Research Paper

Key demographic factors for recovery of the endangered Nightingale Reed-Warbler (*Acrocephalus hiwae*) via population viability analysis

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ABSTRACT. The Nightingale Reed-Warbler (*Acrocephalus hiwae*), a critically endangered songbird, is the last remaining of four reed-warbler species that once inhabited the Mariana Islands. The most recent population estimate for the species is 2915–3742 individuals distributed over the islands of Saipan (n = 2742, 95% CI = 1686–3956) and Alamagan (n = 946, 95% CI = 173–1000), which represents a significant decline for the species on Saipan. Though data on life history parameters such as survival rates are not widely available, other parameters such as clutch size and nest success have been studied. Given the extirpation of three of the four reed-warbler species from the Mariana Islands, the recent significant decline of the larger Saipan population, and the increasing threats faced by the species, it is critical to determine what additional life history information is needed to aid management decisions. Using Vortex, we developed stochastic population models to represent current reed-warbler population dynamics and used sensitivity analysis to identify the life history parameters to which the model was most sensitive. Baseline models without inbreeding indicated declines of the Nightingale Reed-Warbler populations on Saipan and Alamagan, as well as of the overall population. The inclusion of inbreeding further increases the modeled rate of population decline. Parameters such as initial population size, carrying capacity, and male survival have relatively little influence on reed-warbler population models, while female and juvenile survival and, to a lesser degree, fecundity measures, exhibit strong influences on the species' population dynamics. We recommend effort be placed on collecting updated survival data for all life stages, but particularly for females and juveniles. Given model predictions of vulnerability to extinction, we recommend management actions that may increase survival rates of juveniles and females.

Facteurs démographiques clés pour le rétablissement de la Rousserolle de Saipan (*Acrocephalus hiwae*), en voie de disparition critique, au moyen d'analyses de viabilité des populations

RÉSUMÉ. La Rousserolle de Saipan (*Acrocephalus hiwae*), un passereau en voie de disparition critique, est la dernière des quatre espèces de rousseroles qui se reproduisaient autrefois sur les Mariannes. L'estimation la plus récente de la population de cette rousserolle est de 2 915-3 742 individus répartis sur les îles de Saipan (n = 2 742, IC 95 % = 1 686-3 956) et Alamagan (n = 946, IC 95 % = 173-1 000), ce qui représente une baisse importante de l'espèce sur Saipan. Bien que certaines composantes biodémographiques comme le taux de survie ne soient pas disponibles à grande échelle, d'autres paramètres tels que la taille de la ponte et le succès de nidification ont été bien étudiés. Étant donné la disparition de trois des quatre espèces de rousseroles des Mariannes, du récent déclin prononcé de la plus importante population sur Saipan et des menaces grandissantes auxquelles fait face l'espèce, il est primordial de déterminer quels paramètres de la biodémographie sont nécessaires pour orienter les décisions de gestion. Au moyen de Vortex, nous avons développé des modèles de population stochastiques représentant la dynamique actuelle de population des rousseroles et avons utilisé des analyses de sensibilité pour identifier quels paramètres démographiques influaient le plus sur les modèles. Les modèles de base sans consanguinité ont pointé vers une baisse des populations de Rousserolle de Saipan sur Saipan et Alamagan, de même que pour l'ensemble de la population. L'inclusion de la consanguinité dans le modèle a mené à un taux de diminution des populations encore plus élevé. Les paramètres tels que la taille initiale de la population, la capacité de support et la survie des mâles ont relativement peu d'effet sur les modèles de population des rousseroles, alors que la survie des femelles et des jeunes, et à un moindre degré, les mesures de la fécondité, ont un effet important sur la dynamique de population de l'espèce. Nous recommandons d'orienter les efforts sur la collecte de données permettant une mise à jour des taux de survie à tous les stades de vie, mais plus particulièrement pour les femelles et les jeunes. Considérant les prédictions des modèles révélant une vulnérabilité à la disparition, nous recommandons d'appliquer des mesures de gestion qui puissent hausser le taux de survie des femelles et des jeunes.

Key Words: *Acrocephalus hiwae; ga'ga' karisu; Mariana Islands avifauna; PVA; Vortex*

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INTRODUCTION

The Nightingale Reed-Warbler (*Acrocephalus hiwae*), known in Chamorro as *ga'ga' karisu* (bird of the reeds), is an IUCN-critically endangered insectivorous songbird of Saipan and Alamagan, Mariana Islands (Saitoh et al. 2012, BirdLife International 2016), and is listed as Endangered under the U.S. Endangered Species Act (USFWS 1970). The Mariana Islands are an approximately 840 km-long arc comprising 15 main islands, running approximately north-south from Uracas at latitude 20.5° N to Guam at latitude 13.5°N, in the Western Pacific Ocean. The largest island is Guam, and only four (Guam, Rota, Tinian, and Saipan) are permanently occupied. Of the four reed-warbler species that formerly inhabited this island chain, only the Nightingale Reed-Warbler remains. The Nightingale Reed-Warbler's sister species, *A. nijoi, A. luscinius,* and *A. yamashinae,* have been extirpated from Aguiguan, Guam, and Pagan, respectively (Saitoh et al. 2012). Though the Nightingale Reed-Warbler has persisted, the most recent population estimates indicate an estimated total of only about 3688 individuals distributed over the islands of Saipan in 2007 (n = 2742, 95% CI = 1686–3956; Camp et al. 2009) and Alamagan in 2010 (n = 946, 95% CI = 173–1000; Marshall et al. 2011). The population on Saipan appears to have been nearly halved from an estimated 4867 individuals in 1982 (Engbring et al. 1986), although the numbers appear more stable on Alamagan, with a previous estimate of 1125 individuals (95% CI = 504–1539) in 2000 (Cruz et al. 2000*a*).

