

'ALALA, AKOHEKOHE, & PALILA

Population & Habitat
Viability Assessments



CBSG



**'ALALA, AKOHEKOHE, AND PALILA
POPULATION AND HABITAT
VIABILITY ASSESSMENT REPORTS**

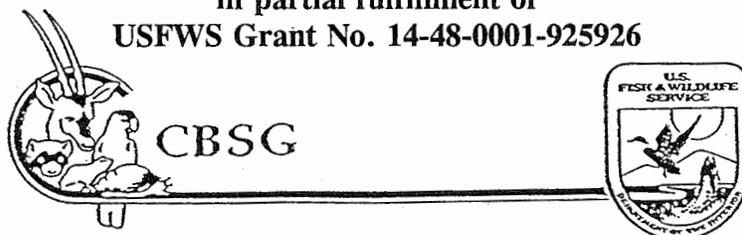
Compiled and Edited by

Susie Ellis, Kimberly Hughes, Cynthia Kuehler, Robert Lacy, and Ulysses Seal

**in conjunction with the participants
of PHVA workshops held in
Hilo, Hawaii
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Robert C. Lacy

SECTION 1.

'ALALA (HAWAIIAN CROW) *Corvus hawaiiensis* POPULATION AND HABITAT VIABILITY ASSESSMENT REPORT

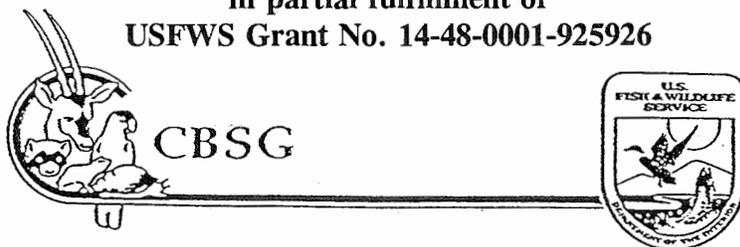
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'Alala PHVA

'ALALA (HAWAIIAN CROW) *Corvus hawaiiensis* POPULATION AND HABITAT VIABILITY ASSESSMENT

Working Group: Kimberly Hughes (Chairperson), Paul Banko, Fern Duvall, Jon Giffin, Peter Harranty, Scott Johnston, Cynthia Kuehler, John Marzluft, and Claire Mirande

INTRODUCTION

The 'Alala (*Corvus hawaiiensis*) is an endangered Corvid that is known only from the Island of Hawai'i (Big Island). At one time, the 'Alala was widespread in the montane forests of the island. By 1974, the wild population had declined to an estimated 61 individuals in three populations (Banko and Banko, 1980). In the past 18 years, all individuals have disappeared from two of those three areas (with the possible exception of a single female that may still reside in the on Mount Hualalai). Currently, only one wild population remains, and it consists of only about a dozen animals.

Compared to other Corvids, the 'Alala exhibits somewhat specialized habitat requirements. It prefers closed-canopy koa-ohia forest, although it also uses more open koa-ohia forest (Giffin et al., 1987). It is omnivorous, but its diet is largely comprised of fruit. A widespread but declining, endemic plant, the ieie (*Freycinetia arborea*), may once have been a primary food source. These specialized requirements and the disappearance of appropriate habitat have likely contributed to the decline of the species.

Overgrazing by introduced ungulates inhibits regeneration of ohia, koa, and understory plants in the 'Alala's historical range. Alien predators are known to have destroyed nests and are thought to be an important source of mortality, especially during the vulnerable fledgling stage of the life. Other threats to the wild bird are disease (e.g., avian pox) and human interference. Direct interference by humans is probably not an important factor in the currently inhabited area in which 'Alala are found, but shooting of birds has occurred in other areas.

The 'Alala is classified as Endangered by the USFWS, the State of Hawaii, and IUCN-The World Conservation Union. A review of the status of this species (Ellis et al., 1993) classified the species as Critical based upon application of the Mace/Lande criteria (Mace and Lande, 1991).

Recommendations for the recovery of the 'Alala have included predator and disease control, supplemental feeding, expansion of the captive breeding program, release of captive-reared birds, nest-site manipulation, and habitat restoration. It was our purpose to evaluate these recovery options by a computer modelling approach known as PHVA (Population and Habitat Viability Assessment). PHVA models simulate demographic and genetic processes in small populations. Because small populations can be subject to large stochastic deviations from the predictions of deterministic models, several sources of random and environmental variability

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are included in the population projections produced by the models.

The parameters for the 'Alala PHVA were formulated by the 'Alala Working Group (Appendix II) at the Hawai'ian Forest Birds CAMP Workshop. This report consists of three sections. The first describes the PHVA of the wild population. The parameters used in the modelling process and the sources of the data are described in the first part of Section 1. Results and conclusions make up the second part. The captive population models are similarly described in Section 2. The third section contains the results of "metapopulation models." (These models are constructed to simulate a management program that uses frequent translocations from the captive to the wild population and vice versa.). The final section presents recommendations for future management of the 'Alala.

1. ANALYSIS OF WILD POPULATIONS

1.1 Assumptions of the baseline models.

1.1.1 Population biology parameters. Population and habitat viability assessment uses available ecological, demographic, and genetic data to predict the fate of a population under various scenarios. The reliability of data on which analyses are based has, of course, a profound impact on the precision of these predictions. For the 'Alala, field data are available from several sources (Banko and Banko, 1980; Temple and Jenkins, 1981; Giffin et al., 1987; and Giffin, 1991). Workshop participants also had access to demographic information from a captive population at the Olinda Captive Propagation Facility on Maui, Hawai'ian Islands (information provided by F. Duvall). Data from both the wild and captive populations from all of the above sources are summarized in the NRC report on the 'Alala. The members of the 'Alala Working Group and other members of the Hawai'ian Forest Bird Conservation Assessment Meeting provided recent, unpublished results. They also provided estimated values for population parameters that could not be precisely determined from the available data. These estimates were then used to construct a range of scenarios to be evaluated in the modelling process.

Throughout this document, models of *current population processes*, under various assumptions about inbreeding effects, catastrophic events, and mortality rates, are jointly referred to as the *basic models*. Models that have been designed to simulate management strategies will be referred to as *management models*.

1.1.2 Current Population Size and Carrying Capacity. Future projections were based on an initial population size of 12 individuals. This number is based on a census conducted in 1992 by Paul Banko and Scott Johnston. The basic projection models were also run with a higher initial population size (15) based on a 1989 estimate by McCandless Ranch staff.

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Carrying capacity was set at 200 for all the models. The 'Alala Working Group had difficulty reaching a consensus on actual carrying capacity because of the very rapid decrease in the range of the species during the last few decades. Some members of the group believe the island of Hawai'i cannot support many more animals than are currently present without extensive habitat restoration. A carrying capacity value of 200 was chosen because it allowed us to evaluate the population growth rate under different scenarios, assuming that future habitat management (and possibly supplemental feeding) would serve to partially offset any resource limitation of population numbers.

1.1.3 Sex and Age Structure. Because no systematic observations of the wild 'Alala have occurred during the last decade, the age distribution of the population is basically unknown. However, one bird is a 15-year-old female, and one bird hatched in 1992. All remaining birds are thought to be at least several years old because of their dark mouth coloration and adult vocalization. The evidence suggests, then, that the population is not near the stable age distribution. We therefore assigned adult ages to all birds, with the exception of the juvenile.

Of 11 birds found in 1992, three pairs were participating in nesting activity. Of the remaining five birds, four may be paired, although they did not nest in 1992. The sex-ratio appears to be approximately even. All models were constructed with approximately even sex ratios.

1.1.4 Reproductive Rates. Reproductive rates in the wild 'Alala were estimated using both fledging and hatching as the measure of birth. The National Research Council (NRC) report (NRC, 1992) measured reproduction at fledging. The proportion of breeding-age females (age 2 or older) that fail to produce young in a given year is summarized in Tables 1 and 2.

Estimates were also made on the yearly proportions of breeding-age females producing eggs, using the data from Temple and Jenkins (1981). These results are summarized in Table 3.

Comparison of models using fledging or hatching as the birth statistic showed that both models predicted comparable population growth rates. Hatching data was chosen for the basic model since it provides the most flexibility in predicting the effects of different management strategies.

Variability in reproductive rates was calculated from field data. A value of 21 percent was used for the standard deviation in reproductive rates.

1.1.5 Mortality. Mortality rates were estimated by several methods. Juvenile (hatch year) mortality was estimated with hatching as the birth statistic. Using the NRC value, adjusted to reflect birth at hatching, the first estimate of juvenile mortality was 67 percent (11 of 20 died). Recent USF&WS survey results (Banko and Johnston, pers. comm.), when combined

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With the previous estimates, indicate juvenile mortality rates of 75 percent.

Yearling (age 1 to 2 years) mortality was estimated at 10 percent in the NRC report. Banko and Giffin noted that sightings of juveniles have been very rare and that the NRC value may be an underestimate. Consequently the model was also run with juvenile mortality set at 50 percent.

Several adult mortality rates were examined. The combined data for the McCandless, Honaunau, and Hualali populations was 27 percent (41 of 56 banded adults were estimated to have died based on resightings, according to Banko and Banko, 1980). Examination of the McCandless data alone indicated adult mortality rates of 19 percent (5/27) based on observation-weighted estimates and 10 percent based on the time-weighted method [NRC Report, based on data of Banko and Banko (1980) and Temple and Jenkins 1981].

We tested the validity of the various estimates by employing historical models based on known population sizes in 1974 and 1980. The mortality schedules evaluated in this manner are shown below. Numbers represent annual mortality, expressed as a percent.

Mortality Rates

	<u>Hatch Year</u>	<u>Yearling</u>	<u>Adult</u>
Scenario 1:	67	10	10
Scenario 2:	67	10	19
Scenario 3:	67	10	27
Scenario 4:	67	50	10
Scenario 5:	75	10	10

The results of this analysis appear in Table 4. Models 1a through 5a are based on a population size of 35 on Mauna Loa in 1974 (Banko and Banko, 1980). Models 6b through 10b on a population size of 19 in 1980 (Temple and Jenkins, 1981; Banko and Banko, 1980). Models were run for 18 and 12 years, and the predictions for probability of extinction, population size, and heterozygosity refer to the same time periods.

Assuming the current population size is between 12 and 20, Scenario 3 appears to be an overestimate of the overall mortality. Our simulation results provide little guidance for discrimination between the other mortality schedules. Scenario 1 appears to predict a current population size considerably larger than is now believed to persist at McCandless. However, the large standard deviation about the mean indicates that current population sizes are well within the range predicted under this scenario. Large Corvids typically have low post-fledgling mortality; at least one of the McCandless birds are known to be 15 years of age. In addition, the estimate of 19 percent adult mortality was calculated by a method that produces

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estimates of the maximum mortality rate. We performed further simulations with Scenarios 1, 2, and 4 that indicated that Model 1 predicts population sizes that are larger than are currently observed (but with very large standard deviations), when modelled over the last 18 years; while Models 1 and 4 predict population sizes that may be too low when projected over the last 12 years. This may indicate that mortality rates have changes over time, as would be expected if mortality rates change with age and if the current population is highly age-structured. The empirical support for this conclusion is weak, however. We consequently decided to use Scenario 1 as an appropriate set of values for mortality in the current population, with the following caveat: actual mortality rates might be substantially higher than those that were used in the basic models. This would mean that the models these models make optimistic predictions of extinction probabilities and population size. These models should probably be viewed as "best-case" scenarios.

Because of the very limited data on banded wild birds, we were not able to calculate a standard deviation for mortality rates. We chose instead to investigate the effects of this variable by running all models at two levels of environmental variation (EV) in mortality. Low levels of EV were produced by setting the standard deviation in age-specific mortality equal to 10 percent of the mortality rate. High EV levels correspond to a standard deviation that equals 30 percent of the mortality rate.

1.1.6 Lifespan. Lifespan was estimated at 30 years based on data on other corvid species.

1.1.7 Catastrophes. Four potentially catastrophic events were recognized as threatening to the wild 'Alala. Because of the small size and limited distribution of the population, as well as the potential for inbreeding effects on resistance, disease was deemed the most likely and the most potentially devastating of these events.

