

WHY ISN'T THE NIHOA MILLERBIRD EXTINCT?

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Abstract. We used the extinction model VORTEX to assess population viability for the Nihoa Millerbird (*Acrocephalus familiaris kingi*), an endangered reed-warbler, endemic to the small Hawaiian Island of Nihoa. VORTEX was used to simulate establishment (via translocation) of new populations. Some population and life history parameters are known and others were estimated based on available data for similar tropical passerine birds. In these simulations, occasional population supplementation was the key to success, probably because it maintained genetic diversity. When current estimates of carrying capacity and environmental variation were used, 1,000-year simulations of 100 iterations each generated very high probabilities of extinction, but 100-year simulations were more optimistic. Because conservative estimates of some parameters (e.g., carrying capacity) always resulted in extinction, we used the more liberal estimates of some values. The model may need to be adjusted for populations such as this one that have had a long history of small size, probable numerous bottlenecks, and may no longer suffer severe negative effects from inbreeding or low levels of heterozygosity. We recommend that conservation measures for this species include an assessment of genetic variation (past and present) and that planning for translocation be undertaken without delay.

Key Words: *Acrocephalus*; conservation; endangered species; extinction; Hawaiian birds; Millerbird; population viability analysis (PVA); translocation; VORTEX.

The Nihoa Millerbird (*Acrocephalus familiaris kingi*) is endemic to tiny (63 ha) Nihoa Island in the Hawaiian Islands National Wildlife Refuge (NWR). Nihoa Millerbird was listed as endangered because of its small population (recent estimates have ranged from 30 to 730 birds), limited natural range, and the fragility of its native ecosystem (USFWS 1984a, Morin et al. 1997). The Laysan Millerbird (*A. f. familiaris*), which was endemic to Laysan Island (1,060 km northwest of Nihoa and also in the NWR), became extinct between 1916 and 1923, during a period when feral rabbits were destroying the vegetation on Laysan Island (Ely and Clapp 1973). According to the Northwestern Hawaiian Islands Passerines Recovery Plan (USFWS 1984a), the major threats to the continued existence of the Nihoa Millerbird are accidental introduction of alien plant and animal pests and environmental catastrophes. Due to difficulty of access, Nihoa may be less susceptible to accidental introductions of alien species than other northwestern Hawaiian islands. Consequently, the U.S. Fish and Wildlife Service has not actively pursued extraordinary conservation measures such as establishment of alternative populations and captive propagation. However, major environmental perturbations, such as hurricanes or severe drought, may occur at any time.

The genus *Acrocephalus* (reed-warblers) is relatively widespread in Eurasia and Africa and among the Pacific islands, where it has colonized numerous islands, many of which are small and often remote (Pratt et al. 1987). Based on its patchy, apparently relictual distribution, Pratt et al. (1987) speculate that the genus has been in the Pacific for a long time and note that

the Pacific island forms have diverged substantially in morphology from continental relatives. In the Hawaiian Islands *Acrocephalus* is known to occur only on Laysan and Nihoa islands. Despite extensive paleontological exploration in a variety of sites in the main islands (James and Olson 1991), no fossils of this genus have been found.

Vertebrate populations with limited ranges and of small size (similar to that of the Nihoa Millerbird) are thought to be at risk of extinction due to demographic and environmental stochasticity and loss of genetic variation (Soulé 1987). In the early 1980s, basing their estimates primarily on genetic considerations, biologists (e.g., Franklin 1980, Soulé 1980, Shaffer 1981) suggested that an effective population size (N_e) of at least 50 was the minimum viable population size (MVP) for which we might expect a species to survive for up to 100 years. The idea of a specific number was quickly recognized to be an oversimplification of the issue. Lande and Barrowclough (1987) and Soulé (1987), among others, revised the notion of MVP, stating that 500 was a much safer MVP for vertebrates, if, indeed, it was wise to specify an MVP in the first place. Those same authors also provided an extensive discussion of the MVP concept, cautioning that numerous factors (e.g., genetic, demographic, environmental, populational) must be considered in any estimation of MVP for a particular species. Recently, Lande (1995) addressed the MVP issue in the context of genetic variation, concluding that most vertebrate populations should number at least 5,000 if they are to survive at least 100 more years. Unfortunately many, if not most, endangered vertebrate popu-

lations number fewer than 5,000. Many conservation biologists and managers generally agree that ecosystem protection is the best way to conserve viable populations (e.g., Tear et al. 1993); nevertheless, recovery plans for endangered species often specify a minimum census population size (often smaller than 5,000) as a means of judging whether a species has sufficiently recovered to be considered "secure."

