from the natal nest to the geometric center of the territory first defended, and (2) the number of territories moved from the natal territory to the territory first defended. These measures represent the minimum distances dispersed; birds may have covered longer distances before settling. In cases where the natal nest location was not known, I used the location within the

natal territory where the bird was banded as a juvenile. All values reported are means  $\pm$  SE.

## RESULTS

### MARKING AND ENCOUNTER SUMMARY AND LONGEVITY RECORDS

During this study, 108 'Elepaio were marked, and 29 individuals marked in previous years were still present, for a total of 137 marked birds, all of which were used in analyses. An average of  $65.6 \pm 7.9$  'Elepaio were captured, recaptured, or resighted each year. The oldest known 'Elepaio was a female captured in ASY plumage (and thus at least two years old) in June 1988 and resighted in April 2004, making it at least 17 years and 10 months old. A male captured in ATY plumage (and thus at least three years old) in March 1994 was still alive on my last visit in March 2008, making it at least 17 years old.

### MARK-RECAPTURE ANALYSES

Model fitting began with the simplest model, in which all factors were constant across all groups (Table 1, model 15). Addition of some factors improved fit; others made fit worse. All models showed that territory holders had substantially higher survival and encounter probabilities than floaters (Table 2), indicating that the multistate approach was appropriate and effective. The most parsimonious model included a time effect and an interaction between sex and size on survival of territory holders, and an effect of sex on encounter probability of territory holders (Table 1, model 1). Models that included an effect of reproduction on survival of territory holders and effects of age and size on recruitment probability of floaters were only slightly less likely (Table 1, models 2, 3, and 4), indicating these factors also should be considered.

Apparent survival of territory holders was generally high but exhibited several annual fluctuations and was particularly low in 1998 (Fig. 1). Survival of territorial males ( $0.87 \pm 0.02$ ) was consistently higher than survival of territorial females ( $0.81 \pm 0.03$ ). Encounter probability of territory holders also was higher in males ( $0.98 \pm 0.01$ ) than in females ( $0.93 \pm 0.03$ ). In six of seven years, males that survived were larger on average than males that disappeared, but females that survived

TABLE 2. Annual survival ( $\phi$ ), encounter probability ( $p$ ), and recruitment probability ( $\psi$ ) of Hawai'i 'Elepaio at Hakalau Forest National Wildlife Refuge from 1991–2000 by social status, sex, and age, estimated with program MARK. HY = hatch year; SY = second year; TY = third year. All values are mean  $\pm$  SE from model 1 in Table 1, except survival and recruitment probabilities of different-aged floaters, which are from models 5 and 2, respectively.

Social status	Sex	Age	Survival ( $\phi$ )	Encounter probability ( $p$ )	Recruitment probability ( $\psi$ )
Territorial	Male	All ages	$0.87 \pm 0.02$	$0.98 \pm 0.01$	0 (fixed)
	Female	All ages	$0.81 \pm 0.03$	$0.93 \pm 0.03$	0 (fixed)
Floater	Both sexes	TY	$0.51 \pm 0.33$	$0.24 \pm 0.30$	$1.0 \pm 0.0$
		SY	$0.40 \pm 0.15$	$0.24 \pm 0.30$	$0.78 \pm 0.25$
		HY	$0.32 \pm 0.19$	$0.24 \pm 0.30$	$0.36 \pm 0.32$



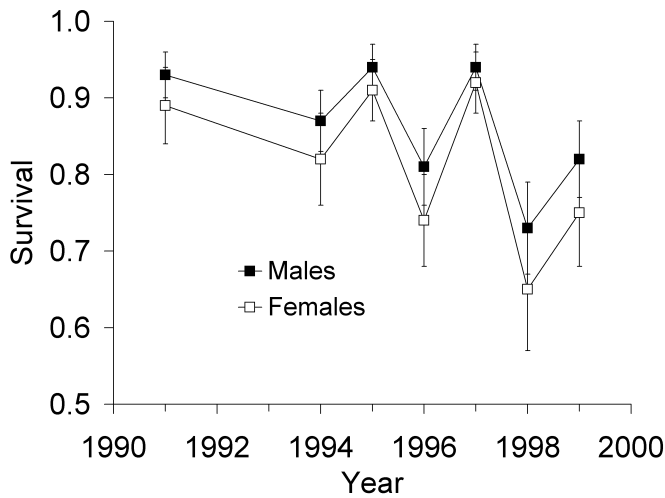


FIGURE 1. Survival (mean  $\pm$  SE) of territorial male and female Hawai'i 'Elepaio at Hakalau Forest National Wildlife Refuge from 1991–2000. Survival varied among years and was consistently higher in males than in females.

were larger than females that disappeared in only two of seven years (Fig. 2). Survival of territory holders did not differ among age classes.