<u>Catastrophe</u>	<u>Frequency</u>	<u>Effect on Survival</u>	<u>Effect on Reproduction</u>
Disease	1/50 years =2%	0.10	0
Drought/Rain	1/100 years =1%	0.99	0
Hurricane	1/200 years = 0.5%	0.50	0.50
Lava flow	1/600 years = 0.17%	0.99	0.20

Effect on survival and reproduction are calculated by multiplying the numbers listed above by the reproductive and mortality rates used in the model.

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1.1.8 Inbreeding Depression. There was a general consensus that inbreeding depression is contributing to the low fertility and hatchability rates of the current population. It is worth noting that estimates of fertility are based on a limited number of eggs analyzed by Temple and Jenkins (1981).

The degree of inbreeding depression that a species is expected to undergo depends on the history of the population and on the particular model of the genetic basis of inbreeding depression that is used. The literature on inbreeding depression includes many investigations of domesticated birds, but very few on wild or captive populations of non-domesticated species. Two published studies of wild birds yield inconclusive results (Van Noordwijk and Scharloo, 1981; Gibbs and Grant, 1989).

Therefore, the amount of inbreeding depression experienced by the 'Alala is unknown. Controlled experiments aimed at measuring inbreeding depression in this species are not likely to occur in the foreseeable future. Because of the paucity of data on inbreeding in this or any other non-domesticated bird, we have used a range of values for this parameter. All the models were constructed with 0.0, 3.12, and 6.28 lethal equivalents. These values are equivalent to: no inbreeding depression, inbreeding depression equivalent to that in captive wild mammals, and twice the average mammalian value, respectively (Ralls et al., 1988).

1.2 Management Strategies.

Because none of the proposed management strategies have been tested on the 'Alala, we do not know with certainty what the effect of any given strategy will be. The 'Alala Working Group spent several days evaluating the likely effects on demographic parameters of each of the management options discussed below. The Working Group consisted of individuals with expertise in the following areas: 'Alala field biology and the captive propagation of 'Alala, field biology and captive propagation of other corvids and other non-corvid passerines, successful recovery and management of avian species in a wide variety of habitats, and theoretical and experimental population biology. We estimated the potential effect of each management strategy on the age-specific mortality rates and the fecundity of wild 'Alala. The values used in the models were consensus values that were arrived at after evaluation of all the available data from both captive and wild populations. We also evaluated data from other corvids and from management programs in other avian species. We believe the estimates we used are the best that can be produced, given the unavoidable constraint of limited data.

Several management strategies were modelled via their expected effects on reproductive and mortality rates. Table 5 present a summary of the reproductive and mortality schedules incorporated into the models of the management strategies discussed in the next several sections. When interpreting the following models, it must be kept in mind that hatching, not fledgling is considered to be birth.

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1.2.1 Assumptions of the baseline models

1.2.1a Predator and Disease Control. We concluded that management practices such as predator control and disease control are likely to influence population demography via effects on mortality rates. Hatch-year (HY) mortality, in particular, is likely to be decreased through intensive predator control or disease-vector eradication programs. These management strategies therefore enter the models as decreases in HY mortality. The Corvid specialists in the group concluded that an extremely effective predator control strategy may reduce HY mortality to half its current level. A more moderate, but still optimistic, expectation is that HY mortality might be reduced from 67 percent in the basic models to 50 percent in the predator control models. We also modelled a scenario in which predator control is only able to reduce the HY mortality to 60 percent. It was felt that these three models provided reasonable coverage of the range of effectiveness of predator control programs in other Corvids (Banko, Harrity, and Marzluft, pers. comm.).

Disease control was modelled as a reduction in HY mortality from 67 percent to 57 percent. We concluded that it was unlikely that even highly effective disease- and predator control would reduce the HY mortality to less than 34 percent. Consequently, a separate model of the combined effects of these two management strategies was not produced, with the assumption that the model using 34 percent mortality would be an adequate description of such a program.

Predator and disease control could also increase birth rates by decreasing egg predation and by mediating any effect of disease on fertility. Therefore a model that combined moderate mortality rate reductions with a 10% increase in birth rate was constructed.

1.2.1b Chick Salvage. Salvaging of chicks or juveniles in poor condition is also a management option. We believe that this option, by itself, will not have as great an impact on mortality rates as the predator- and disease control options. This conclusion was reached mainly because biologists will be restricted in their opportunities to observe chicks in the nests. Reduction of juvenile mortality from 67 percent to 55 percent is the maximum effect expected from the implementation of this option alone. Since this is almost exactly the same magnitude of effect as was predicted for disease control, a separate model was not produced for this effect.

1.2.1c Nest-Site Manipulation. Alternately, techniques such as nest-site artificial incubation or double-clutching will primarily affect reproductive rates. We chose two levels of increased productivity to simulate the potential effects of these practices. Doubling of productivity is not an unreasonable goal for such techniques, so it was decided to model increases in productivity of 75 and 100 percent.

We also investigated methods whereby half the additional chicks produced by double-

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clutching could be used to supplement the captive population, rather than returned directly to the wild. In these models, productivity of the wild population was increased by 33 percent as opposed to the higher values described above.

1.2.1d Supplemental Feeding. Supplemental feeding is another method whereby productivity rates can be elevated. Some members of the Working Group believed that the wild population is not food limited, others suggested that feeding might increase productivity, but not drastically. Again, a range of potential effectiveness was modelled. The low effectiveness program incorporates a productivity increase of 10 percent; the more effective program simulates the effect of a 25 percent increase in production.

1.2.1e Supplementation. Two sets of models were constructed to simulate supplementation from the captive population. In one model, a single female and male bird are added to the wild population every year for 20 years. Supplementation ceases after 20 years. The second model incorporates the addition of two females and two males per year for 20 years. In both models, the birds that are supplemented are assumed to be second-year birds.

1.2.1f "Combination Models." Models were constructed to simulate the effects of integrated management programs that combine several of the strategies outlined above. A model incorporating a 25 percent increase in productivity and a decrease in HY mortality to 50 percent was used to simulate a management program that relies on predator and disease control and supplemental feeding. Such an approach might be used if one wished to minimize invasive procedures that might disturb the birds' nesting activities.

Another approach would be to attempt to increase the population size as much and as rapidly as possible. In this case, a program involving nest-site manipulation techniques (establishing a field incubation station) as well as disease and predator control might be used. To predict the outcome of such a program, we used a model with HY mortality reduced from 67 percent to 34 percent, and a productivity increase of 45 percent.

It should be noted that both the above scenarios incorporate moderately optimistic values for the expected effects of the various management techniques that they encompass.

1.3 Description of Simulations and Output.

1.3.1 Simulations. All simulations were run for 100 years, and were replicated 100 times. One hundred replications yielded consistent results and small standard errors about the predictions for mean population sizes and intrinsic rates of increase. (Standard errors can be calculated directly from the standard deviations reported on the tables.) Very little precision would be gained by increasing the number of replications. At years 20, 50 and 100, the probability of extinction, the population size, the standard deviation of population size, and

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the expected heterozygosity are reported. The probability of extinction is the number of populations, out of 100 that went extinct in the given time interval. Both deterministic (life-table) and stochastic measures of the intrinsic rate of population increase (r) are reported. If more than 50 of the original 100 populations become extinct in a given simulation, the median time to extinction, in years, is also given.

All combinations of the basic models and the previously discussed management strategies were modelled. The results are presented in tabular form as well as in the text of the discussion and conclusion section of further drafts of this report. The tabulations are useful because managers can compare different scenarios by comparing corresponding rows or columns of the appropriate tables.

1.3.2 Explanation of Tables. Results of the models of the wild population appear in Tables 6 through 21. The tables are organized as follows. A particular set of reproductive and mortality schedules will be referred to as a model. Because of our uncertainty about the levels of inbreeding depression and of environmental variation (EV) in demographic parameters, all wild-population models were run with three different levels of inbreeding depression, two levels of environmental variation in mortality rates, and with and without catastrophes. This means there are twelve different permutations of these basic parameters for each model. Each permutation will be referred to as a *scenario*. These scenarios are presented in a single table that is labelled with the name of the model it represents.

The simulations are organized within the table so that the scenarios that incorporate the most optimistic assumptions about inbreeding depression and environmental variability appear at the top of the table and the least optimistic appear at the bottom. For example, the results of the six scenarios that include catastrophic events are displayed in the bottom half of the table; the results from the six scenarios that do not include such events are presented in the top half. Within the "No Catastrophes" group, the results are presented in order of the increasing effects of inbreeding depression. Finally, for each level of inbreeding depression, two levels of environmental variation are considered, and the results of these two permutations are displayed on consecutive lines of the tables.

Each line of the table indicates:

- the level of inbreeding depression (**Ind Dpr**);
- environmental variation in mortality rates (**EV**, designated as "Low" or "High"),
- percent of females breeding in each year (**% Brd**);
- maximum clutch size (**Max Lit**);
- mortality of hatch-year, juvenile, and adult birds (**Mortality: HY, Juv, Ad**, respectively);
- deterministic and stochastic r (**Det r** and **Stoch r**);
- the standard deviation (**SD**) of the stochastic r ;

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the probability of extinction, the population size and SD of population size, and expected heterozygosity at 20, 50, and 100 years (**PE**, **N**, **SD**, **H**); and, the median time to extinction (**TE**).

Stochastic growth rates will often differ substantially from deterministic growth rates. Deterministic growth rates ignore environmental sources of variability and events such as random deviations from an even sex ratio. In very small populations like those of the 'Alala, such probabilistic events can have very large effects. Even positive stochastic growth rates do not guarantee population persistence since they are average values. Many entries in the tables demonstrate that a positive stochastic r can be accompanied by a moderately high probability of extinction. In these cases, extinction may be due to decreases in population size during some years, even though the average growth rate is positive.

1.4 Results.

1.4.1 Basic Model. All basic models predicted a probability of extinction of 59 percent or more during the next 100 years. Tables 6 and 7 show the results for simulations with initial populations of 12 and 15 animals, respectively. These are models of the current population parameters, without incorporation of any effects of potential management options.

The different initial population sizes produce qualitatively and quantitatively similar results. Stochastic growth rates (r) are negative for all scenarios in both tables. The greatest difference is seen in the best-case scenario of no inbreeding depression, low environmental variation in mortality, and no catastrophes. The model that uses an initial population size of 15 individuals yields a 59 percent probability of extinction in 100 years, and a median time to extinction of 80 years. Under the same assumptions, the model with an initial population size of 12 predicts a 67 percent probability of extinction and a median time to extinction of 65 years.

In the worst-case scenario (high inbreeding depression, high environmental variability, and possible catastrophes) both sets of simulations produce a 100 percent probability of extinction in 100 years. The median time to extinction is 28 years when the population initially contains 15 individuals, and 24 years when it initially contains 12 individuals. Based on these results, we conclude that the presence of a few more individuals will not substantially decrease the probability of extinction nor increase the persistence time.

Because increasing the current population size has such a small effect on the projected fate of the population, the initial value of 12 was used in the management models. This allows us to gauge the effectiveness of the management options assuming that there are about 12 animals currently extant. If the actual current population size is somewhat larger, the results described below will still hold approximately, and will still allow us to compare the effectiveness of the

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various management strategies that have been proposed.

1.4.2 Management Models--Predicted Stability of Population.

1.4.2a Predator and Disease Control. As described earlier in this section, we modelled four different levels of effectiveness of predator control. The results of these three different models are shown in Tables 8, 9a, 9b, and 10. Table 8 indicates that a low-effectiveness program somewhat reduces the probability of extinction if inbreeding depression is low and if catastrophes are not included in the models. Even under the most optimistic assumptions, the population becomes extinct with a probability of 25-36 percent over the next 100 years.

Predator control with moderately high effectiveness can substantially reduce the probability of extinction if catastrophes are not included in the models (Table 9a, top half). However, even without catastrophic events, the probability of population extinction within 100 years is greater than 25 percent if moderate or high inbreeding depression is included in the model.