The notion of MVP seems to have been developed largely in a context of concern for the conservation of vertebrate species (or populations) that have undergone relatively recent (in the last century or two) and dramatic declines in total population size and/or geographic range. The MVP concept has no doubt provided a good framework for conservation planning for endangered vertebrates. However, we wondered if the concepts and the models (in this case, VORTEX; Lacy 1993, Lacy et al. 1995) developed for population viability analysis (PVA) of rare vertebrates were appropriate for small populations that may have been "naturally" small for several thousands of years and whose geographic range has also been small for a similar length of time. In other words, do "naturally" small populations, such as those endemic to small, remote islands, have the same risk of extinction as populations that have become small due to recent, dramatic declines?

Frankham (1995) discussed the role inbreeding may play in extinction. He pointed out that the susceptibility of island populations to extinction has been attributed to nongenetic causes and cautioned that inbreeding is probably also an important cause of extinction on islands. But is this really true? And, if it is, how could we distinguish between extinctions due to genetic causes, including inbreeding depression and loss of heterozygosity, and those due to demographic and environmental stochasticity? Although we have not been able to answer that question with the work reported here, our results prompt us to reiterate that genetic, demographic, and environmental factors all need to be addressed when PVAs are used as a basis for planning management actions aimed at conserving rare species (Mills et al. 1996). Although VORTEX allows us to assess all these factors, we found that its estimates of extinction probabilities for the Nihoa Millerbird still seem unrealistic.

METHODS AND MATERIALS

VORTEX is a computer model that provides a stochastic simulation of the extinction process (Lacy et al. 1995). The model uses basic life history (e.g., age at first reproduction, age-specific reproductive success) and genetic parameters to estimate the probability of extinction within a particular time frame (usually 100

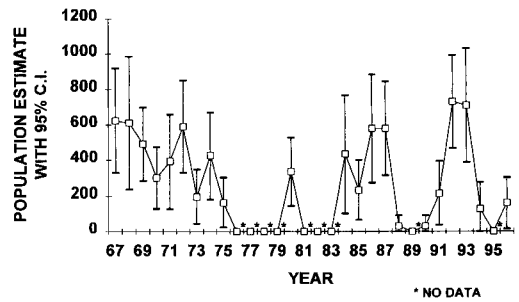


FIGURE 1. Nihoa Millerbird population estimates from 1967 to 1996.

to 1,000 years). Like any model, VORTEX makes a number of assumptions that can be violated for any particular analysis.

Although we have some data about the life history of the Nihoa Millerbird (Conant et al. 1981, Morin et al. 1997), we found it necessary to estimate a number of parameters. To do this we conducted a literature survey on life history of small tropical passerines, including those endemic to islands or archipelagoes and, especially, *Acrocephalus* species (Rowley and Russell 1991; Komdeur 1992, 1994a, 1997). We also examined unpublished data (made available to us by colleagues) on life history parameters of other endemic Hawaiian passerines. Presently we have no data on baseline genetic diversity in this subspecies or in the extinct Laysan Millerbird; however, blood samples from live Nihoa Millerbirds have been collected and tissue samples could be taken from museum specimens to resolve some of the genetic issues.

THE EXISTING KNOWLEDGE

Population size and carrying capacity

Between 1967 and 1996, the U.S. Fish and Wildlife Service (USFWS) censused the Nihoa Millerbird population 21 times. The estimates ranged from a low of 31 birds to a high of 731 birds, with a mean of 380, a median of 395, and an average 95% CI of ± 211.5 ($N = 21$, range 61–374; Fig. 1; see also Appendix 2 in Morin et al. 1997). Strip transects 3 m wide were used for all estimates (see Conant et al. 1981 for a detailed description of the method), and estimates are based on the assumption that all birds are detected within those transects. The 95% CI for these estimates are quite large, due, in large part, to effects caused by observers (Conant et al. 1981, and see Morin and Conant 1994 for a discussion of effects of observer variability on population estimates).

Using spot mapping and habitat evaluation, Conant et al. (1981) estimated that 40 ha of Nihoa Island's 63 ha of habitat are suitable for Nihoa Millerbird territories. Territory size ranges from 0.2 to 0.4 ha, so the number of territories on the island could be 100 to 200. There is insufficient data to assess what proportion of the population consists of pairs with territories and what proportion consists of floaters. According to the recovery plan for the endangered passerines of the Northwestern Hawaiian Islands (USFWS 1984a), the carrying capacity (K) is 600, and, although we used

TABLE 1. EXISTING KNOWLEDGE (MORIN ET AL. 1997) OF NIHOA MILLERBIRD LIFE HISTORY PARAMETERS

40 ha of Nihoa Island's 63 ha useable for territories
Territories are 0.2 to 0.4 ha, permitting 100 to 200 territories
Pairs stay on territories year-round, are monogamous, and retain mate from year to year
Clutch size is 2 to 3 (mean = 2.2, N = 16)
Pairs can breed more than once per year
From 1967 to 1996, population averaged 380 birds (N = 21, range = 31-731).
Carrying capacity (K) for Nihoa Island ~ 600 (USFWS 1984a), SD of environmental variation estimated at 200
K for extinct Laysan Millerbird on Laysan Island estimated at 1,500, SD of environmental variation at 500

this figure in our analyses, we think it may be an overestimate.