Apparent survival of territory holders was higher in years when reproduction was low (Fig. 3), and examination of individual reproductive effort suggested that this pattern was caused by a cost of reproduction. Females that attempted to nest were less likely to survive (0.78,  $n = 63$ ) than females that made no nesting attempts (1.0,  $n = 14$ ;  $\chi^2_1 = 3.8$ ,  $P = 0.05$ ). Males that attempted to nest also tended to survive less often (0.84,  $n = 105$ ) than males that made no nesting attempts (0.90,  $n = 21$ ), but the pattern was not significant ( $\chi^2_1 = 0.6$ ,  $P = 0.44$ ).

Among floaters, apparent survival did not differ between sexes and was not dependent on size. Survival of floaters appeared to differ among age classes (Table 2), but addition of an effect of age on survival of floaters did not improve fit (Table 1, model 5), perhaps because the sample of some ages of floaters was small. Recruitment of floaters was influenced by age and body size. Floaters that were members of older age classes were more likely to acquire territories (Table 2), and floaters that were known to have recruited were larger on average (mean normalized size =  $-0.02 \pm 0.33$ ) than those that disappeared ( $-0.37 \pm 0.23$ ).

#### NATAL DISPERSAL

Natal dispersal distances in 'Elepaio were short but tended to be longer in males ( $539 \pm 68$  m) than in females ( $357 \pm 82$  m; Mann-Whitney  $U = 117$ ,  $P = 0.07$ ). Natal dispersal measured by the number of territories moved also tended to be longer in males ( $4.4 \pm 0.6$ ) than in females ( $2.7 \pm 0.8$ ; Mann-Whitney  $U = 115.5$ ,  $P = 0.10$ ). The distribution of natal dispersal distances was approximately normal (Fig. 4), suggesting few birds dispersed farther than those observed.

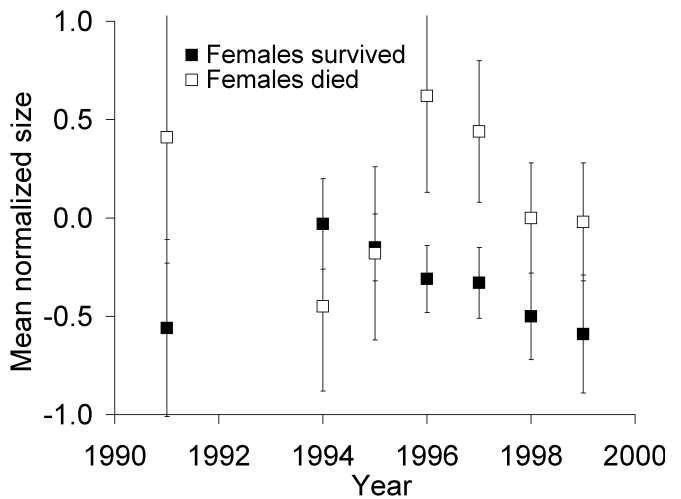
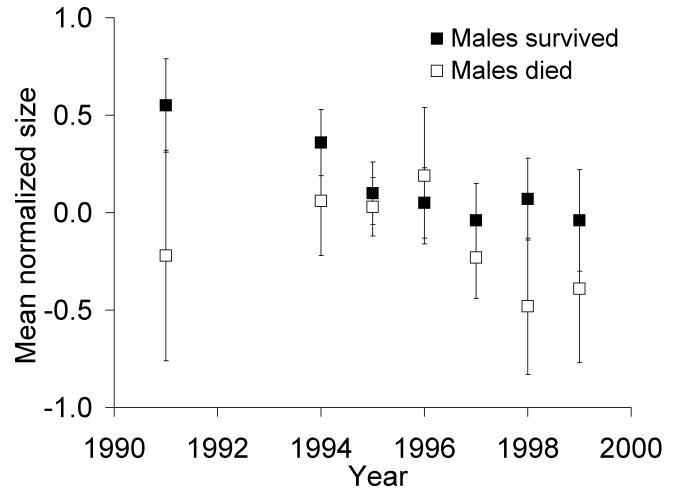


FIGURE 2. Survival of male (top) and female (bottom) Hawai'i 'Elepaio at Hakalau Forest National Wildlife Refuge from 1991–2000 in relation to body size. In six of seven years, males that survived were larger (mean  $\pm$  SE) than males that disappeared, but surviving females were larger than females that disappeared in only two of seven years.