Including increased reproductive rates in the above model (Table 9b) substantially decreases the extinction rate only for moderate and high levels of inbreeding in the "no catastrophe" models. For these scenarios, the rate of extinction is reduced below 25 percent. The rate of loss of heterozygosity is slowed in all the scenarios of Table 9b when compared with Table 9a.

If the possibility of catastrophic events is included in this model, extinction probabilities are quite high (between 69 and 94 percent) depending on the amount of inbreeding depression (Tables 9, bottom half). The amount of genetic variability that is maintained over 100 years is between 70 and 77 percent if catastrophes are excluded and between 65 and 75 percent if they are included.

When predator-control effectiveness is modelled as extremely effective (reducing the total amount of hatch-year mortality to half its current value), the chance that the population persists for 100 years is increased, especially when the possibility of catastrophes is excluded (Table 10). In the "No Catastrophe" scenarios, extinction probabilities are 5 percent or less in cases of low or moderate inbreeding depression, and about 15 percent if inbreeding depression is high. Heterozygosity persists at about 80 percent of its original value in these simulations.

When catastrophic events are included, the probability of extinction increases to 44 to 85 percent, depending on the amount of inbreeding depression. Between 71 and 76 percent of the original heterozygosity is maintained.

1.4.2b Disease Control or Salvaging of chicks. As expected, the model of disease control produced results very similar to those for the low-effectiveness predator control model (Table 11). As explained above, combined disease and predator control is not likely to produce

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results outside the range spanned by the three predator-control models. Consequently, we will not discuss these models further.

1.4.2c Supplemental feeding. Supplemental feeding models produce the results shown in Tables 12 and 13. Table 12 summarizes the fate of the current population if supplemental feeding were implemented and if that feeding resulted in a modest productivity increase of 10 percent. Table 13 presents predictions for a supplemental feeding program that increased the productivity of the current population by 25 percent.

Comparing these results to those from the basic model (Table 6) reveals that a 10 percent increase in productivity has little effect on the current population projections. If a 25 percent increase in productivity can be achieved through this technique, the probability of extinction is lowered and the persistence time is increased when inbreeding depression is low and catastrophes are excluded. The most optimistic scenarios predict a 30 percent chance of extinction within 100 years and 32 percent loss of genetic variability if extinction is avoided.

1.4.2d Double-clutching. Double-clutching techniques could potentially be used to increase the productivity of the wild population. They could also be used to supplement the captive population. Since this technique has never been applied to 'Alala, there is some uncertainty as to its possible effectiveness. Four levels of productivity increase were modelled in order to simulate the possible outcomes of either (1) use of half of these chicks for reintroduction, while retaining the other half for the captive propagation program, or (2) use of all chicks resulting from pulling clutches in a reintroduction program.

1.4.2e Double-clutching I--reintroduction of half the chicks. Tables 14 and 15 represent the range of results that could be expected from such a program. We considered productivity increases of 33 percent (Table 14) and 50 percent (Table 15). When catastrophes are not included, probabilities of extinction are reduced below those in the basic model. Extinction still occurs in over half the simulations when inbreeding depression is high, however. Persistence times are approximately double the times in the basic model. The level of heterozygosity is 70 to 80 percent of its original level after 100 years.

Extinction probabilities in the face of catastrophic events are 65 percent or more in all scenarios. Persistence times are slightly higher than in the basic model, but are always less than 50 years. Heterozygosity falls to 60 to 80 percent of the original value.

1.4.2f Double-clutching II--reintroduction of all the chicks. Productivity increases of 60 and 100 percent were used to simulate this management option. Without catastrophes, the probability of extinction is reduced considerably, compared to the basic model (Tables 16 and 17). At the high levels of productivity increase exemplified in Table 17, the population may have a good chance of persisting for 100 years, but if inbreeding depression is high, there is still about a 15 percent probability of extinction. About 75 percent of the original genetic

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variation is maintained when a population does persist.

Catastrophes will cause the population to become extinct in more than half the runs of this model. The only exception is when both inbreeding depression and environmental variability are low in Table 17. In this case the probability of extinction is 46 percent. Genetic variability falls to 60 to 80 percent of current levels.

1.4.2g Combined Management Strategy I-- non-invasive combination. The combined effects of predator control, disease control, and supplemental feeding are presented in Table 18. The results are very similar to those presented in Table 17 (the high-effectiveness double-clutching model). At low- to-moderate levels of inbreeding depression and no catastrophes, the population has a good chance of persistence for at least 100 years. If catastrophes are included in the model, the probability that the population will persist for 100 years drops to less than 50 percent. Genetic variability will be retained at approximately 70 to 80 percent of current levels.

1.4.2h Combined Management Strategy II-- combination of nest-site manipulation and non-invasive techniques. The combination of predator and disease control and double-clutching techniques (with reintroduction of half the chicks) produce the results shown in Table 19. Extinction probabilities are very low when there are no catastrophes. Average population sizes are near the carrying capacity and about 85 percent of the original genetic variability is maintained.

When Catastrophes are included in the model, the probability of extinction varies between 35 and 59 percent, depending on the severity of inbreeding depression and the amount of environmental variability in mortality rates (Table 19). About 75 percent of the original genetic variability is retained after 100 years when extinction is avoided.

1.4.2i Supplementation from the captive population. Low levels of supplementation from the captive population (1 male and one female bird per year for 20 years) yield the results in Table 20. If catastrophes are excluded and inbreeding depression is low, the probability of extinction within 100 years is below 10 percent. This probability increases to around 20 percent when inbreeding depression is moderate or high. When catastrophes are included, the likelihood of extinction rises to 78 to 92 percent.

The stochastic growth rate (r) for these models is calculated for the years after cessation of supplementation. The short-term effects of supplementation can be judged by considering the state of the population at year 20. For all the scenarios on Table 20, the population grows during years 1 through 20, indicating that supplementation is more than compensating for mortality. However, the growth rate r , calculated for the years during which no supplementation occurs, is negative for most of the scenarios on this table. This indicates that the population is not able to sustain itself after the period of supplementation.

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Higher levels of supplementation (2 females and two males per year for 20 years) do not drastically improve the situation (Table 21). The stochastic growth rate remains negative for all but the most optimistic scenarios. The probability of extinction is below 10 percent if catastrophes are excluded, but rise to high values (68 to 80 percent) when catastrophes are included.

1.4.3 Graphical presentation of results. Figures 1 and 2 provide a graphical comparison of the performance of the various models. The predicted probability of extinction is portrayed as a box with height equal to the number of replicate populations, out of 100, that went extinct within 100 years. The predicted extinction rate for each management model is that predicted by assuming a moderate level of inbreeding depression and low environmental variability in mortality rates. Letters before model names refer to (L) low effectiveness, (M) moderate effectiveness, and (H) high effectiveness. Numbers after basic models refer to the number of animals assumed to be in the current population. Figure 1 presents the results for models when the effects of catastrophes are ignored. Figure 2 shows corresponding results when catastrophes are included in the models.

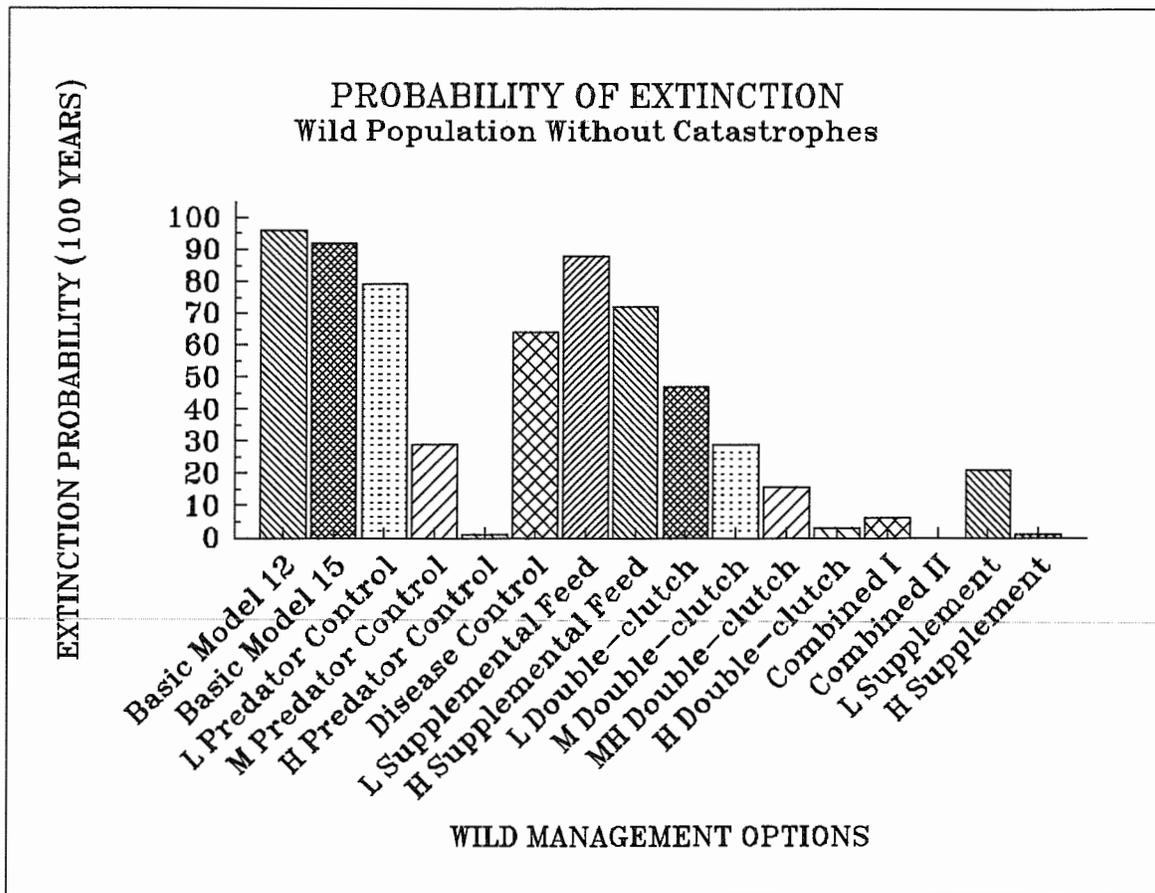


Figure 1. Probability of extinction is x100.

1.5 Conclusions.

Population and Habitat Viability Analyses indicate that the current demographic parameters of the wild 'Alala population yield predictions of likely extinction within 100 years. The fate of the population can be affected through the management options that have been proposed, although the degree to which such strategies improve the chances of persistence vary considerably.