Life history parameters

Pairs remain on their territories year-round, are monogamous, and retain pair bonds from year to year (Morin et al. 1997). Clutch size is two or three eggs (mean = 2.2, N = 16), and pairs may breed more than once per year, though this has been documented for only one pair (Morin et al. 1997). Existing knowledge about the Nihoa Millerbird is summarized in Table 1. We needed to estimate a number of additional parameters in order to use VORTEX.

ESTIMATES OF PARAMETERS FOR A STANDARD RUN OF THE MODEL

Due to the dearth of information about this species, we estimated many of the parameters in order to run the model in VORTEX. In this section we provide a detailed discussion of and justification for those estimates.

Reproduction and mortality

We assumed a monogamous breeding system. The VORTEX model assumes random recombination of pairs each year (Lindenmayer et al. 1995), so that any advantage to reproductive success or survival conferred by mate fidelity is apparently not modeled. We were unable to assess the importance of this attribute of the VORTEX model. We know that banded pairs remained together on their territories, and both parents incubated eggs and cared for their young (Morin et al. 1997); this type of mating system would certainly limit, if not preclude, opportunities for extra-pair copulations. We assumed that the parents at the nest were the genetic parents of the young in that nest, although we do not have genetic information to confirm this assumption. Craig (1992) found that the Nightingale Reed-warbler (*Acrocephalus luscini*), endemic to Saipan, was largely or entirely monogamous and that males defended relatively large territories on which most were sedentary for the two years of the study. In contrast, Brooke and Hartley (1995) found, in a single study season, that Henderson Reed-warblers (*A.*

vaughani taiti) bred cooperatively, as the Seychelles Warbler (*A. sechellensis*) will do under certain conditions (Komdeur 1994b). Age at first breeding is not known for the Henderson or Nightingale reed-warblers.

We assumed that females and males breed at one year of age. Although we do not have data for the Nihoa Millerbird, we do know that the Hawai'i 'Åkepa (*Loxops coccineus*; Lepson and Freed 1997), and the 'Elepaio (*Chasiempis sandwichensis*; VanderWerf 1998a) sometimes breed at one year of age, although quality of habitat and food probably influence the age at which birds breed. Seychelles Warblers may breed as early as eight to nine months of age, or reproduction may be considerably delayed (up to six years) if habitat quality is low (Komdeur 1992, 1994a,b). We assumed that the maximum, cumulative number of young per female per year is four, an assumption based on observations of a single banded pair of birds with two successful clutches in one breeding season (Morin et al. 1997). In the VORTEX equation for percentage of females that breed, we assumed that when the population is well below K, 95% of females breed, and when the population is at K, 65% of females breed. We assumed that all males would be in the breeding pool when the population was below K.

Environmental variation and reproduction

We assumed that environmental variation in reproduction and survival are correlated and that reproduction is density dependent. The population is limited to a small island that probably has a limited food supply, and the quality and amount of food and shelter are strongly affected by environmental factors, such as amount and distribution of rainfall, which, in turn, probably affect reproductive success. Komdeur and colleagues (Komdeur et al. 1991; Komdeur 1992, 1994a,b, 1997) have documented that reproduction in the Seychelles Warbler is strongly influenced by environmental variables, and that reproduction is density dependent. We assumed that the Allee effect would be zero because the island is so small that it is unlikely individuals would have difficulty finding mates if they were available. Territorial males advertise with a distinctive territorial song that "floater" females should be able to detect as they are moving about. VORTEX asks the investigator to choose one of several formulas that describes the shape of the curve (B) describing density dependence. We did not have information on the true shape of this curve for our species. We chose B = 8 because this curve best fit our expectation that, due to limited available habitat, a steep decrease in breeding would occur at high population densities as is the case for the Seychelles Warbler (Komdeur 1992, 1994b). We modeled three types of environmental catastrophes and based our estimates of their frequencies on available weather data and historical accounts of fire on the island. We assumed that there would be a severe drought every 50 years, a remarkable hurricane every 100 years, and a major fire every 200 years. Although hurricanes frequently occur near Hawai'i, between 1904 and 1967 only four came close enough to affect the islands (Mueller-Dombois et al. 1981a). According to Armstrong (1983) 14 hurricanes occurred near Hawai'i between 1950 and 1983, but none of

TABLE 2. STANDARD CONDITIONS FOR VORTEX SIMULATIONS FOR THE NIHOA MILLERBIRD

Simulations to run for 100 or 1,000 years, 100 iterations each
 No inbreeding depression
 Environmental variation in reproduction and survival are correlated
 Three catastrophes in Nihoa Model:

