

## Determining productivity of Maui Parrotbills, an endangered Hawaiian honeycreeper

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**ABSTRACT.** Maui Parrotbills (*Pseudonestor xanthophrys*), critically endangered Hawaiian honeycreepers endemic to the island of Maui, are restricted to a single population of ~500 individuals located in remote, mountainous terrain. From January to June 2006–2011, we located nests and fledglings in the Hanawi Natural Area Reserve (NAR) in east Maui, Hawaii, to document nest success and annual reproductive success. Nest success is a commonly used measure of productivity and is a central component of many demographic studies. Annual reproductive success is less frequently documented because greater effort is required to monitor the reproductive success of breeding pairs through time. However, for species whose nests are difficult to locate or access, such as Maui Parrotbills, the presence or absence of fledged young may provide a more accurate measure of breeding success than monitoring nests. During our study, we located and determined the outcome of 30 nests to document nest success, and monitored 106 territories for the presence or absence of fledglings to calculate annual reproductive success. Nest success probability was 19% ( $N = 30$ ) and seasonal nest success was 46%. During our monitoring efforts, 49 of 106 breeding pairs produced a single fledged young. Because parrotbills typically have single egg clutches and only re-nest after nests fail, the presence or absence of a fledgling is an indication of a pair's overall reproductive success for a breeding season. Based on the number of fledglings per pair, our estimate of annual reproductive success was 46%, confirming our initial productivity estimate from nests. Thus, our results indicate that the two methods, determining annual reproductive success by monitoring fledglings and calculating nest success, provide similar estimates of annual productivity for Maui Parrotbills. Based on our estimates, the parrotbill population appears to be demographically stable. However, our productivity estimate was based only on the population at Hanawi, an area representing just 3% of the total range of parrotbills. Thus, our results may not accurately reflect the status of parrotbills over their entire range.

### RESUMEN. La determinación de la productividad de *Pseudonestor xanthophrys*, un ave hawaiana en peligro de extinción

La especie *Pseudonestor xanthophrys* es un ave en peligro crítico y endémico a la isla de Maui, y se limita a una sola población de ~500 individuos, ubicados en lugares remotos y montañosos. De enero a junio 2006–2011, localizamos nidos y volantones en el Hanawi Natural Area Reserve (NAR) en el este de Maui, Hawaii, para documentar el éxito de nidificación y el éxito reproductivo anual. El éxito de los nidos es una medida de productividad comúnmente utilizada y es un componente central de muchos estudios demográficos. El éxito reproductivo anual es menos documentado porque requiere de un mayor esfuerzo para monitorear el éxito reproductivo de las parejas a través del tiempo. Sin embargo, para las especies cuyos nidos son difíciles de localizar o acceder, como *P. xanthophrys*, la presencia o ausencia de volantones puede proporcionar una medida más precisa del éxito reproductivo que el monitoreo de nidos. Durante nuestro estudio, localizamos y determinamos el resultado de 30 nidos para documentar el éxito de los nidos, y monitoreamos 106 territorios para determinar la presencia o ausencia de volantones, para calcular el éxito reproductivo anual. La probabilidad del éxito de nidos fue de 19% ( $N = 30$ ) y el éxito de nidificación por temporada fue de 46%. Durante nuestros esfuerzos de monitoreo, 49 de 106 parejas produjeron un solo volantón. Por la razón que *P. xanthophrys* suele tener un solo huevo por puesta, y sólo re-nidifican después de que el nido falla, la presencia o ausencia de un volantón indica el total éxito reproductivo de una pareja para una temporada de cría. Basado en el número de volantones por pareja, nuestra estimación del éxito reproductivo anual fue de 46%, lo que confirma nuestra estimación inicial de productividad, usando el éxito de los nidos. Por lo tanto, nuestros resultados indican que los dos métodos (la determinación del éxito reproductivo anual mediante

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el monitoreo de volantones, y el éxito de los nidos), proporcionan estimaciones similares de la productividad anual para *P. xanthophrys*. En base a nuestras estimaciones, la población de *P. xanthophrys* parece ser demográficamente estable. Sin embargo, nuestra estimación de la productividad se basó sólo en la población en Hanawi, un área que representa sólo el 3% de la distribución total de *P. xanthophrys*. Por lo tanto, es posible que nuestros resultados no reflejan precisamente el estado de *P. xanthophrys* en toda su distribución