The decline of the Nightingale Reed-Warbler, and extinction of the other three reed-warbler species in the Mariana Islands, has been driven by several factors. One of the most detrimental has been habitat loss. Reed-warblers of the Marianas occur in a variety of habitats, including thickets, forest edges and openings, native reed-mar, mangrove wetland, as well as upland introduced *Leucaena leucocephala* forest and mosaics of elephant grass (*Pennisetum purpureum*) and tangan-tangan (*Ricinus communis*; Craig 1992, Reichel et al. 1992, USFWS 1998, Mosher and Fancy 2002). However, much of Saipan's wetlands and forests have been converted to agriculture, residential development, and tourist-related facilities over the last several decades, reducing suitable habitat for the Nightingale Reed-Warbler (USFWS 1998). Exacerbating this loss is the spread of non-native vines, especially ivy gourd (*Coccinia grandis*; Liske-Clark 2015), which has invaded ~90% of Saipan's forests since its introduction in the mid-1990s (Deleon Guerrero 2015). This species smothers the forest canopy until it collapses because of tree death (Global Invasive Species Database 2017), thereby destroying reed-warbler nesting habitat.

Degradation of habitat by feral ungulates, e.g., goats, has also contributed to the extirpation of *A. nijoi* on Aguiguan and *A. yamashinae* on Pagan (Cruz et al. 2000*b*). Severe habitat damage from feral goats, pigs, and cows may be causing Nightingale Reed-Warbler population decline on Alamagan, while continued grazing on Aguiguan may limit opportunities for recolonization or reintroduction (Cruz et al. 2000*a, b*). Introduced predators including cats (*Felis catus*), rats (*Rattus* spp.), monitor lizards (*Varanus indicus*), and brown treesnakes (*Boiga irregularis*) also play a significant role in reed-warbler declines throughout the Marianas (USFWS 1998). Predation, mostly by non-native species, was responsible for 75% of nest failures (rats [71%], cats [5%] and unknown predators [24%]; Mosher 2006). Monitor

lizards and the native Mariana kingfisher (*Todiramphus albicilla*) may also deprecate reed-warbler nests. Of particular concern is the brown treesnake, which greatly reduced or extirpated most native birds, including the reed-warbler, within 35–40 years after its accidental introduction on Guam (Reichel et al. 1992). The brown treesnake was the primary cause of extirpation of *A. luscinius* on Guam (Rodda and Savidge 2007), and the potential for invasion by the brown treesnake on Saipan (and, though less likely, Alamagan) places the Nightingale Reed-Warbler population at risk.

To address these threats, current Nightingale Reed-Warbler management protocols include protecting and managing extant populations and core habitat (USFWS 1998). Regular population surveys have been run to assess population trends (Engbring et al. 1986, Cruz et al. 2000*a, b*, Esselstyn et al. 2003, Camp et al. 2009, Marshall et al. 2011, Amidon et al. 2014). Another integral aspect of the species' recovery is continued protection against brown treesnake incursions through monitoring and removal of brown treesnakes.

Population viability analysis (PVA) is a useful tool to assess management options to reduce the risk of extinction (Ellner and Fieberg 2003). PVA incorporates demographic and environmental variables to forecast population persistence and extinction risk, thereby testing the relative importance of model parameters via sensitivity analysis, evaluating management strategies, and identifying priorities for maximizing effective species recovery (Beissinger and Westphal 1998, Brook et al. 2000, Cross and Bessinger 2001, Reed et al. 2002).

Although data on some life history parameters such as survival rates of the Nightingale Reed-Warbler are not widely available, other parameters such as clutch size and nest success have been well-studied (Mosher and Fancy 2002, Mosher 2006). Considering the significant decline in the larger Saipan population in recent years (Camp et al. 2009) and the increasing threats faced by the species, it is critical to determine what additional life history information is needed to aid management decisions, as well as what management actions can assist the Saipan reed-warbler population. To address these needs, our overarching goal was to evaluate possible population trajectories of the Nightingale Reed-Warbler and identify key life history attributes important to understand species population dynamics. Based upon this goal our objectives were the following: (1) to model Nightingale Reed-Warbler population dynamics on both Saipan and Alamagan for the next 100 years; and, (2) to conduct sensitivity analysis on life history attributes to determine which, if any, parameters are most influential in model outcomes.