- Droughts: 2/100 yrs, 0.5 effect on reproduction, 0.8 on survival
- Hurricanes: 1/100 yrs, 0.5 effect on reproduction, 0.75 on survival
- Fires: 1/200 yrs, 0.5 effect on reproduction, 0.5 on survival

Monogamous breeding system
 Females and males breed at 1 year of age
 Maximum age is 10 years
 Sex ratio at birth is 1:1
 Maximum cumulative young fledged per female per year is 4
 Reproduction is density dependent
 In equation for percentage of breeding females: $P(0)^a = 95\%$, $P(K)^b = 65\%$, $B^c = 8$, $A^d = 0$
 For breeding females:

- 35% fledge 1/yr 45% fledge 2/yr
- 15% fledge 3/yr 5% fledge 4/yr
- SD = 5%

70% mortality from fledging to 1 yr (20% EV^e) both sexes

- 15% mortality 1 yr to 10 yrs (5% EV) females
- 10% mortality 1 yr to 10 yrs (3% EV) males

All males in breeding pool
 Stable age population
 Initial (1996) population = 200
 K = 600
 Standard deviation (EV) in K = 200
 No harvest or supplementation

^a P(0) = probability of extinction observed.

^b P(K) = probability of carry capacity.

^c B = curve describing density dependence.

^d A = Allee effect (difficulty in finding a mate).

^e EV = environmental variation.

these did any serious damage. Since then, only two storms, Hurricane Iwa in 1983 and Hurricane 'Iniki in 1992 have caused serious structural damage to natural habitats. Droughts are a regular feature of El Niño events, which occur roughly every 20 years, but remarkable droughts occur less frequently (Armstrong 1983). Smith and Tunison (1992) summarized what is known about the role of fire in Hawai'i's natural ecosystems, concluding that it played a minor role until the establishment of human populations and alien species, particularly grasses. Our estimate that one catastrophic fire would occur every 200 years takes into account a low natural rate of fire and a substantially higher fire risk associated with human visitation to Nihoa Island.

Initial population size, carrying capacity (K), length of runs, and inbreeding depression

We assumed the Nihoa Millerbird population would have a stable age distribution, that K was 600, as stated in the recovery plan, and that the standard deviation of K was 200. We used the 1996 population estimate of 200 birds as the initial population size. There could be no supplementation of this population because it is the only one in existence, and harvesting is not currently permitted. We ran both 100- and 1,000-year simulations of 100 iterations each. For our standard condition runs of the model, we assumed that there would be no inbreeding depression because the population has been small for a substantial, though unknown,

length of time. We included inbreeding depression in a few other runs to see what would happen, and those results are discussed below. Other PVAs (Bustamante 1996) have assumed no inbreeding depression as part of the standard conditions for their VORTEX runs.

Appropriateness of estimates

Although we based our estimates of most life history parameters on data for similar species, we do admit to a certain amount of bias generated by our early attempts at running the model. For example, we feel that the estimate of K = 600 from the recovery plan for this species is rather high. We note that the average population estimate is 380 birds, well below 600. If K is actually 600 and the standard deviation of K is actually about 200, then the average of the population estimates and the confidence intervals for those estimates should more closely approach 600 and 200, respectively. However, we found that if we attempted to run the model with a K lower than 600, the probability of extinction [P(E)] was so high that, if the model is correct, the Nihoa Millerbird should have gone extinct long ago. We regard some of our estimates of other parameters (e.g., age-specific reproductive success for females) "optimistic" as well but found that lower estimates caused the model to "crash" consistently. These problems will be discussed later.

Standard conditions we used to run the model are shown in Table 2.

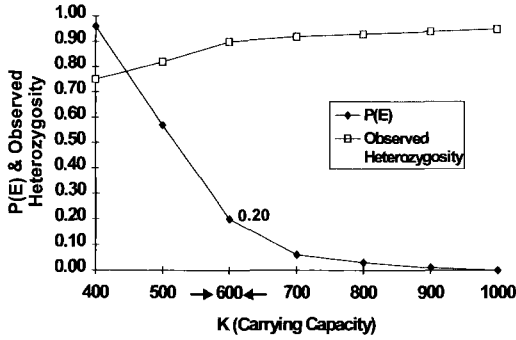


FIGURE 2. Probability of extinction [P(E)] and observed heterozygosity in Nihoa Millerbirds for 100-year VORTEX run of 100 iterations. Environmental variation (EV) = 200 for different carrying capacities K, "standard" condition being K = 600.

RESULTS

RESULTS OF 100- AND 1,000-YEAR SIMULATIONS

The results of the 100-year simulation of 100 iterations at the standard conditions specified above are illustrated in Figure 2. At a K of 600, the probability of extinction [P(E)] is 0.20. In this example (Fig. 2) the model is very sensitive to K; that is, P(E) increases dramatically as K decreases. Observed heterozygosity and the number of alleles increases with K, more rapidly up to K = 700 than at higher K. The results of a 1,000-year simulation (using identical input and also performed with 100 iterations) provide a much less optimistic outlook (Fig. 3). At K = 600, P(E) in the 1,000-year run is 0.96 and decreases to 0.42 at K = 700. Observed hetero-

zygosity and number of alleles are much lower in this simulation, an indication of the effects of heterozygosity on the P(E).