*Key words:* annual reproductive success, demography, nest success, population monitoring

Maui Parrotbills (*Pseudonestor xanthophrys*) are a federally endangered and red-listed critically endangered species of Hawaiian honeycreeper (U.S. Fish and Wildlife Service 1967, IUCN 2011). The species is restricted to a single population occupying an area of  $\sim 50$  km<sup>2</sup> on the northeastern slopes of Haleakala, Maui, Hawaii (Scott et al. 1986, U.S. Fish and Wildlife Service 2006). Historically, Maui Parrotbills (hereafter parrotbills) were distributed across the islands of Maui and Molokai (James and Olson 1991), where they apparently preferred native koa (*Acacia koa*) forests (Perkins 1903). Clearing of lowland forests and introduction of alien diseases (i.e., avian malaria and pox) drastically reduced the range of parrotbills, and they are now restricted to high-elevation (1200–2350 m) wet montane forests, where cool temperatures limit disease vectors (i.e., mosquitoes) and consequently the spread of avian malaria (Scott et al. 1986, Mountainspring 1987, Simon et al. 1997). Population estimates of parrotbill based on data collected in the 1980s suggested a stable population of  $502 \pm 230$  (95% CI) individuals (Scott et al. 1986). Data collected during more recent surveys, however, have been inadequate to allow an accurate population estimate. Although range-wide surveys through 2001 yielded densities similar to those in the 1980s, a trend assessment was inconclusive regarding the stability of the population (Gorreson et al. 2009, Camp et al. 2009).

Parrotbills are insectivorous honeycreepers that defend year-round territories (Pratt et al. 2001) and frequently occur in family groups, with young remaining with parents for five to eight months after fledging (Simon et al. 1997). Parrotbills breed from November to June, with most breeding between February and June. Males and females form long-term monogamous pair bonds, typically foraging together year round. Females typically lay single-egg clutches and only re-nest after nest failure, which often occurs during periods of heavy rain (Lockwood et al. 1994, Simon et al. 1997). Due to their

rarity and tendency to nest high in the forest canopy, information about parrotbill reproductive success is limited and no recruitment data are available.

In the absence of a conclusive population estimate, population modeling may be crucial in guiding management efforts for this species. For example, population viability analyses (PVAs) provide managers with information about extinction risk that is useful in developing management strategies for endangered species (Boyce 1992, Akcakaya and Atwood 1997, Brook et al. 2000). However, all population models rely on accurate demographic data. Unfortunately, the quality of such data is often poorest for endangered species—species that are most commonly in greatest need of accurate PVAs to inform their conservation management (Beissinger and Westphal 1998).

One key demographic component of all population models is productivity, and nest success is a commonly used metric for estimating this variable (Woodworth et al. 2001, Renner and McCaffery 2008, Hartman and Oring 2009, Nappi and Drapeau 2009). The Mayfield estimator or more recently developed methods implemented in Program MARK (White and Burnham 1999) and SAS/STAT<sup>®</sup> software have been used to standardize data from nests found (Mayfield 1961, 1975, Rotella et al. 2004), but information about the success of individual nests does not always reflect reproductive output at the population level (Murray 2000, Jones et al. 2005), especially when it is not possible to monitor all nesting attempts (Thompson et al. 2001). This problem can be particularly acute for cryptic species that are difficult to locate and monitor. Therefore, alternative methods for estimating productivity are necessary for some species. One potential alternative method is the intensive monitoring of breeding pairs and calculation of annual reproductive success (ARS) based on the number of fledged young per pair. Given the difficulty of monitoring individual birds through an entire breeding season, few

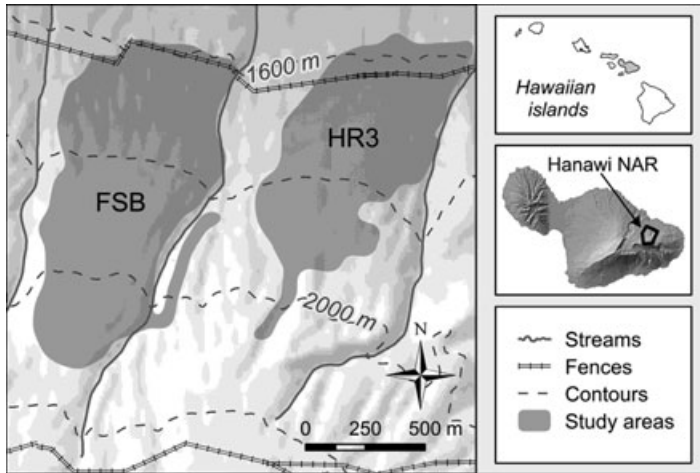


Fig. 1. Study sites where the productivity of Maui Parrotbills was examined in our study. Both Frisbee Meadows (FSB, 77 ha) and Poouli Camp (HR3, 56 ha) are located in the Hanawi Natural Area Reserve, Island of Maui, Hawaii.