## DISCUSSION

### TERRITORY HOLDERS

The higher survival of territory holders than floaters, even among birds of the same age, probably was caused by an advantage in food resource access provided by territory defense (Gill and Wolf 1975, MacLean and Seastedt 1979). Territory holders were not able to completely exclude floaters, but they had greater access to the best sites, foraged without interruption more often (VanderWerf 1994), and presumably had better knowledge of the time since an area was last searched for arthropods, which in theory should allow increased foraging efficiency (Davies 1980, Schoener 1983). Floaters were expelled from a territory when detected by the owner, limiting their use of rich food patches and forcing them to move farther and more often in search of food (VanderWerf 1994).

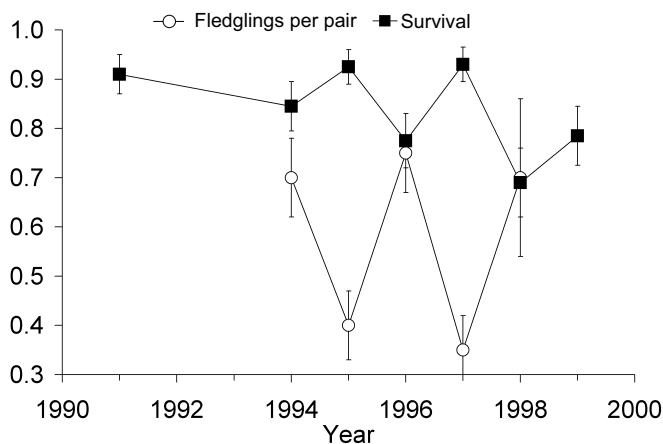


FIGURE 3. Survival of Hawai'i 'Elepaio at Hakalau Forest National Wildlife Refuge from 1991–2000 (mean ± SE, sexes averaged) in relation to annual reproductive success. Survival was lower in years when reproduction was higher.

It is also possible that the lower survival of floaters was due to lower average quality of those individuals. Ability to survive the floater period and compete for territories was probably an important means of selection that removed less proficient individuals from the population. A similar pattern was found by Sandercock et al. (2000) in Green-rumped Parrotlets (*Forpus passerinus*), in which breeders had higher survival than nonbreeders.

The consistently higher apparent survival of male vs. female territory holders could in part have been a result of the slightly lower encounter probability of females. However, two lines of evidence indicate that this difference was caused by higher cost of reproduction in females rather than differ-

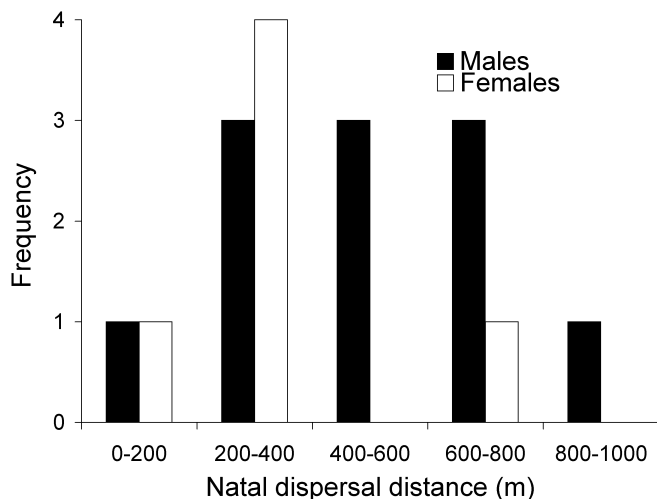


FIGURE 4. Natal dispersal distances, by sex, in Hawai'i 'Elepaio at Hakalau Forest National Wildlife Refuge from 1991–2000. Dispersal distances were short but were longer in males than in females.