EFFECTS OF ENVIRONMENTAL VARIATION

To examine the effect of environmental variation (EV) in K, we varied the standard deviation (EV) of K, which, in the previously discussed simulations, was 200. When EV decreases from 200 to 150 in the 100-year simulation, observed heterozygosity rises from 0.90 to 0.93 and P(E) drops from 0.20 to 0.04 (Fig. 4). For the 1,000-year simulations P(E) remains high regardless of the magnitude of EV; however, it dropped to <0.40 when EV was only 150. We believe that EV may actually be much higher than 150. In the 1,000-year simulations, when EV was 250, all Nihoa Millerbirds in these iterations went extinct by year 400, and when EV was 300, they went extinct by year 200.

Under our "standard conditions" (Table 2), which included no inbreeding depression, the mean final population for successful cases of 100-year simulations was 278 Nihoa Millerbirds (SD = 168.5), and the mean final population for successful cases of 1,000-year simulations was 170 Nihoa Millerbirds (SD = 125.2). When we changed the inbreeding depression to the Recessive Lethal Model and kept all other conditions the same, the mean final population for successful 100-year simulations was 240 Nihoa Millerbirds (SD = 129.6), and the mean final population for successful 1,000-year simulations was 309 Nihoa Millerbirds (SD = 92.2)

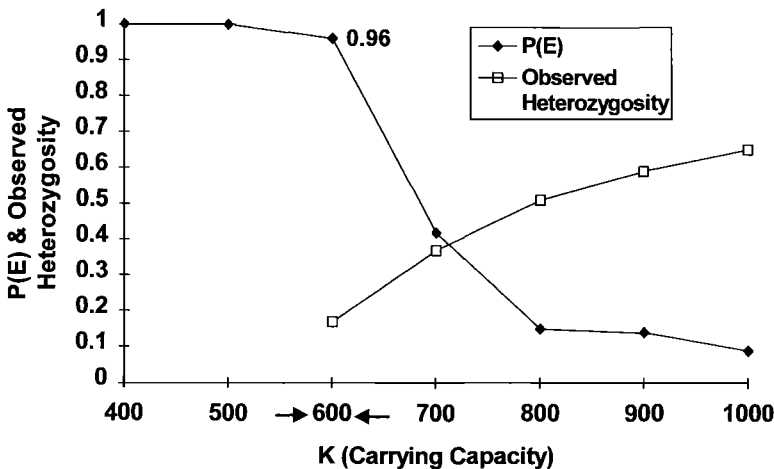


FIGURE 3. Probability of extinction [P(E)] and observed heterozygosity in Nihoa Millerbirds for 1,000-year VORTEX run of 100 iterations. Environmental variation (EV) = 200 for different carrying capacities K, "standard" condition being K = 600.

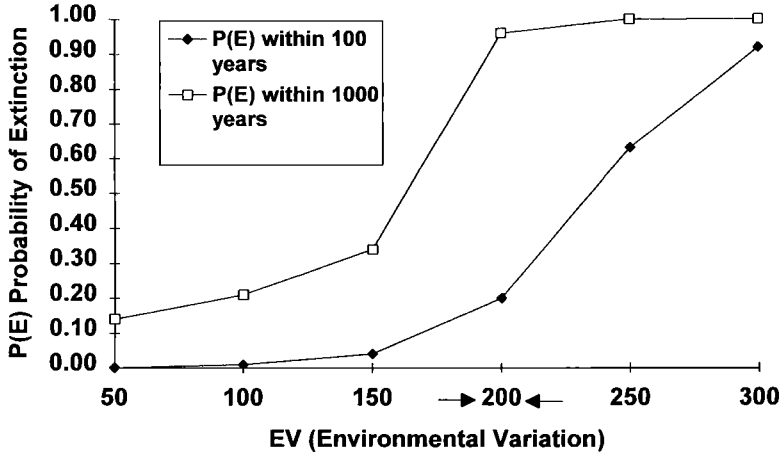


FIGURE 4. Probability of extinction [P(E)] in Nihoa Millerbirds for $K = 600$ when environmental variation (EV) ranges from 50 to 300, for 100-year and 1,000-year VORTEX runs. All runs resulted in extinction by year 400 in the 1,000-year runs when $CV = 250$, and all runs resulted in extinction by year 200 when $EV = 300$.