METHODS

PVA software

We conducted our PVAs using Vortex 10 (Lacy and Pollack 2014), which simulates stochastic demographic and environmental processes. Vortex is an individual-based simulation model that follows the fates of each animal in a simulated population from birth to death, with all events happening according to defined probabilities.

Baseline model input

Using Vortex (Appendix 1), we developed baseline models incorporating all available information on the Nightingale Reed-Warbler. Each model was simulated 1000 times (Owen-Smith 2007) over a time frame of 100 years. We defined extinction as occurring when only one sex remained.

Because little is known about the genetics and effects of inbreeding depression on the Nightingale Reed-Warbler, coupled with the absence of good information on the impact of inbreeding depression, we developed models both with (at the default heterosis model of 6.29 lethal equivalents, 50% due to recessive lethals) and without inbreeding depression included (Appendix 1). We tested this initial parameterization using equivalency testing in Minitab (version 18). Equivalence testing is a statistical tool used to test whether observations from two groups are similar enough to be biologically analogous. In equivalence testing, the null hypothesis is that the difference between the means is greater than a researcher-defined amount, which is referred to as "interval of tolerable difference." We defined the limits at which we thought model output difference would be equivalent as $\pm$ 0.02 stochastic r (essentially $\pm$ 2% annual growth rate) and $\pm$ 10 individuals remaining at 100 years. We found the growth rate of inbreeding depression models to be nonequivalent to noninbreeding models based upon these defined limits (p > 0.7). Although models were equivalent based on population size at 100 years (p < 0.05), this was an artifact of the very small final population sizes ($\leq$ 4), rather than a reflection of equivalency. Given the small population size and current population decline we choose to run all baseline and sensitivity models both with and without inbreeding depression.

We modeled four cohorts or stages: juvenile females, adult females, juvenile males, and adult males. We developed our demographic input parameters from a variety of sources, including original data, previously published information, and discussions with Nightingale Reed-Warbler biologists. We assumed that the effects of environmental variation on reproduction and survival were correlated.

Population dynamics and dispersal

We modeled populations on Saipan and Alamagan separately, as well as together as a total population. We assumed baseline demographics were the same for each island. For several reasons, we further assumed that if dispersal between islands does exist, it is at levels too low to be meaningful. First, populations on both islands were at best stable to declining (Camp et al. 2009, Marshall et al. 2011) and unlikely to be producing emigrants. Furthermore, genetic testing showed little if any recent gene flow between Saipan and Aguiguan (30 km apart), which is much closer to Saipan than Alamagan (250 km; Saitoh et al. 2012). Finally, the closely related Seychelles Warbler (*Acrocephalus sechellensis*) rarely dispersed even when their current habitat was saturated and there were other suitable islands nearby, despite retaining all the morphological structures for such flight (Komdeur et al. 2004).

Reproduction

We assumed Nightingale Reed-Warblers are monogamous within the year, but not between years, because in one study males were not seen to associate with more than one female during a breeding season, but females exhibited low mate fidelity between years (Craig 1992). We further assumed that they would breed at one

year of age because the congeneric Seychelles Warbler breeds as early as 8–9 months (Komdeur 1991, 1992, 1994*a, b*) and the congeneric Nihoa Millerbird (*Acrocephalus familiaris kingi*) is presumed to breed at one year (Conant and Morin 2001). Mosher (2006) found that Nightingale Reed-Warblers nest during two peak seasons (January–March; July–September), and that pairs renested after failure during a given season, but if successful waited to renest until the next season. Thus, we assumed a maximum of two broods per year. However, no data were available on the mean number of successful nests/pair/year. To estimate the distribution of successful broods per year, we used Komdeur and Daan's (2005) distribution of Seychelles Warblers nest attempts/year, adjusted by Mosher's (2006) Nightingale Reed-Warbler nest success. Although Mosher (2006) witnessed one pair lay four eggs on two occasions, the maximum number of young successfully reared to fledging was three (mean = 1.95 $\pm$ 0.65), and we assumed this to be the maximum number of progeny per pair per season. Seychelles Warblers successfully breed until nine years old (Komdeur 1996) and Nihoa Millerbirds are presumed to breed until 10 years (Conant and Morin 2001), so we assumed that Nightingale Reed-Warblers can breed until nine years old and live up to 10 years. We also assumed a 1:1 sex ratio at birth.