ences in foraging proficiency, predation away from the nest, or some intrinsic factor. First, among floaters, there was no difference in survival between the sexes, and second, territorial females that did not nest had higher survival than those that did. Possible costs of reproduction include nest predation and energetic demands associated with egg production and incubation (Martin 1995, Nur 1998, Ghalambor and Martin 2001, Fontaine and Martin 2006). There is no information about such energetic costs in 'Elepaio, but nest predation is known to be a cause of mortality for females in particular. The most serious predator on 'Elepaio nests is the nonnative black rat (*Rattus rattus*), which is primarily nocturnal. There is some diurnal predation away from the nest by the 'Io or Hawaiian Hawk (*Buteo solitarius*) and Pueo or Hawaiian Short-eared Owl (*Asio flammeus sandwichensis*), but it is probably similar in both sexes. Male and female 'Elepaio incubate in alternating shifts during the day, but only the female incubates at night when rats are most active (VanderWerf 1998). In the O'ahu 'Elepaio, nest predation by black rats caused low nest success (33%) and a large difference in annual survival of males (0.79) and females (0.50; VanderWerf and Smith 2002). Black rats are common at Hakalau (Nelson et al. 2002), but the small difference in survival of males and females and the high nest success (65%; VanderWerf 2004) suggest nest predation is less common at Hakalau. The difference in predation on 'Elepaio nests at Hakalau and on O'ahu may be related to the dominant tree species at each site. On O'ahu, 'Elepaio nest in areas dominated by alien trees that bear fruit or nuts, which provide abundant food for rats and may thus attract them into the forest canopy. At Hakalau, 'Elepaio nest primarily in native 'ōhi'a (*Metrosideros polymorpha*) trees, which have tiny, wind-dispersed seeds that do not provide food for rats.

Much of the annual variation in survival of territory holders was inversely related to variation in reproduction. 'Elepaio survival was highest and reproduction was lowest in 1995 and 1997, which were dry years with low arthropod abundance (Fretz 2000). Fewer 'Elepaio attempted to nest in those years (VanderWerf 1999), suggesting some birds were unable to nest or chose to skip nesting, which may have reduced mortality risk from predation exposure or allowed energy conservation and improved body condition (Chastel et al. 1995, Ghalambor and Martin 2001, Fontaine and Martin 2006).

Survival of 'Elepaio was particularly low from 1998 to 1999. High reproduction in 1998 may partly account for low survival that year, but other factors may also have been involved. Freed et al. (2005) showed that prevalence of avian malaria (*Plasmodium relictum*) at Hakalau was higher from 2001–2002 than 1988–1992, and that 'Elepaio exhibited the largest increase in malaria prevalence of any species at the site between the two time periods (0% vs. 67%), though the sample sizes were very small ( $n = 13$  and 9 birds, respectively). Data on malaria prevalence during the intervening period, including 1998, are not yet

available, so it is not known whether this apparent increase was an isolated event or part of a chronic increase in disease transmission. 'Elepaio have greater immunity to alien diseases than do most Hawaiian passerines, but there is some disease-related mortality (VanderWerf 2001b, VanderWerf et al. 2006) and it is possible the low survival of 'Elepaio at Hakalau in 1998 was related to disease.

The association of larger body size with higher survival among territorial males but not territorial females suggests that larger size is advantageous primarily in direct competition for territories. If mate attraction or increased foraging proficiency were responsible for the higher survival of larger individuals, one would expect higher survival in larger birds of both sexes (Webster 1997), but this was not the case. Both sexes of 'Elepaio are active in territory defense, but territory size is more closely related to male status, and males engage in physical contests more often (VanderWerf 2004). I once observed an adult male 'Elepaio at Hakalau kill another male during competition over a territory. The victorious male was one of the largest males ever captured at the site.

#### FLOATERS, NATAL DISPERSAL, AND RECRUITMENT

In order for a young 'Elepaio to recruit into the breeding population, it must survive one or more years as a floater and compete with other floaters for a territory. These two steps appear to be influenced by different factors. Survival of floaters was not related to sex or size, and was at best weakly related to age. Survival of floaters may depend instead on foraging proficiency and ability to learn the diverse foraging behaviors used by 'Elepaio (VanderWerf 1994), and on avoiding aggression from dominant adults (VanderWerf and Freed 2003).

In contrast, the size- and age-related recruitment hierarchy among floaters coincides with plumage patterns and behavioral dominance revealed by model presentations (VanderWerf 2001a, VanderWerf and Freed 2003). Juvenile and first-year subadult 'Elepaio have dull-colored plumages that advertise the subordinate status of these age classes. The plumage of second-year subadults is more conspicuous and adultlike and elicits stronger aggression from adults because birds of this age pose more of a competitive threat. By three years of age, when 'Elepaio produce definitive basic (adult) plumage, all birds have either acquired territories or died. The age-based dominance signaled by plumage and the advantage of larger size are realized only when 'Elepaio physically compete for territories. At other times, older and larger floaters may be unable to enforce their dominance because the commotion that would occur during contests would alert territory owners, causing all floaters to be expelled. Arcese (1989) found that, within each cohort, subordinate Song Sparrows (*Melospiza melodia*) settled later than dominant ones and were more likely to emigrate.