investigators have quantified productivity using this method (Porneluzi and Faaborg 1999, Jones et al. 2005, Vanderwerf 2009, Rogers 2011).

The choice of reproductive measure and the resulting fecundity estimates that different estimators produce can have far-reaching effects when determining population viability. Furthermore, models of population dynamics have been shown to be sensitive to small changes in such estimates (Powell et al. 1999, Woodworth 1999). Consequently, we estimated the productivity of breeding parrotbills using both nest success and annual reproductive success, and compared estimates to evaluate their relative performance in the Hanawi Natural Area Reserve.

## METHODS

The Hanawi Natural Area Reserve (NAR) covers 3036 ha on the windward slopes of Haleakala Volcano. Within the reserve, 800 ha above 1600 m in elevation are fenced and ungulate free; this is the core area used by the current parrotbill population (U.S. Fish and Wildlife Service 2006). We used two study areas in the Reserve, Frisbee Meadows (FSB) and Poouli Camp (HR3). The FSB study area (77 ha) is between 1600 and 2200 m asl, and the HR3 study area (56 ha) between 1550 and 1950 m asl. Non-native rodents are controlled on 35 ha

of the HR3 site (Malcolm et al. 2008; Fig. 1). The area is characterized by steep, rugged terrain and supports a thick montane, wet forest dominated by ohia (*Metrosideros polymorpha*) and olapa (*Cheirodendron trigynum*; Jacobi 1989). The forest has an intact native understory and sub-canopy that provides high-quality foraging habitat for parrotbills.

Parrotbills were captured prior to and throughout the duration of our study using passive mist-netting and targeted mist-netting using playback. Of 212 adult (ASY) birds monitored over the 4-yr period, 130 were marked with a unique color band combination. Unmarked birds could be accounted for when paired with a banded individual during a single breeding season, but could not be identified between years.

Territories were defined by the presence of singing males, males counter-singing with neighboring males, and regular presence of foraging adults; little overlap was observed between adjacent territories. Birds were assumed to be paired if they were observed foraging and travelling together, occupied the same territory, and demonstrated typical breeding behaviors such as mutual preening, mutual feeding, and nest building. To prevent possible double-counting, pairs where both adults were unbanded were only classified as discrete pairs when their territories bordered those of marked individuals.

We searched for nests and fledglings along trails at each study site. Trails were 50 to 100 m apart in a network web that covered the entire study area and were systematically searched at least once per week from 07:00 to 17:30, each observer covering ~2 km per day. We conducted searches along 32.5 km of trails in the two study areas. Once an adult was detected, observers stayed for several hours to identify the individual and note behavioral activity. Three to six observers searched each site daily, except during severe weather. In addition to regular trail coverage, all territories in each study area were visited weekly to locate adults. We located fledglings either using their incessant begging calls (Simon et al. 1997) or by following parents to offspring.

**Nest success.** From January to June 2006–2011, nests were located by observing adults carrying nesting material and the location of courtship displays, copulations, and pair feedings, all of which usually occurred near nest sites. Because of individual variation in the timing of breeding and the length of the breeding season, we could not determine if nests we monitored were first, second, or third nesting attempts for the year. Nests were usually monitored daily for 3 to 6 hrs using spotting scopes or binoculars from a distance of ~30 m until chicks fledged or nest failure was confirmed. Because nest contents were usually not visible, parental behavior at nests was used to determine nesting stage (e.g., constructing, incubating, brooding, or fledged; Becker et al. 2010). Only nests where an egg was presumed to have been laid, based on observation of apparent incubation, brooding, or food delivery, were included in our analyses. Nests were classified as successful if fledglings were observed, with young considered to have fledged when they left nest trees.