Several of the management options appear to have little effect on the basic population projections. Low-effectiveness predator control, salvaging of ill or vulnerable chicks, supplemental feeding, and disease control, implemented as stand-alone strategies, have very small effects, or have effects that are only apparent under the most optimistic of assumptions

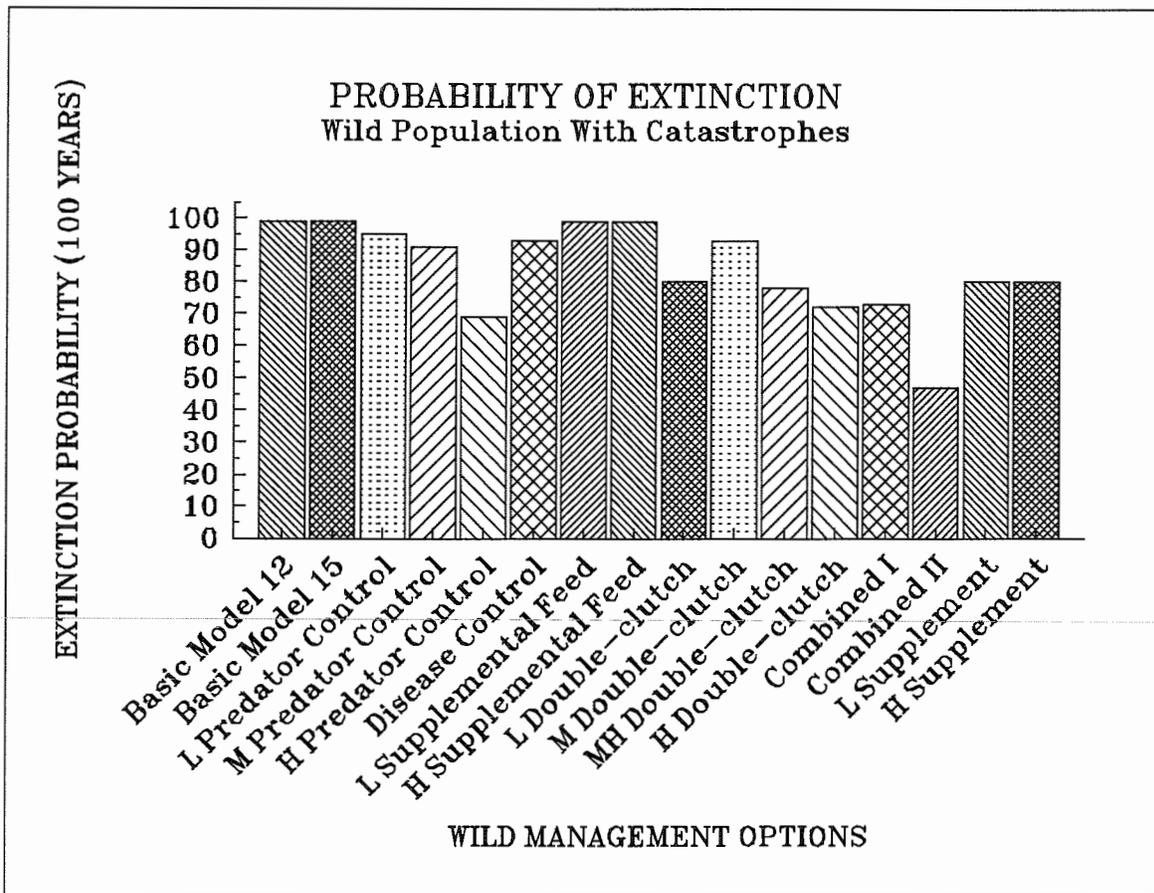


Figure 2. Wild population with catastrophes. Probability of extinction is x100.

about environmental variability and the genetic properties of the population. If one makes the assumption that predator and disease control can have very large effects on hatch-year mortality, these techniques can substantially improve the outlook under some sets of assumptions. Effective double-clutching techniques can also improve the probability of population persistence quite dramatically, under the same sets of assumptions.

The most effective management strategy that we evaluated was the application of the combination of double-clutching techniques, and predator and disease control. Even though we assumed only moderate effectiveness of the individual techniques, the improvement in the probability of extinction and in the persistence time of the population exceeded that for any single technique applied with very high effectiveness.

The most disturbing aspect of this analysis is the apparent susceptibility of the wild

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population to catastrophic disease, weather, or volcanic activity. Even the most effective "combined" strategy could not insure the persistence of the population in the face of such catastrophes. The simulations predict 100-year extinction probabilities of 35 percent or higher even if the 'Alala suffer no inbreeding depression at all.

The most effective way of reducing such susceptibility would be the establishment of distinct subpopulations of wild 'Alala. Spatially separate subpopulations would presumably be somewhat independent of each other with respect to the occurrence of catastrophes. This would lessen the probability that the entire population would become extinct even if one subpopulation experienced catastrophic declines. Theoretically, the probability that two subpopulations will suffer independent catastrophic events at the same time is the square of the probability in either subpopulation.

Immediate establishment of separate subpopulations may be impractical. In this case, the management of the captive and wild populations as a "metapopulation" may be the best way to minimize the chance of catastrophic loss of the wild population. Several metapopulation models are discussed in Section 3. While these models yield more optimistic predictions, implementation of such a program cannot begin until the captive population is itself stabilized. The next section presents the PVA for the captive population of 'Alala.

2. ANALYSIS OF CAPTIVE POPULATIONS

2.1 Population Biology Parameters.

2.1.1 Population Size and Carrying Capacity. The current population size for the captive 'Alala is 11. A goal for target population size has not been established. Population sizes of 50 and 125 were tested. Additional sizes (carrying capacity) may be run to help guide management decisions on the goals for preservation of genetic diversity and on the duration of the captive program.

2.1.2 Reproductive Rates. Reproductive rates were computed in two different ways-- using the number of eggs laid as a measure of offspring production, and using the number of chicks hatched as a measures of offspring production. Egg-laying rate was chosen as the measure of reproductive rate because it allows greater sensitivity in modelling the effects of proposed management strategies. These parameters were estimated based on reproductive histories of captive birds and are summarized in Table 22. Calculations are summarized in Table 23. All years in which females were considered sexually mature were included in the data set (2 years and older).

2.1.3 Mortality. Like the values for wild birds, juvenile mortality was estimated in two different ways. Both the numbers of eggs laid and the number of chicks hatched were tested

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as measures of offspring production. Hatch-year mortality (when eggs are used as the birth statistic) was estimated by dividing the number of eggs hatched by the number of eggs which had a chance to hatch (eliminating those eggs of unknown status and fertile, broken eggs) This equals $7/(82-16-3)$ or 11.1 percent. All chicks that hatched survived to one year, so second-year (juvenile) mortality was set to 0.

Adult mortality was based on life-table analysis from the SPARKS (Small Population Analysis and Record Keeping System) studbook file. The mean value for males and females was 7.6 percent. Slight differences in male (8.4 percent) and female (6.8 percent) rates are attributed to small sample size.

Because the captive environment is presumably less variable than the natural environment of the crows, we have chosen to model only one moderately low level of environmental variation. The value used for the standard deviation of mortality rate was 10 percent.

2.1.3 Lifespan. As in the models of the wild population, 30 years was used as the lifespan of captive 'Alala.

2.1.4 Catastrophes. The Working Group believes disease is the major catastrophic threat to the captive population. Meteorological and geological catastrophes are not thought to be a substantial threat to the captive population. A 5 percent probability of a catastrophic disease within 100 years was included in some of the models. Because of the continuous maintenance and care available to captive birds, the effect of disease in the captive population is less than that modelled for the wild population. The models assume that the population suffers a 50 percent reduction in reproduction and survival in the event of a disease epidemic.

2.1.5 Inbreeding Depression. The poor captive breeding success of 'Alala and the production of a relatively large proportion of abnormal eggs and chicks has led many biologists to speculate that the population is suffering from inbreeding depression. In fact, the captive birds did demonstrate high band-sharing coefficients in a DNA fingerprint analysis (Duvall et al. 1991). Some of the individuals in the current population are known to have high inbreeding coefficients. However, inbreeding itself does not always lead to inbreeding depression. As stated in the section on inbreeding in wild 'Alala, the degree of inbreeding depression that a species experiences is not necessarily related to the amount of inbreeding that is presently occurring. All the models were therefore constructed with 0.0, 3.14, and 6.28 lethal equivalents, just as in the models of the wild population. To reiterate, the low value corresponds to no inbreeding depression at all and the high value to two times the average inbreeding depression in captive mammalian species.

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2.2 Management Strategies.

In addition to the basic models, we have constructed models of several proposed management scenarios. Table 24 presents a summary of the reproductive and mortality schedules that were incorporated into the models of the captive management strategies discussed below.

2.2.1 Improved hatchability of eggs. This scenario is incorporated into the models by reducing juvenile (hatch year) mortality from 89 percent to 64 percent. The latter is the rate of juvenile mortality that would be observed in the captive flock if hatchability were raised to the level observed for wild eggs.

2.2.2 Prevention of breakage. Complete prevention of breakage would result in a 35 percent increase in productivity in the captive population. This assumes that the eggs that have been broken in the past were a random sample of all eggs that were laid. That is, the eggs were not broken because they were infertile or defective in some other way. We constructed these models to reflect the increase in productivity resulting from minimizing egg breakage.

2.2.3 Improved hatchability of eggs and breakage prevention. We also constructed a model that incorporates both improved hatchability and prevention of breakage. This was accomplished by simply combining the mortality rate reduction embodied in the first model with the productivity increase characterizing the second. We expected the model of this two-pronged strategy to yield more optimistic results than either of the two strategies considered individually.

Because this is the best-case scenario for the management of the captive population independently from the wild population, we tried to determine if a sustainable harvest, for the purposes of reintroduction, could be conducted with a captive population managed under this scenario. We therefore performed an additional set of simulations in which 2 female and 2 male birds are harvested each year, starting in year 20. Year 20 was chosen because the captive population should be close to carrying capacity by that time. If the populations should actually reach carrying capacity earlier or later than this, the model will still provide insight into the sustainability of a harvest that is begun whenever carrying capacity is reached.

2.2.4 Supplementation from the wild population by double-clutching of wild nests. Two levels of supplementation are modelled. Low level supplementation is the addition to the captive population of 1 female and 1 male chick from the wild population every year. High supplementation is 2 female and 2 male chicks per year. Supplementation at these rates is maintained for 20 years, after which supplementation ceases. Inspection of the 20-year columns of the tabulated results will give an indication of the short-term effects of this management option.

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2.3 Description of Simulations and Output.

2.3.1 Simulations. Simulations for the captive population were run in the same manner as was described for the wild population in Section 1.3. Again, all combinations of the basic assumptions (level of inbreeding depression, incorporation or absence of catastrophes from the model) and the management strategies were modelled. The results will be presented in tabular as well as in the text of the discussion a conclusion section of further drafts of this report. The tabulations are useful because managers can compare different scenarios by comparing corresponding rows or columns of the appropriate tables.

2.3.2 Explanation of Tables. Tables are organized in the same manner as those for the wild population, with the following exceptions. We were interested in the effects of different carrying capacities of the captive facilities. The results for the two different values appear in the same tables. Results produced from simulations assuming the captive program could support 125 animals appear in the top half of each table. Results produced by assuming a maximum capacity of 50 animals appear in the bottom half of the tables.

We chose to model only one level of environmental variability in mortality rates. Consequently, the column labelled "EV in mort" has been deleted from the tables for the captive population models.

2.4 Results.

2.4.1 Basic Model. Current demographic parameters yield predictions of almost certain extinction of the captive population within 100 years. Table 25 presents results for three levels of inbreeding depression, inclusion and exclusion of catastrophes, and two different values for the carrying capacity of captive facilities. Deterministic r values are below zero for all sets of assumptions. The probability of extinction is always above 90 percent after 100 years. Median time to extinction is between 19 and 37 years, depending on the assumptions about inbreeding depression, carrying capacity, and catastrophes. In the unlikely event that the population persists, levels of genetic variability decline to 43 to 64 percent of original levels.

2.4.2 Management Models--Predicted Stability of Population.

2.4.2a Improved Hatchability. Improving hatchability in the captive population decreases the probability of extinction substantially, particularly if catastrophes are excluded from the models (Table 26). Without catastrophes, the extinction rate is below 5 percent after 100 years, population size is near carrying capacity, and heterozygosity is 66 percent to 81 percent of the original value.

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When catastrophes are included in the simulations, extinction rates are high (37 to 68 percent) if inbreeding depression is moderate or high. If inbreeding depression is low, extinction rates are below 30 percent. Maintained genetic variability is also lower in these scenarios.

Deterministic r values are positive and large in all the improved-hatchability scenarios, but catastrophic disease events appear to overwhelm even large growth rates.

2.4.2b Prevention of Egg Breakage. This management strategy appears to have little effect on the predicted fate of the captive population (compare Table 27 to Table 25). Extinction probability and median time to extinction are barely reduced below the values reported for the basic model.

2.4.2c Improved Hatchability and Prevention of Egg Breakage. As expected, when the two methods above are combined, more optimistic predictions can be made for the future of the captive population. Table 28 demonstrates improved chances for population survival for all scenarios. However, scenarios that include catastrophes still predict a substantial likelihood that the population will become extinct within 100 years.

In Table 29, the sustainability of harvest is modelled. In general the scenarios that exclude the possibility of catastrophe predict that a harvest of 2 pairs of birds per year could be sustained. The only exception is the scenario with high inbreeding depression and a carrying capacity of 50. In this case, Vortex predicts an probability of extinction of 51 percent. This is the clearest example that we obtained of an effect of carrying capacity on the expected probability of extinction. (The expected effects of carrying capacity on numbers of animals and on genetic variability are obvious and the results for all the models conform to expectations.)