The marginally longer natal dispersal distances of male vs. female 'Elepaio are opposite to the pattern observed in many birds (Greenwood 1980, Greenwood and Harvey 1982, Clarke

et al. 1997). The mechanism most often proposed to explain dispersal patterns in vertebrates is mating system. Sex-biased dispersal can arise if there are sexual differences in effort expended on territory or mate defense that lead to differential costs and benefits of dispersal (Greenwood 1980, Plissner and Gowaty 1996). Potential costs of dispersal include passage through unsuitable habitat, decreased resource-holding ability in unfamiliar areas, increased exposure to predators, uncertain mating opportunities, and energetic expense, while the primary benefit is thought to be inbreeding avoidance (Pusey 1987, Arcese 1989, Payne 1991). In systems where males defend resources rather than mates, males may gain a greater advantage in resource defense from remaining in a familiar (natal) area, leading to greater dispersal by females to avoid inbreeding (Greenwood 1980, Pusey 1987). In 'Elepaio, sex-biased dispersal is not related to sexual differences in costs and benefits of dispersal. 'Elepaio are socially monogamous; a male defends a territory and its resources to attract and maintain exclusive access to a female. The female drives off other females to ensure exclusive access to resources controlled by the male and exclusive male parental care, which is essential for reproduction (VanderWerf 1998, 1999). Neither sex seems likely to incur greater costs of dispersal, and any benefits to philopatry through increased resource-holding ability should be similar in both sexes (Arcese 1989, Zack and Stutchbury 1992).

Alternatively, natal dispersal may be driven by competition, in which case sex-biased dispersal can arise if there are sexual differences in demography or intensity of competition (Dobson 1982, Moore and Ali 1984, Arcese 1987). Demographic models have shown that sex-biased dispersal can be caused entirely by a difference in adult survival that produces sexually asymmetrical territory availability (Waser 1985, Buechner 1987). This appears to be true for 'Elepaio; natal dispersal is driven by intrasexual competition. Survival of territorial males was higher than survival of territorial females, resulting in fewer vacancies and greater competition among males and requiring males to move farther on average to find vacancies.

Natal dispersal distances of 'Elepaio were short compared to those of many bird species (Weatherhead and Forbes 1994), but similar to that of another tropical resident insectivore, the Checker-throated Antwren (*Myrmotherula fulviventris*), in which most individuals settled within two territories of their natal territory (Greenberg and Gradwohl 1997). Observed dispersal may underestimate true dispersal because birds that disperse farther are less likely to be found (Barrowclough 1978, Koenig et al. 1996), but in this study, the bias did not appear serious. The approximately normal distribution of natal dispersal distances suggested that few birds dispersed farther than those observed, and dispersal distances were short compared to the size of the study sites. Moreover, mortality and recruitment of locally marked individuals was sufficient to account for the population trend at each site (stable at Pua 'Ākala, increasing at Maulua;

VanderWerf 2004), indicating no long-distance immigrants were required to support local populations and suggesting there were few long-distance emigrants. In Wrentits (*Chamaea fasciata*), recruitment based on observed dispersal was much less than that required to balance adult mortality, indicating there was considerable recruitment through immigration, and probably also emigration that was not observed (Baker et al. 1995).

Survival of Hawai'i 'Elepaio has been estimated previously using simple enumeration (the proportion of birds encountered from one year to the next; VanderWerf 2004), which produced only slightly lower and less precise estimates ( $0.86 \pm 0.04$  for males,  $0.79 \pm 0.05$  for females) than those calculated with MARK ( $0.87 \pm 0.02$  for males,  $0.81 \pm 0.03$  for females). Enumeration resulted in fairly accurate estimates of apparent survival because the study population at Hakalau had high site fidelity and high encounter probability. Survival of O'ahu 'Elepaio also has been estimated by enumeration, but site fidelity and encounter probability of females are lower on O'ahu because more females switch territories and mates due to low nest success caused by predation (VanderWerf and Smith 2002). Application of mark-recapture methods to O'ahu 'Elepaio likely would produce higher and more accurate estimates of female survival.

The long lifespan, low fecundity, and extended parental care of Hawai'i 'Elepaio are typical of many tropical and south-temperate resident birds (Martin 1996, Sandercock et al. 2000, Peach et al. 2001). As noted by Karr et al. (1990) and Faaborg and Arendt (1995), island birds often exhibit extremes of this life-history pattern. The high annual survival estimates of 'Elepaio and other Hawaiian passerines provide further support for this idea (Kilpatrick 2006). There are several notable exceptions to this pattern, however, such as the unusually low survival estimates of 0.63 for Palila (*Loxioides bailleui*; Lindsey et al. 1995) and 0.55 for 'I'iwi (*Vestiaria coccinea*; Ralph and Fancy 1995). These low values may indicate populations that are under threat, but it is also possible these estimates could be improved by refining analyses to include sex, additional age classes, time, and use of multistate models to stratify analyses by social class or reproductive status.