Previously active nests where no activity was documented for  $\geq 3$  h were classified as failures. Over a 3-h time period, adults typically visit nests at least two to three times (Becker et al. 2010). All failed nests were checked at least once more 1–3 days after failure was documented. Causes and timing (nest stage) of failures could not be determined for most nests because nests were located high (~11 m) in the canopy. When possible, we used mirrors or climbed nest trees to view nest contents.

Parrotbill nest success was calculated using PROC GENMOD (SAS Institute 2008) to fit

a logistic-exposure model (Shaffer 2004). This generalized linear model with a modified link function uses the appropriate likelihood estimator for interval data, avoiding assumptions about when failure occurs and allowing variable intervals between observations. We pooled nest data across all years to increase our sample size because there was no apparent annual variation (Kershner et al. 2001). For nests found under construction, the first day of incubation was determined by female behavior (i.e., when first observed incubating). Because only single-egg clutches have been documented (U.S. Fish and Wildlife Service 2006), we assumed incubation began immediately after an egg was laid. Because we were unable to determine the contents of most nests, we did not differentiate between egg and nestling survival.

**Annual reproductive success.** From January to June 2008–2011, we systematically monitored the territories of 106 pairs of parrotbills for the presence of fledglings to calculate annual reproductive success. Because parrotbills typically have single-egg clutches and only re-nest after nest failure, the presence or absence of a fledgling is an indication of a pair's reproductive success for a breeding season (Simon et al. 1997). Therefore, annual reproductive success was estimated by dividing the number of pairs with offspring by the total number of pairs observed during a breeding season.

**Population growth model.** To determine the overall effect of each estimate of productivity (nest success and annual reproductive success), we calculated the finite rate of population growth ( $\lambda$ ) using the formula:

$$\lambda = P_A + P_J\beta (0.5),$$

with  $P_A$  = adult survival,  $P_J$  = juvenile survival, and  $\beta$  = average productivity per pair. Values of  $\lambda > 1$  indicate a population increase and values of  $\lambda < 1$  indicate decline. Adult and juvenile survival estimates derived from the same study population were drawn from Vetter et al. (2012).

Due to re-nesting, our nest success estimate did not reflect seasonal productivity (Streby and Anderson 2011). Parrotbills have been observed to make up to three nesting attempts per season after nest failures (MFBRP, unpubl data). We adjusted our  $\beta$  value for nest success with the following equation to have comparable seasonal productivity estimates based on each method:

Table 1. Maui Parrotbill annual reproductive success based on number of pairs observed with fledglings at two study sites (FSB and HR3) in Hanawi NAR, 2008–2011.

Site	Year	Number of pairs observed	Number of pairs with juveniles	Percent success
FSB	2008	11	3	27.3%
	2009	15	8	53.3%
	2010	18	6	33.3%
	2011	19	10	52.6%
HR3	2008	10	4	40.0%
	2009	8	6	75.0%
	2010	9	5	55.6%
	2011	16	7	43.8%
FSB totals		63	27	42.9%
HR3 totals		43	22	51.2%
Totals		106	49	46.2%

Seasonal nest success = Observed nest success  
+ Observed nest success  
\* (1 - Observed nest success)  
+ [Observed nest success  
\* (1 - Observed nest success)  
\* (1 - Observed nest success)]

## RESULTS

**Nest success.** During six breeding seasons (2006–2011), we located 30 Maui Parrotbill nests (24 at HR3 and six at FSB). Eight nests either did not progress past the nest-building stage or nest outcome could not be determined; these nests were not included in our analyses. All nests were located in Ohia trees, most in outer canopy branches 5.2–18.2 m above ground (mean = 10.9 m). Fifteen of 22 nests failed (68.2%). The logistic-exposure method resulted in a nest success probability of  $0.185 \pm 0.056$  and a daily nest survival probability of  $0.953 \pm 0.007$ . One egg that did not hatch after 31 days of incubation was presumed to be infertile. Seven of the 15 failures occurred during the first 10 days of the nestling period, and one chick was predated by a Pueo (*Asio flammeus sandwichensis*; Mounce 2008). The cause of failure of the other 14 nests could not be determined. Seasonal nest success, adjusted for re-nesting, was 46% ( $N = 22$  nests).