Density dependence

Vortex models density dependence in terms of its effect on reproduction as: $P(N) = (P(0)-((P(0)-P(K))*((N/K)^B)))*(N/(A+N))$; where P(0) is the percentage of adult females breeding at low density; P(K) is the percentage of adult females breeding at carrying capacity; N is initial population size; K is carrying capacity; B is a steepness parameter, which determines the shape of the curve relating the percentage of adult females breeding to population size; and A is the Allee parameter, which accounts for the decrease in the proportion of females breeding at low densities. We assumed that Nightingale Reed-Warblers would be density-dependent, given that it is a territorial bird that defends prime nesting sites and food sources. In the absence of data to the contrary and given that Nightingale Reed-Warblers are currently confined to small remnant habitat areas we assumed the Allee effect was zero. To determine the appropriate steepness parameter, we graphed a series of density-dependent population projection plots using steepness parameters from 0.25 to 16. A steepness parameter of 8 looked the most reasonable, though 4 and 16 also seemed plausible. To test the influence of the steepness parameter, we ran three versions each of the baseline with and without inbreeding, with steepness values of 4, 8, and 16, and as with inbreeding, tested for equivalency with Minitab (version 18), within the self-defined limits of $\pm$ 0.02 stochastic r and $\pm$ 10 individuals remaining at 100 years. Because all models showed equivalent results (p < 0.01) we chose to use a steepness value of 8 in our baseline model. We used data from the Seychelles Warbler (Brouwer et al. 2009) to estimate the percent breeding at high and low population densities. At carrying capacity, Seychelles Warblers delay breeding and help breeding birds at the nest, resulting in an average group size of 2.8 $\pm$ 0.1 birds, which means about 71% of adult birds are breeding. At low densities, however, no nest helpers are seen, and most territories consist of a pair of breeding birds, with some unpaired floaters. Thus, we assumed 95% of adult birds breed at low densities. Vortex used the parameters of percent breeding at low density and percent breeding at high density, the Allee parameter and the steepness

parameter to automatically calculate the percent of adult females breeding. For the environmental variation in percent breeding, we used default values in the absence of other data. Given that the Nightingale Reed-Warbler lives in a somewhat stable, maritime climate, we would not expect large variations from year to year. Finally, we assumed that 100% of males would be in the breeding pool, though not all find mates.

Mortality

To determine survival, we developed a series of models in Program MARK (version 8.0) using unpublished data collected on the Nightingale Reed-Warbler by Steven Mosher. Mosher followed 57 marked adult males over 19 months from January 1997 until July 1998, with monthly resighting intervals. We created an encounter history for each bird using the month of initial capture and all resightings in subsequent months. We used the Live Recaptures data type which is a form of Cormack-Jolly-Seber (CJS) model. We compared five models: Phi(.)p(.), which provided mean monthly estimates of survival (Phi) and detection (p) across sex/life stages; Phi(.)p(g), which provided mean monthly estimates of survival (Phi) across sex/life stages and detection (p) for each sex/life stage; Phi(g)p(.), which provided estimates of mean monthly survival for each sex/life stage (g) and the average monthly detection probability (p) across all sex/life stages; Phi(g) p(g), which provided mean monthly estimates of survival (Phi) and detection (p) for each sex/life stage; and Phi(g)p(g+covar), which provided mean monthly estimates of survival (Phi) and detection (p) for each sex/life stage and included an additive effect of typhoons as a covariate of detection. We used the product of monthly survival rates (Phi^{12}) to estimate annual survival. Based on AICc, the model Phi(g)p(g+covar) (AICc = 884.19, k = 6, Dev. = 872.06) was far superior (Δ = 272.43) to the next best model, Phi(g)p(g) (AICc = 1156.93, k = 6, Dev. = 1144.80). The monthly survival probability of adult males was 0.9735 (SE 0.0083, CI 0.9515, 0.9856). The mean monthly detection probability of adult males in the absence of typhoons was 0.8325 (SE = 0.0180, CI 0.7942, 0.8649). The annual survival probability of adult males was 0.7243 (CI 0.0700, 0.9978). The dataset was insufficient to estimate female and juvenile survival. Given that at least one of 13 (~8%) marked females was depredated on the nest and others have found higher female mortality in passerine species where rat nest predation is an issue (VanderWerf et al. 2011, 2014), we assumed that female survival would be 10% lower than males (62%). For modeling purposes when better information was unavailable, a juvenile survival rate, which is half of adult survival (generally resulting in ~30% juvenile survival), has been assumed for migratory passerines (Ricklefs 1973, Donovan et al. 1995). Based on our calculated Nightingale Reed-Warbler male survival, this would produce an annual juvenile survival of 36%. However, Seychelles Warbler juveniles exhibit considerably higher survival than 36%, and ostensibly juvenile survival should be slightly higher for a resident, nonmigratory bird species. Thus, we assumed 40% survival for juveniles. We used these survival estimates in our baseline model because they represent the only estimate of Nightingale Reed-Warbler survival rates. In the absence of better data, as with percent breeding, we felt that in this relatively stable island environment we would not see large annual fluctuations in mortality rates. Thus, we used Vortex's default, relatively modest deviation in mortality rate of 10% for juvenile mortality and 3% for adult mortalities.

Catastrophes

Typhoons and super-typhoons commonly occur in the Marianas Islands. However, the survival and reproductive data used to calculate our parameters (Mosher 2006) were collected during an intense El Nino year, in which four super-typhoons occurred within five months. Since these data represent most of what parameterizes our model, the effect of super-typhoons is already built into our model. To avoid double counting their effect, we have not included them as a separate effect in the model.