The demographic information from this study on a large, stable 'Elepaio population at Hakalau Forest National Wildlife Refuge will be useful in understanding dynamics of other 'Elepaio populations and other species of Hawaiian forest birds, and in designing conservation strategies to combat the causes of their decline. In the O'ahu 'Elepaio, control of nonnative black rats, the principal nest predator, improved nest success and survival of females (VanderWerf and Smith 2002). Comparison of nest success and female survival on O'ahu with values from Hakalau indicate that current predator control techniques can largely ameliorate the predation threat on a local scale, that a small difference in survival of males and females can be expected to occur naturally due to costs of reproduction, and that efforts to improve management

should be made by expanding the geographic scale at which predators are controlled. It has proven difficult to collect information about juvenile survival, recruitment, and dispersal in the O'ahu 'Elepaio. Data from this study can be substituted in demographic calculations and to help evaluate the likelihood of dispersal among fragmented populations on O'ahu. Other bird species with similar life histories involving long lifespan, low fecundity, and extended parental care, such as the endangered Maui Parrotbill (*Pseudonestor xanthophrys*) and 'Akiapolā'au (*Hemignathus munroi*), likely exhibit similar patterns of sex-specific and status-dependent survival and encounter probability. Information about 'Elepaio can be used to augment our understanding of these rare and difficult-to-study species, and to design efficient data collection and analytic protocols for field projects aimed at their conservation.

#### ACKNOWLEDGMENTS

For permission to work at Hakalau Forest National Wildlife Refuge, I thank the U.S. Fish and Wildlife Service, especially refuge biologist Jack Jeffrey and refuge manager Richard Wass. Help in mist-netting and resighting 'Elepaio was provided by Patrick Hart, Scott Fretz, Matthew Burt, Joby Rohrer, and Jason Bennett. I thank Leonard Freed and Jaan Lepson for information about 'Elepaio banded before my study began and Gus Bodner and Wendy Kuntz for information about 'Elepaio recaptured after my study was over. I thank Paul Doherty for advice in using program MARK. The manuscript was improved by comments from Brett Sandercock, Steve Beissinger, Scott Stoleson, and David Dobkin. Fieldwork was supported by the Ecology, Evolution, and Conservation Biology Program of the University of Hawaii, the ARCS Foundation, Sigma Xi, the Hawaii Audubon Society, and the John D. and Catherine T. MacArthur Foundation. Data analysis and manuscript preparation were supported in part by the Pacific Islands Office of the U.S. Fish and Wildlife Service.

#### LITERATURE CITED

- ANDERS, A. D., AND M. R. MARSHALL. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* 19:66–74.
- ARCESE, P. 1987. Age, intrusion pressure and defence against floaters by territorial male Song Sparrows. *Animal Behaviour* 35:773–784.
- ARCESE, P. 1989. Intrasexual competition, mating system and natal dispersal in Song Sparrows. *Animal Behaviour* 38:958–979.
- ARNOLD, J. M., S. BRAULT, AND J. P. CROXALL. 2006. Albatross populations in peril: a population trajectory for Black-browed Albatrosses at South Georgia. *Ecological Applications* 16:419–432.
- BAKER, M., N. NUR, AND G. R. GEUPEL. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and application using Wrentits. *Condor* 97:663–674.
- BARROWCLOUGH, G. F. 1978. Sampling bias in dispersal studies based on finite area. *Bird Banding* 49:333–341.
- BUECHNER, M. 1987. A geometric model of vertebrate dispersal: tests and implications. *Ecology* 68:310–318.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.