**Annual reproductive success.** During four breeding seasons (2008–2011), we monitored 43 pairs at HR3 and 63 pairs at FSB. Annual reproductive success estimates were 51% and 43% for HR3 and FSB, respectively, result-

ing in an overall estimate of 46% (Table 1). For all four years combined, we found no difference in productivity between the two study sites ( $\chi^2 = 6.5$ ,  $k = 3$ ,  $P = 0.10$ ).

**Population growth model.** According to Vetter et al. (2012), adult survival in our population of parrotbills was estimated at  $0.84 \pm 0.04$  and juvenile survival at  $0.76 \pm 0.09$ . Based on both our seasonal nest success estimate and our annual reproductive success estimate, our model predicts a stable population ( $\lambda = 1.02 \pm 0.07$ ).

## DISCUSSION

Demographic modeling relies on accurate estimates of reproductive success. Therefore, using the reproductive monitoring method that provides the most accurate productivity data is critical. We suspected that our estimates of annual reproductive success based on observations of family groups would be the superior method because we calculated annual reproductive success using a larger subset of the population than for nest success, and because this method more accurately reflected season-long productivity. However, we found that the two methods (seasonal nest success and annual reproductive success) produced similar estimates of annual productivity for our Maui Parrotbill population.

Our productivity estimate suggests a stable population. This is supported by results from population monitoring using point transect distance-sampling throughout the species' range that were unable to detect any recent changes in

population size (Gorreson et al. 2009, Camp et al. 2009). However, these transect surveys are only repeated every 5 yrs and, because parrotbills are long-lived birds (up to 16 yrs), any changes in population could take several years to detect and thus our productivity values may be more valuable to managers than range-wide survey data.

For species like parrotbills that occur at low densities (as few as 10 birds/km<sup>2</sup>) and have difficult-to-locate nests, determining productivity by documenting the number of young fledged per pair confirmed the validity of our seasonal nest success estimates despite low sample sizes. However, these two methods may not yield similar results for all species. Although monitoring nests is critical for identifying factors that might limit productivity (i.e., weather or predation; Jones et al. 2005), nest success has been shown to provide inaccurate estimates of productivity in other passerines (Murray 2000, Underwood and Roth 2002, Grzybowski and Pease 2005). In a review of methods for estimating productivity, Anders and Marshall (2005) noted that quantifying the season-long productivity of individuals in a population provides the most accurate estimate of population productivity. When obtaining such data is not logistically practical, productivity can still be estimated more accurately by incorporating other variables into population models (Anders and Marshall 2005). For example, for species where nests are difficult to locate or access, like those of Maui Parrotbills in our study, surveying territories for the presence of fledglings can be less time-consuming than locating and monitoring nests because fledglings often beg loudly and adults give alarm calls or chips when potential predators approach (Anders and Marshall 2005).

Although our data suggest some variation in annual reproductive success of parrotbills between our two study areas, we found no significant spatial and temporal differences, even though predator control was conducted at over 62% of the HR3 site during our study, but was not conducted at FSB. Populations of non-native mammalian predators, including rats (*Rattus* spp.) and mongooses (*Herpestes javanicus*), were controlled using bait stations loaded with rodenticide and snap traps (Malcolm et al. 2008). These non-native mammals are considered major threats to Hawaiian birds and, although rats have not been documented as

predators of parrotbill nests, they have been documented preying on Akohekohe nests at heights similar to those of parrotbill nests (Scott et al. 1986, Simon et al. 2001). To increase nest success, predator control efforts that do not include all breeding territories may not be sufficient; efforts may need to be expanded to encompass the territories of all breeding pairs.

Based on our annual productivity estimate, the parrotbill population appears to be demographically stable at Hanawi, close to the core of their range. However, our productivity estimate was based only on the population at Hanawi, an area that represents just 3% of the total range of parrotbills. Thus, our results may not accurately reflect the status of parrotbills over their entire range. Survey efforts using point transect distance-sampling throughout their range indicate that parrotbill densities may be lower outside of Hanawi (Maui Forest Bird Recovery Project, unpubl. data), but there has been no detailed demographic monitoring in other areas of the species' range. Expanding our productivity estimate techniques to the outer edges of the species' range will enhance the utility of population modeling studies and will help managers to develop a more sophisticated assessment of population-wide levels of productivity.