Population size and carrying capacity

In the absence of information to the contrary, we assumed Nightingale Reed-Warbler achieve a stable age distribution. We used the most recent estimates of current population size on Saipan (Camp et al. 2009) and Alamagan (Marshall et al. 2011) in our models. No estimates of carrying capacity exist for either island. However, the amount of suitable habitat is declining (Camp et al. 2009, Marshall et al. 2011) and it is unlikely that K is much higher than current populations. Thus, to allow for some population growth while reflecting the current decline in habitat, we assumed carrying capacity to be 25% greater than current populations. In the absence of better information, we assumed fluctuation in K due to environmental variation to be ± 10%.

Software output

Vortex's standard output provided us with stochastic r, probability of extinction within 25 years, average population size at 25 years, median time to extinction (provided 50% of simulations went extinct), and mean time to extinction for populations that went extinct within 25 years.

Sensitivity analysis

We performed sensitivity analysis to understand how data errors or variations affect model outcomes (Akçakaya and Sjögren-Gulve 2000). We individually varied starting population, carrying capacity, and juvenile, male, female, and combined adult mortalities, number of reproductive attempts per year, and number of young produced per attempt by ± 10%, ± 25%, and ± 50%, while holding all other parameters to baseline values. We used a standard sensitivity index (S_x; Morris and Doak 2002). Baseline model values were used to compute the standard sensitivity index for each parameter, which was calculated as:

$$S_x = (x_{new} - x_{baseline})/(P_{new} - P_{baseline}) \qquad (1)$$

where x is the output value (stochastic r/λ or N extant) and P is the parameter of interest.

RESULTS

Baseline models without inbreeding indicated declines of the Nightingale Reed-Warbler numbers on both Saipan (stochastic r = -0.0820) and Alamagan (stochastic r = -0.0849) as well as in the total population (stochastic r = -0.0815; Table 1, Fig. 1). Including inbreeding decreased growth rates further (Saipan = -0.1059, Alamagan = -0.1125, total population = -0.1091). Vortex predicted an 82.5% chance of total population extinction within

Table 1. Nightingale Reed-warbler (*Acrocephalus hiwae*) candidate baseline model results. Note that because of the length of time since population estimation (~10 years), the times we report here reflect predicted time to extinction since population estimation, rather than from the present.

Model	Inbreeding	Steepness	Population	Mean stochastic r	r SD	Probability of extinction (PE)	Population size at 100 years (N)	N SD	Median time to extinction	Mean time to extinction (TE)
Baseline	No	8	Saipan	-0.082	0.167	0.858	3.17	13.1	76	72.8
			Alamagan	-0.0849	0.178	0.957	1.04	5.97	61	61.4
			Total	-0.0815	0.157	0.825	4.21	14.7	80	76.9
Baseline	No	4	Saipan	-0.084	0.168	0.893	2.03	8.03	75	72.6
			Alamagan	-0.0846	0.179	0.966	0.51	3.8	62	62.3
			Total	-0.0833	0.157	0.868	2.55	8.91	79	77
Baseline	No	16	Saipan	-0.0816	0.166	0.874	2.92	11	76	73.5
			Alamagan	-0.0837	0.179	0.95	0.95	5.33	62	61.8
			Total	-0.0813	0.155	0.832	3.87	12.4	80	77.4
Baseline	Yes	8	Saipan	-0.1059	0.161	0.999	0.02	0.36	61	62
			Alamagan	-0.1125	0.171	1	0	0	49	49.1
			Total	-0.1091	0.152	0.999	0.02	0.36	62	64
Baseline	Yes	4	Saipan	-0.1066	0.163	1	0.01	0.15	61	62
			Alamagan	-0.1114	0.171	1	0	0	48	49.3
			Total	-0.1093	0.153	1	0.01	0.15	62	64.1
Baseline	Yes	16	Saipan	-0.1065	0.162	1	0.01	0.13	61	61.9
			Alamagan	-0.1128	0.171	1	0	0	48	48.8
			Total	-0.1094	0.154	1	0.01	0.13	62	64

100 years without accounting for inbreeding (Saipan = 85.8%, Alamagan = 95.7%) and a 99.9% chance of total population extinction with default inbreeding levels (Saipan = 99.9%, Alamagan = 100%) incorporated into the models. Vortex yielded a mean final population size of 4.2 ± 14.7 for the total population (Saipan = 3.2 ± 13.1, Alamagan = 1.0 ± 6.0) without inbreeding and populations of zero when inbreeding was incorporated. The mean time to extinction for the total population was 76.9 years without inbreeding and 64.0 years with inbreeding included (Saipan = 72.8 vs. 62.0 years, Alamagan = 61.4 vs. 49.1 years). The median time to extinction for the total population was 80 years without inbreeding and 62 years with inbreeding included (Saipan = 76 vs. 61 years, Alamagan = 61 vs. 49 years). Thus, with inbreeding as a factor, mean time to extinction will be 13 years (median time to extinction = 18 years) earlier than if inbreeding depression is not a factor. Notably, the baseline population estimates used to calculate these times to extinction are approximately 10 years old at time of publication. Thus, the times we report here reflect predicted time to extinction since population estimation, rather than from the present.