The scenarios with catastrophes do not perform nearly so well. It should be noted, however, that these are also the scenarios in which the population generally has not reached carrying capacity before harvest begins. Considering that these same scenarios predict a substantial probability of population extinction even with no harvesting (see Table 28) this probability could only increase with the introduction of a harvest.

2.4.2d Low Rate of Supplementation from the Wild Population. Table 30 shows that this option decreases the probability of extinction when compared to the basic model, but not substantially. For all scenarios, extinction occurs in more than 60 percent of the simulation runs. Deterministic r values are negative in all cases. This indicates that the supplementation provides only a temporary boost to the population growth rate. After supplementation ceases, the population size resumes its downward trend.

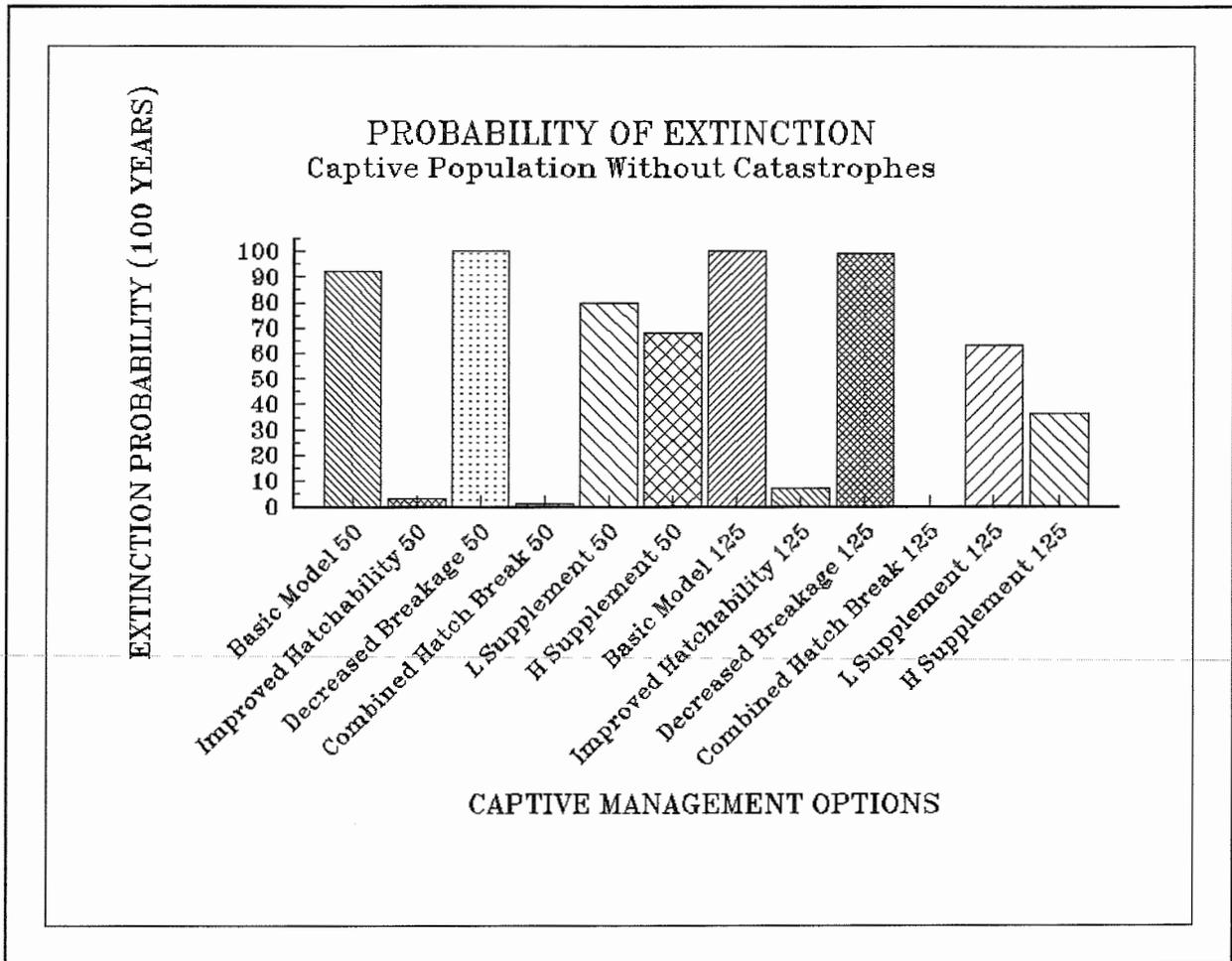


Figure 3. Probability of extinction is x100. Numbers after model names refer to the captive carrying capacity.

As is the case with the wild population, catastrophes pose a very serious threat to population persistence, even under the most successful management strategies. The establishment of two or more spatially separate captive breeding facilities is the best way of reducing the risk of extinction due to catastrophic disease outbreaks. Management of the wild and captive populations as metapopulations, as described in Section III, will also reduce this risk.

3. ANALYSIS OF METAPOPOPULATIONS

3.1 Population Biology Parameters.

Three different models were constructed to describe the unified management of both captive

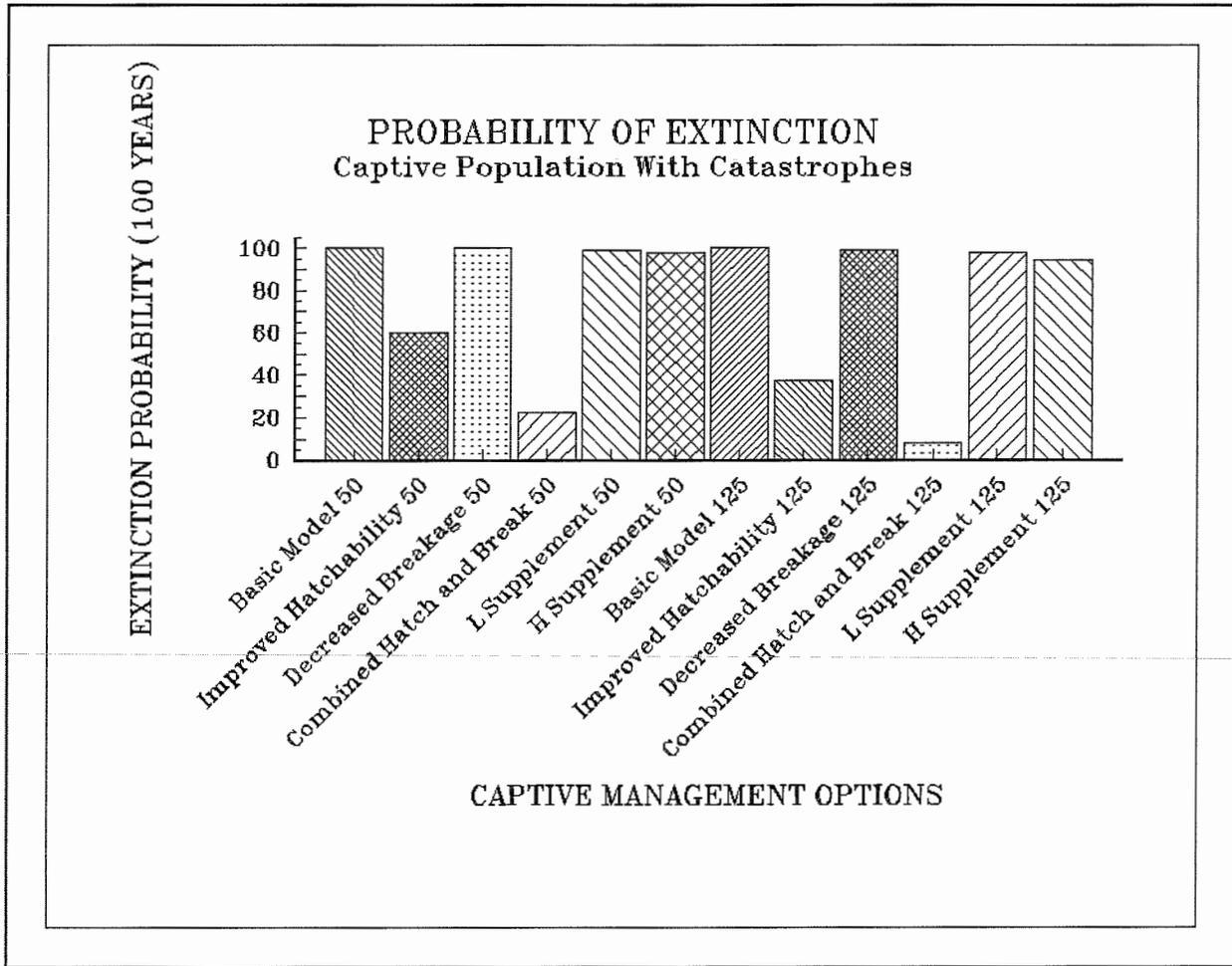


Figure 4. Probability of extinction is x100. Numbers after the model names refer to captive carrying capacity.

and wild populations. The basic approach was to combine one of the captive management strategies with one of the wild management strategies. A migration rate of 5 percent per year was then introduced between the captive and wild subpopulations.

Four different combinations of strategies were constructed. All four models assumed the captive population would be managed under the "Improved hatchability" strategy described in Section 2. This captive management plan was then combined with one of two non-invasive forms of wild management and with one of two more invasive forms. The non-invasive forms of wild-population management correspond to the "Predator and Disease Control" strategy and the "Combined Management Strategy I" of Section 1. "Combined Strategy I" includes supplemental feeding as well as disease and predator control. The invasive forms

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correspond to the "Double-clutching I" (reintroduction of half the chicks) and the "Combined Strategy II" (reintroduction of all chicks) strategies of Section 1.

All the biological parameters correspond exactly to those used in the single-population models. The effects of the strategies on the population parameters are also the same as those assumed in the single-population models.

3.2 Results.

Results for the metapopulation models are shown in Tables 32 through 35. Tables 32 and 33 present the predictions for population viability when non-invasive methods of wild management are combined with captive management that increases the hatchability of eggs in the captive population. Tables 34 and 35 present the results when double-clutching alone or double-clutching and predator and disease control are used in wild management. All the models assume migration between the wild and captive populations of 10 percent per year.

3.2.1 Metapopulation Model 1. Increased hatchability in the captive population and predator and disease control in the wild population produce extinction probabilities of 20 to 50 percent if inbreeding effects and catastrophes are included in the models (Table 32). Extinction occurs with 8 percent probability or less if there is no inbreeding depression, even with catastrophes. This represents moderate improvement over the best single-population strategies.

3.2.2 Metapopulation Model 2. If productivity gains through supplemental feeding are added to the above model, the predictions in Table 33 are produced. The probability of extinction is now 33 percent or less in all cases. The amount of inbreeding depression and the carrying capacity of the captive population have noticeable effects on the predictions, however.

3.2.3 Metapopulation Model 3. Combining low-effectiveness double-clutching methods of wild management with improvements in captive hatchability produce the results in Table 34. These results are very similar to those presented for Metapopulation Model 1, with slightly higher probabilities of extinction.

3.2.4 Metapopulation Model 4. Table 35 presents results for a unified strategy of management that incorporates double-clutching, predator, and disease control in the wild population with improved hatchability in the captive population. This strategy appears to be the most effective metapopulation approach. Even with high levels of inbreeding depression the probability of extinction is only 10-14 percent after 100 years. Lower inbreeding depression yields extinction probabilities of 10 percent or less, even at low carrying capacity. The carrying capacity of the captive population does not have much of an effect on the

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correspond to the "Double-clutching I" (reintroduction of half the chicks) and the "Combined Strategy II" (reintroduction of all chicks) strategies of Section 1.

All the biological parameters correspond exactly to those used in the single-population models. The effects of the strategies on the population parameters are also the same as those assumed in the single-population models.