- CHASTEL, O., H. WEIMERSKIRCH, AND P. JOUVENTIN. 1995. Influence of body condition on reproductive decision and reproductive success in the Blue Petrel. *Auk* 112:964–972.
- CLARKE, A. L., B. E. SÆTHER, AND E. ROSKAFI. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438.
- COOCH, E., AND G. WHITE. [ONLINE]. 2002. Program MARK: a gentle introduction. 4th ed. <[phidot.org/software/mark/docs/book](http://phidot.org/software/mark/docs/book)> (14 April 2004).
- DAVIES, N. B. 1980. The economics of territorial behaviour in birds. *Ardea* 68:63–74.
- DOBSON, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* 30:1183–1192.
- FAABORG, J., AND W. J. ARENDT. 1995. Survival rates of Puerto Rican birds: are islands really that different? *Auk* 112:503–507.
- FONTAINE, J. J., AND T. E. MARTIN. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428–434.
- FREED, L. A., R. L. CANN, M. L. GOFF, W. A. KUNTZ, AND G. R. BODNER. 2005. Increase in malaria at high elevation in Hawaii. *Condor* 107:753–764.
- FRETZ, J. S. 2000. Relationship of canopy arthropod prey to distribution and life history of the Hawai'i 'Akepa. Ph.D. dissertation, University of Hawaii at Mānoa, Honolulu, Hawaii.
- GARDALI, T., AND N. NUR. 2006. Site-specific survival of Black-headed Grosbeaks and Spotted Towhees at four sites within the Sacramento Valley, California. *Wilson Journal of Ornithology* 118:178–186.
- GHALAMBOR, C. K., AND T. E. MARTIN. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* 292:494–497.
- GILL, F. B., AND L. L. WOLF. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. *Ecology* 56:333–345.
- GONZÁLEZ, J. A. 2003. Harvesting, local trade, and conservation of parrots in the Northeastern Peruvian Amazon. *Biological Conservation* 114:437–446.
- GORRESEN, P. M., R. J. CAMP, T. K. PRATT, AND B. L. WOODWORTH. 2005. Status of forest birds in the central windward region of Hawai'i Island. USGS Open-File Report 2005–1441.
- GREENBERG, R., AND J. GRADWOHL. 1997. Territoriality, adult survival, and dispersal in the Checker-throated Antwren in Panama. *Journal of Avian Biology* 28:103–110.
- GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1–21.
- INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE. [ONLINE]. 2006. 2006 IUCN Red list of threatened species. <[www.iucnredlist.org](http://www.iucnredlist.org)> (2 November 2006).
- JOHNSON, M. D., T. W. SHERRY, R. T. HOLMES, AND P. P. MARRA. 2006. Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. *Conservation Biology* 20:1433–1444.
- KARR, J. R., J. D. NICHOLS, M. K. KLIMKIEWICZ, AND J. D. BRAWN. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? *American Naturalist* 136:277–291.
- KILPATRICK, A. M. 2006. Facilitating the evolution of resistance to avian malaria in Hawaiian birds. *Biological Conservation* 128:475–485.
- KOENIG, W. D., D. VAN VUREN, AND P. N. HOOGE. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution* 11:514–517.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- LINDSEY, G. D., S. G. FANCY, M. H. REYNOLDS, T. K. PRATT, K. A. WILSON, P. C. BANKO, AND J. D. JACOBI. 1995. Population structure and survival of Palila. *Condor* 97:528–535.
- MACLEAN, S. F., AND T. R. SEASTEDT. 1979. Avian territoriality: sufficient resources or interference competition? *American Naturalist* 114:308–312.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- MARTIN, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* 27:263–272.
- MARTIN, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London Series B* 269:309–316.
- MARTIN, T. E., J. CLOBERT, AND D. R. ANDERSON. 1995. Return rates in studies of life history evolution: are biases large? *Journal of Applied Statistics* 22:863–875.
- MOORE, J., AND R. ALI. 1984. Are dispersal and inbreeding avoidance related? *Animal Behaviour* 32:94–112.
- NELSON, J. T., B. L. WOODWORTH, S. G. FANCY, G. D. LINDSEY, AND E. J. TWEED. 2002. Effectiveness of rodent control and monitoring techniques for a montane rainforest. *Wildlife Society Bulletin* 30:82–92.
- NICHOLS, J. D., J. E. HINES, K. H. POLLOCK, R. L. HINZ, AND W. A. LINK. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. *Ecology* 75:2052–2065.
- NUR, N. 1998. The cost of reproduction in birds: an examination of the evidence. *Ardea* 76:151–162.
- NUR, N., AND W. J. SYDEMAN. 1999. Demographic processes and population dynamics of seabirds: implications for conservation and restoration. *Current Ornithology* 15:149–188.
- PAYNE, R. B. 1991. Natal dispersal and population structure in a migratory songbird, the Indigo Bunting. *Evolution* 45:49–62.
- PEACH, W. P., D. B. HANMER, AND T. B. OATLEY. 2001. Do southern African songbirds live longer than their European counterparts? *Oikos* 93:235–249.
- PLISSNER, J. H., AND P. A. GOWATY. 1996. Patterns of natal dispersal, turnover and dispersal costs in Eastern Bluebirds. *Animal Behaviour* 51:1307–1322.
- PRADEL, R., J. E. HINES, J.-D. LEBRETON, AND J. D. NICHOLS. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53:60–72.
- PRATT, H. D., P. L. BRUNER, AND D. G. BERRETT. 1987. A field guide to the birds of Hawai'i and the tropical Pacific. Princeton University Press, Princeton, NJ.
- PUSEY, A. E. 1987. Sex-biased breeding dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution* 2:295–299.
- RALPH, C. J., AND S. G. FANCY. 1995. Demography and movements of Apapane and Iiwi in Hawaii. *Condor* 97:729–742.
- RAPPOLE, J. H., AND M. V. McDONALD. 1994. Cause and effect in population declines of migratory birds. *Auk* 111:652–660.
- ROBERTSON, H. A., J. R. HAY, E. K. SAUL, AND G. V. MCCORMACK. 1994. Recovery of the Kakerori: and endangered forest bird of the Cook Islands. *Conservation Biology* 8:1078–1086.
- SANDERCOCK, B. K., S. R. BEISSINGER, S. H. STOLESON, R. R. MELLAND, AND C. R. HUGHES. 2000. Survival rates of a neotropical parrot: implications for latitudinal comparisons of avian demography. *Ecology* 81:1351–1370.