Models showed no difference in relative sensitivity to parameter perturbations whether inbreeding was incorporated into the model or not (Table 2). Growth rate had very little sensitivity to changes in either initial population size or carrying capacity (Table 2). In fact, varying either initial population size or carrying capacity even ± 50% had very little impact. The growth rate was slightly more sensitive to perturbations in fecundity measures and male mortality, though not nearly so sensitive as it was to female and juvenile mortality measures (Table 2). Except at the highest mortalities, growth rate was most sensitive to changes in female mortality (Table 2). As with growth rate, population size at 100 years was relatively insensitive to changes in initial population, carrying capacity, and male mortality (Table 2). Although population size was relatively insensitive to increases in female and juvenile mortality it was quite sensitive to decreases in these

parameters (Table 2). Conversely, population size became relatively more sensitive to fecundity measures as these parameters increased (Table 2).

Fig. 1. Average Nightingale Reed-warbler (*Acrocephalus hiwae*) population size over 100 years for Saipan, Alamagan, and the total population. Note that because of the length of time since population estimation (~10 years), these trajectories commence at population estimation, rather than the present. Population viability was modeled in Vortex, with and without inbreeding.
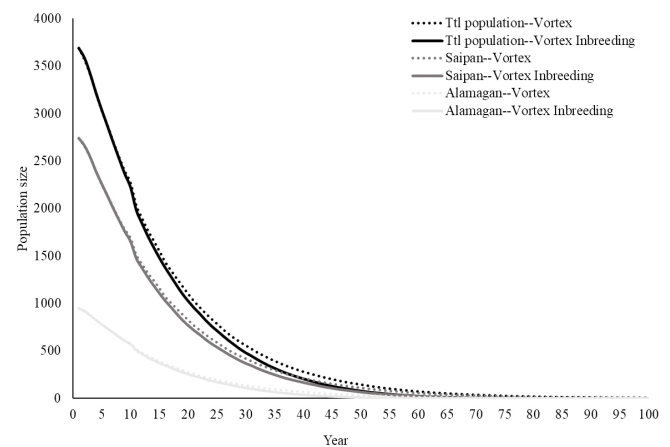
DISCUSSION

Our models indicate that the Saipan and Alamagan populations of Nightingale Reed-Warbler will be severely decreased, and without management intervention, will likely go extinct within the next 100 years or persist at population sizes that were so low as to signal a strong likelihood of future extinction (Fig. 1). Although these results indicate populations in decline, extinction

Table 2. Sensitivity analysis of key input parameter influencing Nightingale Reed-Warbler (*Acrocephalus hiwae*) growth rate and population size at 100 years, without and with inbreeding.

Model	Magnitude of variation	Growth rate sensitivity index ($\Delta r/\Delta x$)		Pop size at 100 years sensitivity index ($\Delta N/\Delta x$)	
		No Inbreeding	Inbreeding	No Inbreeding	Inbreeding
Initial Population	50%	0.0000	0.0000	-0.0009	0.0000
	25%	0.0000	0.0000	-0.0001	0.0000
	10%	0.0000	0.0000	-0.0025	0.0000
	-10%	0.0000	0.0000	0.0035	0.0000
	-25%	0.0000	0.0000	0.0015	0.0000
	-50%	0.0000	0.0000	0.0013	0.0000
Carrying Capacity	50%	0.0000	0.0000	-0.0002	0.0000
	25%	0.0000	0.0000	0.0000	0.0000
	10%	0.0000	0.0000	-0.0010	0.0000
	-10%	0.0000	0.0000	0.0018	0.0000
	-25%	0.0000	0.0000	0.0018	0.0000
	-50%	0.0000	0.0000	0.0013	0.0000
Juvenile Mortality	50%	-1.0360	-0.9640	-14.0333	-0.0667
	25%	-0.9147	-0.8220	-28.0667	-0.1333
	10%	-0.9017	-0.7950	-70.1667	-0.3333
	-10%	-0.9467	-0.9417	-8609.8333	-1837.6667
	-25%	-0.5927	-0.7553	-23912.0000	-20800.7333
	-50%	-0.3903	-0.4700	-14056.7000	-13702.2333
Female Mortality	50%	-0.9179	-0.8411	-22.1579	-0.1053
	25%	-0.9811	-0.9084	-44.3158	-0.2105
	10%	-1.0211	-0.9526	-110.2632	-0.5263
	-10%	-1.1421	-1.0868	-5040.7895	-732.8947
	-25%	-0.8400	-1.0653	-26047.6842	-17834.1053
	-50%	-0.5958	-0.7258	-21774.4737	-21316.7368
Male Mortality	50%	-0.0871	-0.0786	-22.7143	-0.1429
	25%	-0.0929	-0.0729	-24.5714	0.1429
	10%	-0.0964	-0.0821	-41.4286	0.0000
	-10%	-0.0536	-0.0929	-0.7143	-1.4286
	-25%	-0.0400	-0.0957	2.4286	-0.7143
	-50%	-0.0443	-0.0807	-3.1429	-0.2143
Adult Mortality	50%	-1.2552	-1.1836	-25.5152	-0.1212
	25%	-1.2618	-1.1939	-51.0303	-0.2424
	10%	-1.2485	-1.1606	-126.9697	-0.6061
	-10%	-1.3364	-1.2818	-5778.1818	-1021.8182
	-25%	-0.9782	-1.2303	-31215.7576	-20539.0303
	-50%	-0.6848	-0.8364	-25227.7576	-24970.3030
#Attempts/Year	50%	0.2238	0.2785	8377.5289	7842.4711
	25%	0.3473	0.4028	8582.1709	3580.9700
	10%	0.4353	0.3995	1481.5242	168.8222
	-10%	0.2702	0.2460	46.8822	0.2309
	-25%	0.3081	0.2808	19.4457	0.0924
	-50%	0.3236	0.2954	9.7229	0.0462
#Offspring/Attempt	50%	0.1040	0.1292	3841.7231	3712.4308
	25%	0.1594	0.1965	4395.0769	2560.7179
	10%	0.1969	0.1754	715.6410	74.2051
	-10%	0.1795	0.1585	21.5385	0.1026
	-25%	0.1848	0.1670	8.6359	0.0410
	-50%	0.1909	0.1720	4.3179	0.0205