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#### LITERATURE CITED

- AKCAKAYA, H. R., AND J. L. ATWOOD. 1997. A habitat-based metapopulation model of the California Gnatcatcher. *Conservation Biology* 11: 422–434.
- ANDERS, D. A., AND M. R. MARSHALL. 2005. Increasing the accuracy of productivity and survival estimates in

- assessing landbird population status. *Conservation Biology* 19: 66–74.
- BECKER, C. D., H. L. MOUNCE, T. A. RASMUSSEN, A. RAUCH-SASSEEN, K. J. SWINNERTON, AND D. L. LEONARD. 2010. Nest success and parental investment in endangered Maui Parrotbill (*Pseudonestor xanthophrys*) with impacts for recovery. *Endangered Species Research* N278: 189–194.
- BEISSINGER, S. R., AND M. I. WESTPHAL. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62: 821–841.
- BOYCE, M. S. 1992. Population Viability Analysis. *Annual Review of Ecology and Systematics* 23:481–497.
- BROOK, B. W., J. J. O'GRADY, A. P. CHAPMAN, M. A. BURGMAN, H. R. AKCAKAYA, AND R. FRANKHAM. 2000. Predictive accuracy of Population Viability Analysis in conservation biology. *Nature* 404: 385–387.
- CAMP, R. J., P. M. GORRESON, T. K. PRATT, AND B. L. WOODWORTH. 2009. Population trends of native Hawaiian forest birds: 1976–2008: the data and statistical analyses. Hawaii Cooperative Studies Unit Technical Report HCSU-012, University of Hawaii, Hilo, HI.
- GORRESON, P. M., R. J. CAMP, M. H. REYNOLDS, B. L. WOODWORTH, AND T. K. PRATT. 2009. Status and trends of native Hawaiian songbirds. In: *Conservation biology of Hawaiian forest birds: implications for island avifauna* (T. Pratt, C. Atkinson, P. Banko, J. Jacobi, and B. Woodworth, eds.), pp. 108–136. Yale University Press, New Haven, CT.
- GRZYBOWSKI, J. A., AND C. M. PEASE. 2005. Renesting determines seasonal fecundity in songbirds: what do we know? What should we assume? *Auk* 122: 280–291.
- HARTMAN, C. A., AND L. W. ORING. 2009. Reproductive success of Long-billed Curlews (*Numenius americanus*) in northeastern Nevada hay fields. *Auk* 126: 420–430.
- INTERNATIONAL UNION FOR CONSERVATION OF NATURE (IUCN). 2011. IUCN Red List of threatened species, version 2011.2. <<http://www.iucnredlist.org>> (4 January 2012).
- JACOBI, J. D. 1989. Vegetation maps of the upland plant communities on the islands of Hawai'i, Maui, Molokai, and Lanai. Cooperative National Park Resources Study Unit Technical Report 68, University of Hawaii, Manoa, HI.
- JAMES, H. F., AND S. L. OLSON. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands. Part II. Passeriformes. *Ornithological Monographs* 46: 1–88.
- JONES, J., P. J. DORAN, L. R. NAGY, AND R. T. HOLMES. 2005. Relationship between Mayfield nest-survival estimates and seasonal fecundity: a cautionary note. *Auk* 122: 306–312.
- KERSHER, E. L., E. K. BOLLINGER, AND M. N. HELTON. 2001. Nest-site selection and re-nesting in the Blue-gray Gnatcatcher (*Polioptila caerulea*). *American Midland Naturalist* 146: 404–413.
- LOCKWOOD, J. L., J. E. GREENE, K. WAKALEE, E. VANGELDER, S. ASHE, AND R. ABURROMIA. 1994. A description of Maui Parrotbill (*Pseudonestor xanthophrys*) nests and nesting behavior. *'Elepaio* 54: 61–64.
- MALCOLM, T. R., K. J. SWINNERTON, J. J. GROOMBRIDGE, B. D. SPARKLIN, C. N. BROSIUS, J. P. VETTER, AND J. T. FOSTER. 2008. Ground-based rodent control in a remote Hawaiian rainforest on Maui. *Pacific Conservation Biology* 14: 206–214.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87: 456–466.
- . 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73: 255–261.
- MOUNCE, H. L. 2008. What threat do native avian predators pose to Hawaiian honeycreepers? Two cases of predation by Pueo (*Asio flammeus sanduwinchensis*). *'Elepaio* 68: 19–20.
- MOUNTAINSPRING, S. 1987. Ecology, behavior, and conservation of the Maui Parrotbill. *Condor* 89: 24–39.
- MURRAY, B. G. 2000. Measuring annual reproductive success in birds. *Condor* 102: 470–473.
- NAPPI, A., AND P. DRAPEAU. 2009. Reproductive success of the Black-backed Woodpecker (*Picoides arcticus*) in burned boreal forests: are burns source habitats? *Biological Conservation* 142: 1381–1391.
- PERKINS, R. C. L. 1903. *Vertebrata*. In: *Fauna Hawaiiensis* (D. Sharp, ed.), pp. 365–466. Cambridge University Press, Cambridge, England.
- PORNELUZI, P. A., AND J. FAABORG. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology* 13: 1151–1161.
- POWELL, L. A., M. J. CONROY, D. G. KREMENTZ, AND J. D. LANG. 1999. A model to predict breeding-season productivity for multibrooded songbirds. *Auk* 116: 1001–1008.
- PRATT, T. K., J. C. SIMON, B. P. FARM, K. E. BERLIN, AND J. R. KOWALSKY. 2001. Home range and territoriality of two Hawaiian honeycreepers, the Akohekohe and Maui Parrotbill. *Condor* 103: 746–755.
- RENNER, H. M., AND B. J. MCCAFFERY. 2008. Demography of Eastern Yellow Wagtails at Cape Romanzof, Alaska. *Wilson Journal of Ornithology* 120: 85–91.
- ROGERS, C. M. 2011. Use of fecundity measured directly throughout the breeding season to test a source-sink demographic model. *Conservation Biology* 25: 1212–1219.
- ROTELLA, J. J., S. J. DINSMORE, AND T. L. SHAFFER. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27: 187–205.
- SAS INSTITUTE. 2008. SAS/STAT 9.2 user's guide. SAS Institute, Cary, NC.
- SCOTT, J. M., S. MOUNTAINSPRING, F. R. RAMSEY, AND C. B. KEPLER. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. *Studies in Avian Biology* 9: 1–431.
- SHAFFER, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121: 526–540.
- SIMON, J. C., P. E. BAKER, AND H. BAKER. 1997. Maui Parrotbill (*Pseudonestor xanthophrys*). In: *The Birds of North America*, no. 311 (A. Poole and F. Gill, eds.). Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, D.C.