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Results for the metapopulation models are shown in Tables 32 through 35. Tables 32 and 33 present the predictions for population viability when non-invasive methods of wild management are combined with captive management that increases the hatchability of eggs in the captive population. Tables 34 and 35 present the results when double-clutching alone or double-clutching and predator and disease control are used in wild management. All the models assume migration between the wild and captive populations of 10 percent per year.

3.2.1 Metapopulation Model 1. Increased hatchability in the captive population and predator and disease control in the wild population produce extinction probabilities of 20 to 50 percent if inbreeding effects and catastrophes are included in the models (Table 32). Extinction occurs with 8 percent probability or less if there is no inbreeding depression, even with catastrophes. This represents moderate improvement over the best single-population strategies.

3.2.2 Metapopulation Model 2. If productivity gains through supplemental feeding are added to the above model, the predictions in Table 33 are produced. The probability of extinction is now 33 percent or less in all cases. The amount of inbreeding depression and the carrying capacity of the captive population have noticeable effects on the predictions, however.

3.2.3 Metapopulation Model 3. Combining low-effectiveness double-clutching methods of wild management with improvements in captive hatchability produce the results in Table 34. These results are very similar to those presented for Metapopulation Model 1, with slightly higher probabilities of extinction.

3.2.4 Metapopulation Model 4. Table 35 presents results for a unified strategy of management that incorporates double-clutching, predator, and disease control in the wild population with improved hatchability in the captive population. This strategy appears to be the most effective metapopulation approach. Even with high levels of inbreeding depression the probability of extinction is only 10-14 percent after 100 years. Lower inbreeding depression yields extinction probabilities of 10 percent or less, even at low carrying capacity. The carrying capacity of the captive population does not have much of an effect on the

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results. Genetic variability is maintained at 81 to 87 percent of current levels.

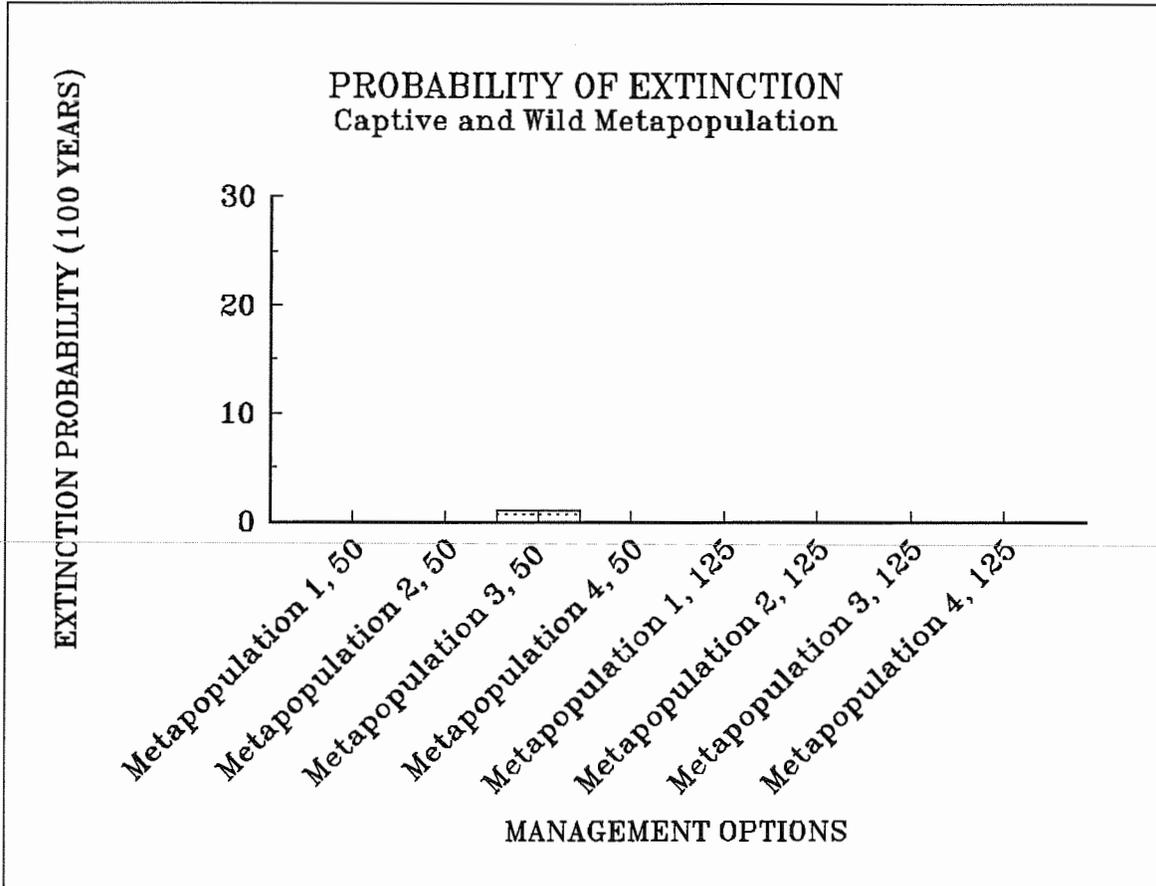


Figure 5. Metapopulation models without catastrophes. Probability of extinction is $\times 100$.

3.2.5 Graphical presentation of results. Figures 5 and 6 are the graphical representation of extinction probabilities for the metapopulation models. They were constructed in the same manner as were figures 1 through 4.

3.3 Conclusions.

The results of the metapopulation models indicate that greater stability of both the captive and wild 'Alala can be provided by an integrated management plan that includes interchange of animals between captivity and the wild. All these models included the catastrophic events

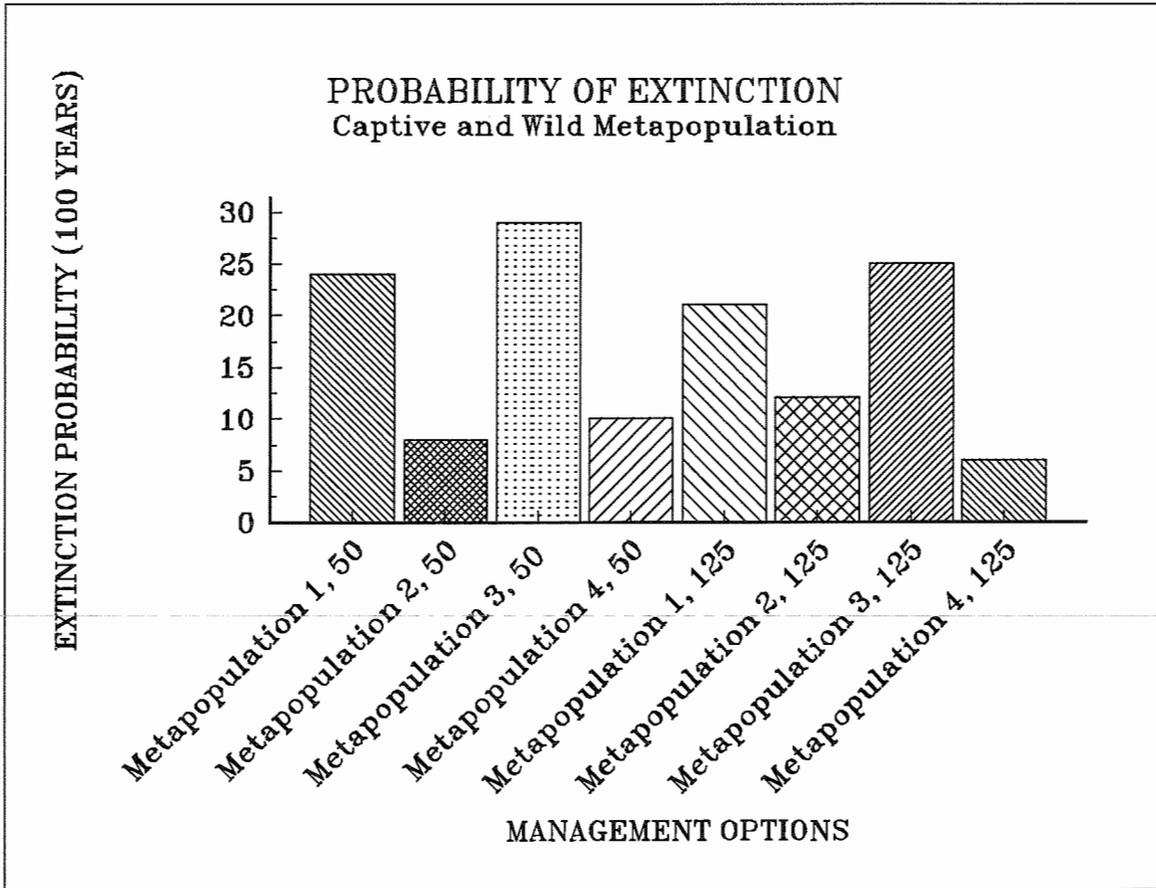


Figure 6. Metapopulation models with catastrophes. Probability of extinction is x100.

that appear devastating in the single-population (wild or captive) models. Even so, a low probability of extinction can be achieved if the multi-faceted approach exemplified by Model 4 is adopted. This approach has the added benefit of maintaining more genetic variability than any of the other single- or metapopulation models considered.

4. RECOMMENDATIONS

The results of the PHVA suggest that short-term management efforts be focused on instituting double-clutching and field-incubation techniques as well as predator and disease control programs for the wild population. Prevention of further degradation of the 'Alala's habitat is, of course, essential for the long-term survival of the species. In fact, this analysis suggests that extensive habitat restoration may be necessary, since the birds are very unlikely to

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maintain or increase their numbers without considerable human intervention.

The efforts in captive management should be primarily directed toward increasing the rate successful hatching. Establishing a second captive facility and reintroduction of birds into a second wild location should also be priorities, as multiple populations are the best insurance against catastrophic extinction. Finally, a commitment should be made to a long-term program of interchange between the captive and wild populations. Management of captive and wild animals as a metapopulation provides the best hope of insuring the continued existence of the 'Alala.

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Table 1. Percentage of breeding age female 'Alala (2 years or older) which were in a territorial pair but did not appear to initiate egg laying (NRC Report, 1992).

Year	Reproductive Pairs Found	Non-reproductive Pairs on Territories	Total Number of Pairs	Proportion Not Breeding
1970	3	0	3	0/3 = 0
1971	1	2	3	0.66
1972	5	2	7	0.29
1973	9	1	10	0.10
1974	12	2	14	0.14
1975	8	4	12	0.33
1976	11	4-5	15-16	(0.27-0.31) 0.3
1977	9	0	9	0
1978	9	1	10	0.1
Total	67	16 (17)		0.21 SD=0.21

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Table 2. Proportion of breeding age females producing different numbers of young per year based on data collected by Giffin (1983).

# Fledged	# Nests	Proportion Fledged	Adjusted Proportion Fledged ^a
0	8	0.36	0.36 X 0.79 = 0.29
1	9	0.41	0.32
2	5	0.23	0.18
Total	22	1.00	0.79

^a The estimate of non-reproductive pairs on territories from Table A indicates that on average only 79 percent of territorial pairs initiate eggs laying ($1 - 0.21 = 0.79$). The proportion of females producing different clutch sizes was adjusted to total 0.79.

Total proportion of non-breeding females:

Non-reproductive pairs on territories (from Table A)	0.21
Females which attempted to breed, but were unsuccessful (see above)	0.29
Total proportion of breeding age females not producing	0.50
SD (from Table A)	0.21

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Table 3. Percentage of breeding age female 'Alala (2 years or older) producing different number of young per year based on data collected by Temple and Jenkins (1981).

# Young	# Nests	Proportion of Females	Adjusted Proportion Hatched ^a
0	4	4/11 = 0.36	0.36 X 0.79 = 0.29
1	3	0.27	0.21
2	3	0.27	0.21
3	1	0.10	0.08
Total	11	1.00	0.79

^a The estimate of non-reproductive pairs on territories from Table A indicates that on average only 79 percent of territorial pairs initiate eggs laying ($1 - 0.21 = 0.79$).