- SCHOENER, T. W. 1983. Simple models of optimal feeding-territory size: a reconciliation. *American Naturalist* 121:608–629.
- SCOTT, J. M., S. MOUNTAINSPRING, F. L. RAMSEY, AND C. B. KEPLER. 1986. Forest bird communities of the Hawaiian islands: their dynamics, ecology, and conservation. *Studies in Avian Biology* No. 9.
- SILLETT, T. S., AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- U.S. FISH AND WILDLIFE SERVICE. 2006. Final revised recovery plan for Hawaiian forest birds. U.S. Fish and Wildlife Service, Portland, OR.
- VANDERWERF, E. A. 1994. Intraspecific variation in foraging behavior of Elepaio in Hawaiian forests of different structure. *Auk* 111:917–932.
- VANDERWERF, E. A. 1998. 'Elepaio (*Chasiempis sandwichensis*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 344. The Birds of North America, Inc., Philadelphia, PA.
- VANDERWERF, E. A. 1999. Delayed plumage maturation and demography of Hawai'i 'Elepaio. Ph.D. dissertation, University of Hawaii at Mānoa, Honolulu, HI.
- VANDERWERF, E. A. 2001a. Two-year delay in plumage maturation of male and female 'Elepaio. *Condor* 103:756–766.
- VANDERWERF, E. A. 2001b. Distribution and potential impacts of avian poxlike lesions in 'Elepaio at Hakalau Forest National Wildlife Refuge. *Studies in Avian Biology* 22:247–253.
- VANDERWERF, E. A. 2004. Demography of Hawai'i 'Elepaio: variation with habitat disturbance and population density. *Ecology* 85:770–783.
- VANDERWERF, E. A. 2007. Biogeography of Elepaio: evidence from inter-island song playbacks. *Wilson Journal of Ornithology* 119:325–333.
- VANDERWERF, E. A., M. D. BURT, J. L. ROHRER, AND S. M. MOSHER. 2006. Distribution and prevalence of mosquito-borne diseases in O'ahu 'Elepaio. *Condor* 108:770–777.
- VANDERWERF, E. A., AND L. A. FREED. 2003. 'Elepaio subadult plumages reduce aggression through graded status signaling, not mimicry. *Journal of Field Ornithology* 74:406–415.
- VANDERWERF, E. A., J. L. ROHRER, D. G. SMITH, AND M. D. BURT. 2001. Current distribution and abundance of the O'ahu 'Elepaio. *Wilson Bulletin* 113:10–16.
- VANDERWERF, E. A., AND D. G. SMITH. 2002. Effects of alien rodent control on demography of the O'ahu 'Elepaio, an endangered Hawaiian forest bird. *Pacific Conservation Biology* 8:73–81.
- WASER, P. M. 1985. Does competition drive dispersal? *Ecology* 66:1170–1175.
- WEATHERHEAD, P. J., AND M. R. L. FORBES. 1994. Natal philopatry in passerine birds: genetic or ecological influences. *Behavioral Ecology* 5:426–533.
- WEBSTER, M. S. 1997. Extreme sexual size dimorphism, sexual selection, and the foraging ecology of Montezuma Oropendolas. *Auk* 114: 570–580.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Suppl.):120–139.
- ZACK, S., AND B. J. STUTCHBURY. 1992. Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behaviour* 123:194–219.