- , T. K. PRATT, K. E. BERLIN, AND J. R. KOWALSKY. 2001. Reproductive ecology and demography of the Akohekohe. *Condor* 103: 736–745.
- STREBY, H. M., AND D. E. ANDERSEN. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. *Ecosphere* 2: 1–15.
- THOMPSON, B. C., G. E. KNADLE, D. L. BRUBAKER, AND K. S. BRUBAKER. 2001. Nest success is not an adequate comparative estimate of avian reproduction. *Journal of Field Ornithology* 72: 527–536.
- UNDERWOOD, T. J., AND R. R. ROTH. 2002. Demographic variables are poor indicators of Wood Thrush productivity. *Condor* 104: 92–102.
- UNITED STATES FISH AND WILDLIFE SERVICE. 2006. Revised recovery plan for the Hawaiian forest birds. U. S. Fish and Wildlife Service, Portland, OR.
- . 1967. Office of the Secretary; Native Fish and Wildlife; Endangered Species. *Federal Register* 32: 4001.
- VANDERWERF, E. A. 2009. Importance of nest predation by alien rodents and avian poxvirus in conservation of Oahu Elepaio. *Journal of Wildlife Management* 73: 737–746.
- VETTER, J. P., K. J. SWINNERTON, E. A. VANDERWERF, J. C. GARVIN, H. L. MOUNCE, H. E. BRENISER, D. L. LEONARD, AND J. S. FRETZ. 2012. Survival estimates for two Hawaiian honeycreepers. *Pacific Science* 66: 299–309.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Suppl.): 120–138.
- WOODWORTH, B. L. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conservation Biology* 13: 67–76.
- , J. T. NELSON, E. J. TWEED, S. G. FANCY, M. P. MOORE, E. B. COHEN, AND M. S. COLLINS. 2001. Breeding productivity and survival of the endangered Hawaii Creeper in a wet forest refuge on Mauna Kea, Hawaii. *Studies in Avian Biology* 22: 164–172.