Total proportion of non-breeding females:

Non-reproductive pairs on territories (from Table A)	0.21
Females which attempted to breed, but were unsuccessful (see above)	0.29
Total proportion of breeding age females not producing	0.50
SD (from Table A)	0.21

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Table 4a. Historical Models. Predictions of current population status based on historical population size.												
Label	Input Values					Results						
	% Brd	Max Lit	HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H
Projections based on population size in 1974 (N=35)												
Model 1a	50	3	67	10	10	0.020	-0.005	14	0	37	20	94
Model 2a			67	10	19	-0.060	-0.100	20	29	11	8	93
Model 3a			67	10	27	-0.132	-0.180	28	70	6	2	81
Model 4a			67	50	10	-0.040	-0.060	17	1	15	9	90
Model 5a			75	10	10	-0.007	-0.030	14	1	24	16	92
Projections based on population size in 1980 (N=19)												
Model 1b	50	3	67	10	10	0.02	0.00	0.14	1	22	10	92
Model 2b			67	10	19	-0.06	-0.12	0.23	25	8	4	84
Model 3b			67	10	27	-0.132	-0.26	0.37	90	5	0	88
Model 4b			67	50	10	-0.04	-0.06	0.19	2	11	6	89
Model 5b			75	10	10	-0.007	-0.05	0.16	0	12	7	7

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Table 4b. Historical Models. Predictions of current population status based on historical population size. Results based on simulations of populations for either 18 years (Models 1a to 5a) or 12 years (Models 1b to 5b).													
Label	EV Mort	Input Values					Results						
		% Brd	Max Lit	HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H
Projections based on population size in 1974 (N=35)													
Model 1a	Low	50	3	67	10	10	0.023	0.004	0.093	0	40	14	94
Model 1a	High			67	10	10	0.023	-0.008	0.132	0	35	20	94
Model 2a	Low			67	10	19	-0.056	-0.095	0.169	25	10	6	85
Model 2a	High			67	50	19	-0.056	-0.106	0.214	29	10	7	83
Projections based on population size in 1980 (N=19)													
Model 1b	Low	50	3	67	10	10	0.023	0.0015	0.119	0	21	9	92
Model 1b	High			67	10	10	0.023	-0.003	0.148	0	21	12	92
Model 2b	Low			67	10	19	-0.056	-0.099	0.183	15	8	4	84
Model 2b	Highl			67	50	19	-0.056	-0.118	0.243	26	8	5	82

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Table 5. Reproductive and Mortality Schedules used in the Simulation Models.											
Model Name	Table #	Percent of Females that Produce Clutches of Size:							Age-Specific Mortality Rate		
		0	1	2	3	4	5	6	HY	Juv	Ad
Basic 12	Table 5	50	21	21	8	0	0	0	67	10	10
Basis 15	Table 6	50	21	21	8	0	0	0	67	10	10
Predator Control L	Table 7	50	21	21	8	0	0	0	60	10	10
Predator Control M	Table 8	50	21	21	8	0	0	0	50	10	10
Predator Control H	Table 9	50	21	21	8	0	0	0	34	10	10
Disease Control	Table 10	50	21	21	8	0	0	0	57	10	10
Supplemental Feeding L	Table 11	50	15	20	10	5	0	0	67	10	10
Supplemental Feeding H	Table 12	40	25	24	11	0	0	0	67	10	10
Double-clutching Low	Table 13	35	25	30	5	5	0	0	67	10	10
Double-clutching Mod	Table 14	35	20	30	10	5	0	0	67	10	10
Double-clutching M/High	Table 15	35	20	20	20	5	0	0	67	10	10
Double-clutching High	Table 16	35	12	15	25	10	2	1	67	10	10
Combined I	Table 17	40	25	24	11	0	0	0	67	10	10
Combined II	Table 18	35	26	26	13	0	0	0	67	10	10
Supplement from Captive L	Table 19	50	21	21	8	0	0	0	67	10	10
Supplement from Captive H	Table 20	50	21	21	8	0	0	0	67	10	10

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Table 6. 'Alala Wild Population. Basic Model--initial population size of 12 individuals.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	50	3	67	10	10	0.023	-0.013	0.157	10	14	8	82	37	22	23	66	67	53	54	62	65
	High						0.023	-0.020	0.169	13	15	9	82	50	20	15	66	73	33	31	57	48
3.14	Low						0.023	-0.036	0.170	18	12	7	83	63	11	8	67	96	8	6	60	41
	High						0.023	-0.040	0.179	18	11	6	83	70	10	9	70	96	5	1	60	38
6.28	Low						0.023	-0.046	0.176	18	10	7	82	87	11	9	70	99	2	0	38	33
	High						0.023	-0.051	0.194	19	11	8	82	80	8	6	60	99	6	0	65	33
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	50	3	67	10	10	-0.002	-0.048	0.180	45	14	10	81	85	23	23	70	95	55	44	61	21
	High						-0.002	-0.041	0.267	36	15	11	83	81	29	21	75	93	48	44	58	30
3.14	Low						-0.002	-0.058	0.284	44	11	5	88	93	16	12	73	99	3	0	61	22
	High						-0.002	-0.068	0.326	43	11	7	81	93	7	4	64	100	--	--	--	23
6.28	Low						-0.002	-0.058	0.270	42	11	7	83	91	8	7	71	100	--	--	--	20
	High						-0.002	-0.071	0.314	44	11	7	83	92	6	2	64	100	--	--	--	24

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Table 7. 'Alala Wild Population. Basic Model--initial population size of 15 individuals.

Ind Dpr	EV in mort	Input Values					Results														TE	
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD		H
No Catastrophes																						
0.00	Low	50	3	67	10	10	0.023	-0.012	0.142	5	17	9	85	27	19	17	71	59	43	47	59	80
	High						0.023	-0.012	0.158	8	17	11	85	34	24	27	67	59	51	50	62	67
3.14	Low						0.023	-0.034	0.156	10	17	10	86	44	15	16	75	92	13	19	65	54
	High						0.023	-0.036	0.171	8	15	9	86	50	13	13	70	95	23	31	71	49
6.28	Low						0.023	-0.048	0.169	9	13	7	86	68	7	4	72	100	--	--	--	41
	High						0.023	-0.043	0.172	11	17	8	91	65	12	13	74	99	10	--	--	43
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	50	3	67	10	10	-0.002	-0.044	0.300	28	14	8	83	75	21	22	70	95	38	31	66	33
	High						-0.002	-0.050	0.310	36	14	10	83	72	17	13	69	96	14	5	64	30
3.14	Low						-0.002	-0.065	0.313	39	13	7	85	85	14	12	67	99	4	--	--	25
	High						-0.002	-0.056	0.308	30	15	9	84	85	16	13	71	99	2	--	--	29
6.28	Low						-0.002	-0.068	0.306	47	16	9	86	85	9	11	69	100	--	--	--	23
	High						-0.002	-0.066	0.288	31	11	9	84	90	6	4	71	100	--	--	--	28

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Table 8. 'Alala Wild Population. Management Options--Predator Control Low Effectiveness.

Ind Dpr	EV in mort	Input Values					Results															TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	50	3	60	10	10	0.047	0.015	0.133	10	18	12	83	25	51	56	69	36	136	71	63	--
	High						0.047	0.020	0.127	2	19	12	83	20	54	47	72	25	136	72	66	--
3.14	Low						0.047	-0.019	0.153	8	15	9	84	44	26	33	72	79	43	50	67	55
	High						0.047	-0.014	0.152	12	19	13	83	41	28	26	73	71	45	47	70	59
6.28	Low						0.047	-0.030	0.156	9	17	9	84	49	16	13	76	91	8	6	56	51
	High						0.047	-0.033	0.172	8	15	10	83	57	12	13	69	95	19	14	73	47
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	50	3	60	10	10	0.021	-0.031	0.322	42	13	7	88	70	30	45	62	87	68	74	60	28
	High						0.021	-0.036	0.342	38	17	14	80	71	34	45	64	94	89	89	61	26
3.14	Low						0.021	-0.041	0.301	35	18	12	82	77	16	12	66	95	5	2	40	31
	High						0.021	-0.040	0.285	34	17	13	83	77	19	18	69	95	21	16	74	32
6.28	Low						0.021	-0.059	0.322	43	14	8	81	84	13	9	70	100	--	--	--	24
	High						0.021	-0.052	0.306	39	16	12	84	85	18	20	74	99	62	0	81	25

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Table 9a. 'Alala Wild Population. Management Options. Predator Control--Moderate Effectiveness.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	50	3	50	10	10	0.077	0.056	0.164	2	36	24	84	4	147	67	78	4	192	23	74	--
	High						0.077	0.054	0.113	5	35	24	85	5	133	67	79	8	196	17	77	--
3.14	Low						0.077	0.016	0.115	3	25	15	86	11	62	49	77	29	131	74	73	--
	High						0.077	0.014	0.127	4	25	18	85	25	74	63	79	37	126	72	73	--
6.28	Low						0.077	-0.007	0.135	5	25	16	85	30	47	44	79	60	81	73	70	79
	High						0.077	-0.009	0.139	6	25	20	85	28	42	42	78	66	65	69	75	74
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	50	3	50	10	10	0.052	-0.003	0.350	29	32	22	84	53	82	70	76	69	109	87	68	38
	High						0.052	-0.010	0.369	27	30	27	82	57	89	76	72	78	103	87	67	39
3.14	Low						0.052	-0.033	0.361	35	25	20	83	66	46	51	72	91	94	88	71	32
	High						0.052	-0.020	0.302	31	29	19	85	55	64	57	77	80	68	75	72	41
6.28	Low						0.052	-0.045	0.349	34	22	18	83	77	39	46	78	94	63	80	75	29
	High						0.052	-0.040	0.331	37	23	17	85	77	46	51	78	92	60	87	65	34

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Table 9b. 'Alala Wild Population. Management Options. Predator Control--Moderate Effectiveness, including the effects of reduced predation on birth rate.

Ind Dpr	EV in mort	Input Values					Results															TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	60	3	50	10	10	0.108	0.088	0.098	1	62	34	87	2	193	23	84	2	199	6	81	--
	High						0.108	0.089	0.109	2	65	39	87	4	193	19	84	4	198	8	81	--
3.14	Low						0.108	0.055	0.096	1	48	29	87	3	164	59	83	6	192	29	81	--
	High						0.108	0.054	0.104	0	52	34	87	6	155	64	84	10	186	39	81	--
6.28	Low						0.108	0.028	0.106	2	42	23	87	7	116	71	82	19	158	65	80	--
	High						0.108	0.026	0.111	1	40	25	87	10	106	72	83	21	144	74	79	--
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	60	3	50	10	10	0.081	0.028	0.364	26	58	43	85	39	130	80	79	53	116	83	71	89
	High						0.081	0.020	0.395	29	58	43	84	49	125	82	79	67	136	76	70	51
3.14	Low						0.081	-0.008	0.371	38	46	32	85	59	109	79	77	73	97	86	66	28
	High						0.081	-0.002	0.359	30	41	31	85	53	108	85	79	72	94	87	69	46
6.28	Low						0.081	-0.016	0.333	29	37	22	86	53	75	66	78	80	90	76	75	45
	High						0.081	-0.023	0.332	24	31	22	84	56	63	66	78	82	82	79	75	40

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Table 10. 'Alala Wild Population. Management Options. Predator and Disease Control--Very Effective.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	50	3	34	10	10	0.121	0.101	0.105	2	80	50	87	2	194	24	84	2	200	6	81	--
	High						0.121	0.109	0.111	0	89	51	88	1	197	16	86	1	199	6	83	--
3.14	Low						0.121	0.067	0.097	0	65	42	87	0	170	56	84	1	190	30	81	--
	High						0.121	0.071	0.105	5	71	42	88	5	183	42	85	5	192	25	82	--
6.28	Low						0.121	0.041	0.104	2	52	35	87	9	143	70	84	17	179	4	82	--
	High						0.121	0.038	0.11	0	51	35	88	5	132	72	84	14	166	56	82	--
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	50	3	34	10	10	0.094	0.041	0.373	21	75	48	86	35	129	82	80	50	150	75	71	100
	High						0.094	0.052	0.336	16	51	51	85	26	144	74	78	44	158	68	72	--
3.14	Low						0.094	0.006	0.365	31	55	36	85	51	121	86	81	69	98	87	75	46
	High						0.094	0.012	0.365	25	48	41	87	48	127	78	80	66	126	80	76	54
6.28	Low						0.094	-0.018	0.371	36		39	86	65	106	83	82	85	49	62	77	32
	High						0.094	-0.009	0.344	25		34	87	45	101	78	81	76	96	85	76	53