is not inevitable because there is still time left to conduct management activities that have potential to reverse these trends.

Sensitivity results indicate that parameters such as initial population, carrying capacity, and male mortality/survival have relatively little influence on the Nightingale Reed-Warbler total population model relative to other parameters (Table 2). On the other hand, sensitivity analyses suggested that we need to gain further understanding of female and juvenile survival and, to a

lesser degree, annual fecundity measures, because they exhibit strong influence on the Nightingale Reed-Warbler's population dynamics. Unfortunately, no data on female and juvenile survival currently exist, and thus we estimated these parameters from male survival and patterns of survival in congeners and other species. Although several parameters were insensitive to changes in terms of model output, it is important to note that they are still important to measure accurately. For instance, although changes in initial population size did not strongly affect model outputs,

such as growth rate and final population size, it will affect time to extinction, and as a result, the time left to try to take management actions to prevent extinction. All else being equal, the Alamagan population, with its smaller initial population size, will likely go extinct quicker than the larger Saipan population, simply because of its smaller initial size. Similarly, while incorporating effects of inbreeding into the models did not significantly change model outcome, it did speed up the population decline. Thus, having a better understanding of whether inbreeding affects Nightingale Reed-Warbler populations, and if so, how it does so, will refine model predictions. In some cases, life history and demographic information for a species is simply absent, and while related species can provide important information for PVA models, if they exist in entirely different environments, or are not closely related, their value may be limited. Several specific demographic measures used in the PVA were developed based on the best available data. However, as additional species-specific data become available, it will likely lead to better parameter estimation, and eventually, more accurate model results.

Although all models suggest a species in decline, there are several caveats that may have strong relevance for future modeling and management efforts. First, we assumed that the populations on Alamagan and Saipan operate in a similar manner and that they have the same demographic attributes. Although both populations occur in the same archipelago, they do have unique environmental settings and thus may differ in terms of population dynamics. In fact, the two islands have somewhat different historic population trends with Alamagan showing an essentially steady, though perhaps slowly declining, population of Nightingale Reed-Warblers (Marshall et al. 2011) compared to Saipan which has been declining more quickly (Camp et al. 2009). One limitation of our analysis is that all previous research has been on Saipan reed-warblers, such that both the Alamagan and Saipan populations have been modeled with Saipan demographics. As a result, the models of Saipan's population may be more robust than Alamagan's. Because Alamagan's reed-warbler population is declining more slowly, it is conceivable that its population outlook may be more optimistic than what we have modeled. Second, nearly all the data used to parameterize the models were over 20 years old. Although many bird species exhibit some consistencies in life history attributes, e.g., average clutch size, many vary based upon environmental conditions, e.g., mortality and fecundity. Given that the populations face the threats of non-native predators, habitat degradation due to feral species on Alamagan, and habitat loss due to development on Saipan, it is quite likely that the species demographics have changed over time. Third, as previously noted, the parameters to which PVA models are sensitive may change as the model changes. It is important to remember that all population and management inferences drawn from the current models assumed that parameter estimates were reasonable approximations of the Nightingale Reed-Warbler's true demography and life history. As new data are collected, and the model is refined and developed, new conclusions may be drawn, and management decisions updated. For instance, our current model was relatively insensitive to changes in carrying capacity, which would be expected if the populations are currently declining for reasons other than declining carrying capacity, such that carrying capacity has little effect on population dynamics.

However, if recovery efforts succeed and the populations increase, carrying capacity may become quite important, and would need to be better understood to effectively model the populations. The same may be said of the true effects of density dependence on reproductive efforts and other parameters as well.