EFFECTS OF VARIATION IN MORTALITY REGIMES

Because we lack data on mortality regimes for this species, we decided to examine how P(E) would vary with different mortality regimes. Figure 5 shows the results of both 100- and 1,000-year simulations in nine different mortality regimes. We ran a simulation with three different adult mortality regimes and three different first-year mortality regimes. Perhaps the most striking result shown in Figure 5 is the difference in P(E) for the 100- and 1,000-year simulations. Only in the most pessimistic mortality

regime (shown in the first column of Fig. 5) does the P(E) for the 100-year simulation resemble that of the 1,000-year simulation. The P(E) for any single 1,000-year simulation was never less than 0.70; whereas all but one of the 100-year simulations had P(E) values of less than 0.25.

DISCUSSION

INFLUENCE OF CARRYING CAPACITY K ON PROBABILITY OF EXTINCTION P(E)

As we mentioned above, we believe that the estimation of $K = 600$ in the recovery plan

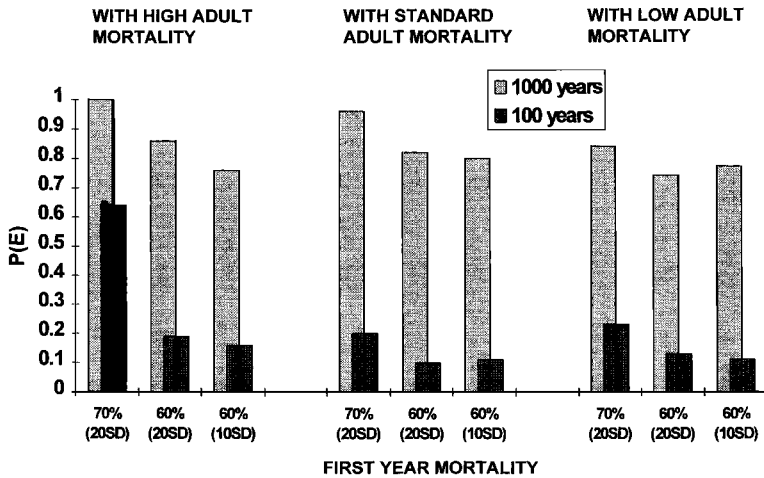


FIGURE 5. Probability of extinction [P(E)] for Nihoa Millerbirds under three different first-year and adult mortality regimes. First year mortality was 70% ($SD = 20$) or 60% ($SD = 10$ and $SD = 20$). In addition there were three adult mortality regimes. High mortality: adult females 20% ($SD = 10\%$), adult males 15% ($SD = 5\%$); “standard” conditions: adult females 15% ($SD = 5\%$) adults males 10% ($SD = 3\%$); low mortality: adult females 10% ($SD = 3\%$), adult males 10% ($SD = 3\%$).

(USFWS 1984a) for this species is a substantial overestimate. We feel it would be more realistic to use the mean population estimate (380) derived from 21 censuses that were made during the last 30 years (Fig. 1). However, when we attempted to use $K = 380$, all simulations had very high $P(E)$. Furthermore, we feel that 200 may be an unrealistically low estimate of EV , again because the censuses (Fig. 1) show such a great deal of variation from year to year. However, if we use an even higher estimate of EV than 200, all simulations result in extinction very quickly. This suggests to us that environmental variation could, in reality, be much smaller than we think. Furthermore, the possibility that K changes, perhaps considerably, from year to year seems very reasonable. The negative effects of the 1997–1998 El Niño phenomenon on environmentally mediated reproduction and survival of many Hawaiian birds appears to have been dramatic (P. Banko, H. D. Pratt, and A. Engilis, pers. comm.)

LIFE HISTORY PARAMETERS

In the model, the percentage of breeding females is a function of population size, but the percentage of breeding males is fixed for any single simulation. We speculate that the percentage of breeding males may also be a density dependent function. If we have underestimated reproductive potential, the population may be more resistant to extinction than our results suggest. For example, if Nihoa Millerbirds breed in response to vegetation flushes brought on by rainfall, then they may have much higher reproductive rates in some years, making the results of our simulations overly pessimistic. It could be that Nihoa Millerbirds, like the Seychelles Warbler (Komdeur 1994a, 1997), may often raise two broods a year. Another consideration here is that, because this model assumes random reassignment of mates each year, it may underestimate reproductive success associated with multiyear mate fidelity. Thus, the effects of multiyear mate fidelity on the probability of extinction remain unknown for the Nihoa Millerbird.

However, even if we have underestimated reproductive potential and overestimated mortality, these values are considerably less important than overestimates of K in the model. As mentioned above, because the simulations using lower values for K almost always went to extinction rapidly (much higher $P(E)$ values), we were somewhat liberal in estimating some life history parameters.

We were surprised at how insensitive the model seemed to be to different mortality regimes (see Fig. 5). Lower mortality regimes did not always have higher probabilities of extinc-

tion. Perhaps the mortality regimes we used overlapped sufficiently to mask such differences.

THE ROLE OF GENETIC VARIATION IN THE MODEL

VORTEX allows the investigator to specify whether or not the population experiences inbreeding depression. The VORTEX simulations used to generate Figures 2–5 were run without inbreeding depression. However, using the rest of the standard conditions (Table 2), we added inbreeding depression for a 100-year and a 1,000-year simulation with both the Heterosis Model (using the default mammalian values of 3.14 lethal equivalents per genome; Ralls et al. 1988) and the Recessive Lethal Model. The $P(E)$ for 100 and 1,000 years for the Heterosis Model were: 0.28 (28 of the 100 simulations went extinct in 100 years) and 1.0 (all simulations went extinct by the year 300), respectively. In contrast, the $P(E)$ for the Recessive Lethal Model were actually the same or slightly more optimistic than those values VORTEX generated when no inbreeding depression was specified: $P(E) = 0.18$ for 100 years and $P(E) = 0.93$ for 1,000 years. The choice of “no inbreeding depression” (standard conditions in Table 2) generated a 100-year $P(E) = 0.20$ and a 1,000-year $P(E) = 0.96$ (Figs. 2, 3).

We decided to eliminate inbreeding depression from our simulations because our population was so small, and had been small for possibly thousands of years. Population estimates over the last 30 years show considerable fluctuation in population size, which is not surprising because of the harsh, variable habitat Nihoa provides. Thus, we expect the population has been subject to frequent and severe bottlenecks, allowing it to adapt a relatively high level of inbreeding. We note that our populations lost heterozygosity quickly in the simulations, and that this factor may have played an important role in the generation of high extinction probabilities. We speculate that our population may not be as severely affected by this factor as populations that have undergone recent, dramatic declines but are at a loss to do more than speculate on the role such a difference might play in scaling the model somewhat differently for our population. This issue could be addressed if we could make a comparison of genetic variation between Laysan and Nihoa Millerbird populations (via the use of museum specimens), as well as a comparison of Nihoa specimens collected in the 1920s and blood samples collected 70 years later in 1992 and 1993. The latter comparison would allow us to compare VORTEX estimates of genetic change in the population over time with actual data.

100-YEAR SIMULATIONS VERSUS 1000-YEAR VORTEX SIMULATIONS

A number of PVAs reported in the literature or performed by or for management agencies report on the results of simulations that are much shorter than 1,000 years (e.g., Ellis et al. 1992a,b; Bustamante 1996, Mills et al. 1996). Our results indicate that 100-year simulations are not very useful for long-term conservation goals, since they give the illusion that populations may be secure, when this may only be true for the short-term (i.e., 100 years) and not the long-term. If management programs are based on results of short-term simulations, they may become locked into simplified or superficial short-term goals due to lack of in-depth understanding of how the population could behave. Populations judged to be "secure" in the short-term may become genetically depleted to the point that they may not recover from their endangered status if management goals are based on results of short-term PVAs.

SHOULD THE NIHOA MILLERBIRD BE TRANSLOCATED TO OTHER ISLANDS?

VORTEX predicts that as K increases $P(E)$ will decrease, all else being equal. This suggests that management efforts for this species should focus strongly on increasing K . Our simulations clearly showed that the higher the value of K , the more extinction resistant the population will be. Because Nihoa Island is limited in size, predator free, and relatively undisturbed, there is little likelihood that managing the habitat there could increase the carrying capacity. The most expedient method of increasing the carrying capacity of Nihoa Millerbird would be to establish one or more additional populations that are geographically separated from the Nihoa population, so that environmental, demographic, and genetic factors affecting extinction probabilities will vary independently for the different populations. Establishment of two alternative populations of the Seychelles Warbler by translocations has certainly brought the species back from the brink of extinction (Komdeur 1997). The potentially devastating effects of an accidental rat introduction (see Fisher and Baldwin 1946a for a description of the extinction of the Laysan Finch [*Telespiza cantans*] and Laysan Rail [*Porzana palmeri*] from Midway within two years of accidental rat introduction) suggest that establishing additional Nihoa Millerbird populations would probably be the single most effective conservation measure that could be undertaken at this time.

To explore translocation as a means of increasing Nihoa Millerbird K , we simulated an

TABLE 3. VORTEX SIMULATIONS OF NIHOA MILLERBIRD INTRODUCTION TO LAYSAN ISLAND, HAWAII¹

	P(E) ^a	Observed heterozygosity	Final number of alleles
100-year scenarios			
40 males and 40 females	0.24	0.92	30.1
No supplementation			
Suppl: 5yr-old males	0.0	0.96	74.1
5yr-old females			
1 × per 10 yrs			
1,000-year scenarios			
20 males and 20 females	0.0	0.77	29.5
Suppl: 5yr-old males			
5yr-old females			
1 × per 10 yrs			

^a P(E) = Probability of extinction.

introduction to Laysan Island. Laysan is probably the best choice for establishing a second population because the Laysan Millerbird once occurred there, the island is predator-free, and there are a number of native and introduced arthropods for food sources. Based on the size of Laysan Island, in particular the size of its vegetated area (~190 ha), we estimated that $K = 1,500$ Nihoa Millerbirds. We estimated that on Laysan, $EV = 500$, then we simulated several scenarios for the introduction (Table 3). In these simulations, we incorporated hurricanes and droughts with the same frequencies and effects as those in the Nihoa simulations (see Table 2), but we did not include fire because we felt that fires on Laysan are far less likely to get started, as well as to move very far due to damp soil conditions and lack of significant dry fuel.