Research and management implications

As evidenced by the PVA results, the Nightingale Reed-Warbler is a species under severe threat. All models suggested that the species will rapidly decline and may go extinct within the next 100 years without management intervention. Based upon the underlying data used in the models and the model output, we recommend the following research and management items. First, given the models' sensitivity to survival and the fact that these estimates are the least robust, we recommend effort be placed on collecting additional survival data for all life stages, but particularly females and juveniles. If current survival estimates prove to be reasonable, we recommend management actions that would increase survival of juveniles and females. Potential management activities could include reducing non-native predators (particularly rats), increasing Nightingale Reed-Warbler food resources, and restoring high-quality native habitat.

Second, given the length of time since reproductive data have been collected and the moderate sensitivity of models to these parameters, we recommend collecting new data on reproduction and other demographic factors. Because environmental conditions may have changed since the data were collected, it is important to evaluate if reproduction has decreased. Furthermore, because data collected during 1997–1998 were during a time of atypical weather patterns, including four super-typhoons, it is difficult to discern what reproduction and other demographic factors may look like during periods of more stable weather patterns. Ideally, data would be collected over a longer interval to allow for evaluation of demographic factors during periods of stable weather and periods of typhoons. Such data could allow for evaluation of reproduction under different storm and typhoon frequencies and severities. Given the potential effects of global change on regional climatic patterns and El Nino and typhoon frequencies, understanding such variability is of considerable importance.

Third, given that Saipan and Alamagan show different population trends, we recommend collecting new data on species demography and life history attributes from both islands to determine if the two populations behave similarly. If they do, it may allow for a simpler management approach. However, if the populations are displaying different dynamics, then management may need to be individualized by island. For example, if Alamagan's population is stable, understanding the differences between its population dynamics and Saipan's may aid in understanding how to better manage reed-warblers on Saipan. Although additional data would provide much needed answers to Nightingale Reed-Warbler population dynamics, it is extremely important to concurrently implement management actions in the near term. It is critical that management of other invasive species commence, including eliminating feral ungulates, controlling ivy gourd, and controlling predators, with the aim of restoring habitat, including food resources. Beyond management within the existing habitat, it will likely be necessary to set aside protected areas, in addition

to the existing Saipan Upland Mitigation Bank, the Nightingale Reed-Warbler Conservation Area, and other conservation areas on Saipan for enough quality habitat to exist. One approach being considered to increase habitat and reduce extinction risk is translocating reed-warblers from Saipan and/or Alamagan to at least two islands—Pagan and Aguiguan, because closely related reed-warblers once occurred on both islands—to create new populations (MAC Working Group 2013). Engaging in management in the near-term future, before the populations' exhibit further large reductions, is critical.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1289

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Appendix 1. Parameter inputs for the baseline Nightingale Reed-Warbler (*Acrocephalus hiwae*) population as modeled in Vortex.

Parameter/variable	Estimate
Scenario Settings	
# iterations	1000
# years	100
Duration of year (days)	365
Extinction definition	Only 1 sex remains
# of populations	2
Species Description	
Inbreeding Depression	
Lethal Equivalent	Default = 6.29
% due to Recessive Lethals	Default = 50%
EV Concordance of Reproduction and Survival?	yes, 0.5 between populations
Dispersal	Did not incorporate due to lack of data and high rate of island endemism
Reproductive System	
Reproductive System	monogamous within year
Age of 1st Offspring Females	1 year
Age of 1st Offspring Males	1 year
Max Age of Reproduction	9 years
Max Lifespan	10 years
Max # Broods/Year	2
Max # Progeny/Brood	3
Sex Ratio at birth in % Males	1:1
Density Dependent Reproduction	Yes
% Breeding at Low Density	95%
% Breeding at K	71%
Allee Parameter	0
Steepness Parameter	8
Reproductive Rates	
% Adult Females Breeding	Calculated from density dependence information
EV (SD) in % Breeding	10
Distribution of Broods each Year	0—32.47%; 1—48.41%; 2—19.1% mean = 0.866 ± 0.710
# Offspring/Female/brood (mean ± SD)	1.95 ± 0.65
Mortality Rates	
Female Mortality as %	
Mort from 0 to 1	60%

SD in Mort from 0 to 1	10%
Annual Mort after Age 1	38%
SD in Mort after Age 1	3%
Male Mortality as %	
Mort from 0 to 1	60%
SD in Mort from 0 to 1	10%
Annual Mort after Age 1	28%
SD in Mort after Age 1	3%

Catastrophes — Did not incorporate as an additional parameter as survival and reproduction are calculated from data collected during a period with four super-typhoons

Mate Monopolization
  % Males in Breeding Pool — 100%
Initial Population Size
  Stable Age Distribution? — Yes
  Initial Population Size — Alamagan—946; Saipan—2742
Carrying Capacity
  K — Saipan—3430; Alamagan—1180
  SD in K due to EV — Saipan—343; Alamagan—118