In the first pair of 100-year simulations, we introduced 40 males and 40 females each time. In one case, there was no supplementation, and, in the second case, the population was supplemented with five-year-old males and five-year-old females every ten years. Without supplementation, the first introduction had a 0.24 $P(E)$ in 100 years. With supplementation the $P(E)$ was zero. Although observed heterozygosities at the end of the 100 years were similar (0.92 for the unsupplemented introduction and 0.96 for the supplemented introduction), the final number of alleles in the supplemented was 74.1, compared to only 30.1 in the unsupplemented population. VORTEX predicts that even a very modest level of supplementation will give the population much higher odds for survival. Supplementation is the key to success for these translocation scenarios, because it allows a much higher level of heterozygosity to be maintained. To mimic an even more practical translocation, we ran a 1,000-year simulation that involved the intro-

duction of 20 males and 20 females, and which was supplemented every 50 years with five-year-old males and five-year-old females. This simulated translocation had an extinction probability of zero as well, a most encouraging result.

We have not suggested the establishment of an alternative population in captivity because it seems likely that this alternative would be prohibitively expensive and may carry unacceptable risks. The passerines of Laysan and Nihoa islands have been isolated from avian diseases such as pox and malaria for a long, though unknown, period of time. Current knowledge of the serious impacts of these diseases on endemic Hawaiian passerines (e.g., van Riper and van Riper 1985, van Riper et al. 1986, Feldman et al. 1995, Jarvi et al. *this volume*, Shehata et al. *this volume*, van Riper and Scott *this volume*), as well as documentation of the Laysan Finch's susceptibility to avian malaria (Warner 1968, Throp 1970) suggest that the risks of moving birds from a captive propagation facility to one of these remote and isolated islands are likely to be quite serious. Furthermore, insectivorous birds are known to be highly sensitive to capture and captive conditions (Komdeur et al. 1994a), so that the remoteness of the population will make any kind of hands-on management involving transport of birds very risky.

The results of both our VORTEX Nihoa Millerbird PVA, as well as the translocation simulations, encouraged us to speculate that the Nihoa Millerbird's historical distribution may have included additional islands (e.g., Lisianski, French Frigate Shoals, Necker, Kaua'i), although this is not yet substantiated by paleontological findings (but note that Curnett et al., *this volume*, discuss how recent paleontological discoveries have reduced the number of single-island endemics throughout Pacific island groups). Alternatively, or perhaps additionally, there may have been a small, nevertheless significant, amount of gene flow between the Laysan and Nihoa populations of this species. Either of these possibilities might well provide the answer to the question posed by our title. More importantly, our results suggest that the species is in serious danger of going extinct during the next two or three decades if an alternative population is not established.

We should be able to refine our population viability analysis of this species if we have bet-

ter data on several life history parameters: age-specific mortality, annual age-specific reproductive success, proportion of breeding adults of each sex in the population. In addition, we need a more realistic idea of what the carrying capacity really is on Nihoa Island and how much it varies. Finally, and perhaps this will be the easiest issue to assess, we need to know the nature of genetic variation in both the Laysan and Nihoa Millerbird populations.

In his paper, "Inbreeding and Extinction: a threshold effect," Frankham (1995) warns that, "there may be little warning of impending extinction due to inbreeding in wildlife, especially with species that are not intensively monitored." We concur and further add that monitoring should include assessing genetic variability as well as the usual parameters examined for rare populations, such as population size and annual reproductive success. Because samples are readily available, an assessment of genetic variation in the species should be undertaken immediately. This assessment should include a comparison of the Laysan and Nihoa Millerbird populations as well as an examination of genetic variation over time for the Nihoa population. Although the population is censused in most years, there is no monitoring aimed at assessing variation in reproductive success, which is unfortunate. Lack of access to the island and the disturbance such monitoring may cause to other wildlife and plants can be serious, however. If establishment of new populations by translocation to Laysan Island (or other islands, such as Midway Atoll or Lisianski Island) is a possibility, planning and data acquisition should begin immediately.

At this point in time we have the luxury of being able to ask, "Why isn't the Nihoa Millerbird extinct?" If action to conserve the species is not taken soon, we may be asking, "Why did the Nihoa Millerbird go extinct?"

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