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Table 11. 'Alala Wild Population. Management Options. Disease Control.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	50	3	57	10	10	0.056	0.030	0.120	4	23	17	83	16	78	64	74	21	163	58	70	--
	High						0.056	0.031	0.121	4	27	17	84	16	84	61	76	19	173	45	72	--
3.14	Low						0.056	-0.007	0.136	5	21	12	85	24	31	28	75	64	74	67	71	82
	High						0.056	-0.006	0.142	9	20	14	81	31	35	34	73	61	75	69	75	76
6.28	Low						0.056	-0.029	0.160	8	17	10	84	47	17	18	74	93	19	23	73	52
	High						0.056	-0.030	0.167	7	16	11	84	46	19	22	75	93	23	19	73	53
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	50	3	57	10	10	0.031	-0.019	0.359	37	24	20	83	65	57	57	72	81	110	81	66	28
	High						0.031	-0.019	0.320	32	25	22	83	66	54	57	70	84	134	79	66	39
3.14	Low						0.031	-0.040	0.313	31	17	12	83	72	41	39	76	93	67	62	71	30
	High						0.031	-0.044	0.314	36	17	7	82	72	23	25	72	98	16	13	53	26
6.28	Low						0.031	-0.050	0.305	31	16	9	84	84	10	10	70	99	3	0	72	30
	High						0.031	-0.047	0.298	25	16	11	83	86	24	34	75	99	9	0	53	30

'Alala PHVA

Table 12. 'Alala Wild Population. Management Options. Supplemental feeding--10% increase in productivity.

Ind Dpr	EV in mort	Input Values					Results																TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years					
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
No Catastrophes																							
0.00	Low	60	3	67	10	10	0.033	0.001	0.139	9	16	9	83	32	28	34	69	49	78	61	65	--	
	High						0.033	0.002	0.143	6	18	10	84	30	35	37	75	46	87	69	65	--	
3.14	Low						0.033	-0.029	0.160	13	14	9	84	58	17	14	71	88	16	18	60	47	
	High						0.033	-0.029	0.169	15	14	9	84	50	13	12	71	92	17	21	65	50	
6.28	Low						0.033	-0.039	0.165	22	13	8	84	68	11	8	71	97	3	1	59	32	
	High						0.033	-0.039	0.175	12	13	8	83	72	10	10	73	99	3	--	--	38	
Catastrophes: Disease, Drought, Hurricane, Volcano																							
0.00	Low	60	3	67	10	10	0.009	-0.053	0.341	39	13	9	80	85	28	23	67	97	21	120	66	24	
	High						0.009	-0.034	0.281	38	15	10	83	69	19	25	61	95	40	36	47	30	
3.14	Low						0.009	-0.052	0.289	42	13	6	81	80	13	10	64	99	9	--	--	22	
	High						0.009	-0.062	0.317	45	11	9	80	87	12	14	71	99	13	--	--	25	
6.28	Low						0.009	-0.059	0.299	38	12	7	83	88	10	10	73	100	--	--	--	21	
	High						0.009	-0.063	0.313	46	11	7	81	94	8	6	70	100	--	--	--	24	

'Alala PHVA

Table 13. 'Alala Wild Population. Management Options. Supplemental feeding--25% increase in productivity.

Ind Dpr	EV in mort	Input Values					Results																
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE	
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
No Catastrophes																							
0.00	Low	60	3	67	10	10	0.047	0.018	0.125	10	21	12	83	27	25	46	75	33	147	66	68	--	
	High						0.047	0.019	0.134	7	22	16	83	21	50	41	72	30	138	68	67	--	
3.14	Low						0.047	-0.016	0.146	7	19	12	84	39	29	28	74	72	42	59	68	68	
	High						0.047	-0.016	0.154	12	18	11	84	43	32	37	45	78	59	65	70	62	
6.28	Low						0.047	-0.034	0.164	6	14	8	83	52	13	12	73	96	5	3	46	49	
	High						0.047	-0.036	0.172	13	16	9	85	57	13	13	70	99	6	0	71	46	
Catastrophes: Disease, Drought, Hurricane, Volcano																							
0.00	Low	60	3	67	10	10	0.022	-0.025	0.326	37	19	13	83	62	49	45	71	84	82	84	63	25	
	High						0.022	-0.032	0.330	44	21	16	83	73	44	54	74	87	86	80	69	32	
3.14	Low						0.022	-0.056	0.333	45	15	9	82	81	13	12	70	99	9	0	35	23	
	High						0.022	-0.048	0.311	41	16	10	82	78	22	14	74	97	14	20	40	25	
6.28	Low						0.022	-0.057	0.314	41	14	8	84	90	11	6	74	100	--	--	--	23	
	High						0.022	-0.052	0.288	35	14	10	82	83	11	8	73	100	--	--	--	25	

'Alala PHVA

Table 14. 'Alala Wild Population. Management Options. Double-clutching--33% increase in productivity.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	65	67	10	10	10	0.064	0.040	0.110	4	27	18	85	13	103	67	78	19	192	21	74	--
	High						0.064	0.031	0.155	9	30	22	84	16	83	68	77	23	159	51	72	--
3.14	Low						0.064	0.001	0.129	5	24	13	86	16	45	46	76	47	93	77	71	--
	High						0.064	0.003	0.156	5	24	18	84	31	60	56	77	51	97	69	73	98
6.28	Low						0.064	0.021	0.149	6	23	16	85	26	25	29	76	82	39	64	69	65
	High						0.064	0.020	0.169	6	23	16	85	33	27	29	76	83	53	63	70	59
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	65	4	67	10	10	0.038	0.009	0.330	40	24	16	84	63	69	64	75	75	106	83	67	33
	High						0.038	0.012	0.342	38	27	21	85	68	61	59	75	78	99	77	67	28
3.14	Low						0.038	0.010	0.336	33	35	28	86	55	109	74	80	80	115	87	80	43
	High						0.038	0.029	0.311	33	26	16	84	62	44	45	77	84	63	81	67	36
6.28	Low						0.038	0.044	0.291	31	19	12	83	71	16	17	74	99	3	0	72	31
	High						0.038	0.046	0.318	38	21	18	84	90	27	25	77	95	27	50	60	28

'Alala PHVA

Table 15. 'Alala Wild Population. Management Options. Double-clutching (50% increase in productivity).

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	65	4	67	10	10	0.075	0.057	0.105	2	34	20	85	6	142	61	80	6	193	27	78	--
	High						0.075	0.047	0.153	4	42	34	81	11	127	68	79	14	178	38	75	--
3.14	Low						0.075	0.017	0.115	5	28	16	85	14	73	58	79	29	130	73	75	--
	High						0.075	0.011	0.153	9	29	19	86	24	69	58	80	36	110	78	74	--
6.28	Low						0.075	-0.013	0.137	4	22	13	85	26	34	31	78	65	44	63	73	82
	High						0.075	-0.013	0.160	6	25	16	95	31	39	42	77	75	60	53	74	71
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	65	4	67	10	10	0.050	-0.001	0.353	23	32	19	85	50	100	81	77	65	120	79	69	50
	High						0.050	-0.003	0.352	36	28	21	84	61	93	73	77	73	105	78	69	32
3.14	Low						0.050	-0.029	0.322	34	24	17	85	64	110	55	73	93	117	93	80	36
	High						0.050	-0.034	0.348	32	23	19	82	73	56	61	77	89	61	78	58	27
6.28	Low						0.050	-0.048	0.329	42	20	16	84	74	23	18	76	95	11	9	65	27
	High						0.050	-0.041	0.333	35	24	22	83	79	30	29	76	96	59	63	70	27

'Alala PHVA

Table 16. 'Alala Wild Population. Management Options. Double-clutching--60% increase in productivity.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	65	4	67	10	10	0.084	0.065	0.103	6	44	26	85	9	171	51	80	9	198	6	78	--
	High						0.084	0.059	0.159	8	24	13	90	12	145	66	81	13	183	23	78	--
3.14	Low						0.084	0.028	0.109	1	33	19	86	9	101	69	80	16	157	66	76	--
	High						0.084	0.021	0.153	9	35	27	87	21	96	72	80	33	143	68	76	--
6.28	Low						0.084	0.025	0.124	2	28	16	86	18	63	61	79	44	97	84	73	--
	High						0.084	-0.023	0.159	10	29	20	86	28	52	53	78	56	80	65	75	84
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low						0.058	0.015	0.336	27	34	25	83	42	110	84	76	59	120	83	68	65
	High						0.058	0.010	0.355	35	40	32	84	50	113	74	80	64	109	85	70	50
3.14	Low						0.058	-0.015	0.345	36	31	21	85	57	85	71	81	78	107	75	73	39
	High						0.058	-0.028	0.363	34	34	29	84	67	79	72	80	88	91	85	76	32
6.28	Low						0.058	-0.030	0.309	33	24	17	85	70	40	31	79	91	78	59	72	37
	High						0.058	-0.042	0.354	40	25	19	84	70	45	64	75	96	82	90	61	25

'Alala PHVA

Table 17. 'Alala Wild Population. Management Options. Double-clutching--100% increases in productivity.

Ind Dpr	EV in mort	Input Values					Results																TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years					
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
No Catastrophes																							
0.00	Low	65	6	67	10	10	0.120	0.102	0.104	0	83	46	88	1	196	22	85	1	198	7	81	--	
	High						0.120	0.093	0.169	2	79	56	87	5	189	84	84	5	189	18	81	--	
3.14	Low						0.120	0.069	0.098	0	64	41	88	1	176	49	83	3	196	18	81	--	
	High						0.120	0.064	0.136	2	72	51	88	2	166	54	84	4	182	36	81	--	
6.28	Low						0.120	0.039	0.103	2	52	32	88	6	140	70	83	12	165	64	80	--	
	High						0.120	0.036	0.126	1	53	37	87	8	126	72	84	17	156	64	82	--	
Catastrophes: Disease, Drought, Hurricane, Volcano																							
0.00	Low						0.094	0.042	0.372	21	72	52	85	31	136	80	79	46	123	80	74	--	
	High						0.094	0.037	0.375	32	56	50	84	48	133	82	77	56	139	72	70	59	
3.14	Low						0.094	0.005	0.359	35	43	39	85	59	113	86	80	72	116	82	77	33	
	High						0.094	0.007	0.359	20	49	42	85	51	105	81	80	66	128	80	73	50	
6.28	Low						0.094	-0.011	0.005	26	42	32	86	56	112	82	80	78	86	86	79	43	
	High						0.094	-0.013	0.005	26	45	33	85	53	92	76	80	79	75	78	74	42	

'Alala PHVA

Table 18. 'Alala Wild Population. Management Options. Disease Control, Predator Control and Supplemental Feeding.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	60	3	50	10	10	0.108	0.088	0.098	1	62	34	87	2	193	23	84	2	199	6	81	--
	High						0.108	0.089	0.109	2	65	39	87	4	193	19	84	4	198	8	81	--
3.14	Low						0.108	0.055	0.096	1	48	29	87	3	164	59	83	6	192	29	81	--
	High						0.108	0.054	0.104	0	52	34	87	6	155	64	84	10	186	39	81	--
6.28	Low						0.108	0.028	0.106	2	42	23	87	7	116	71	82	19	158	65	80	--
	High						0.108	0.026	0.111	1	40	25	87	10	106	72	83	21	144	74	79	--
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	60	3	50	10	10	0.081	0.028	0.364	26	58	43	85	39	130	80	79	53	116	83	71	89
	High						0.081	0.020	0.395	29	58	43	84	49	125	82	79	67	136	76	70	51
3.14	Low						0.081	-0.008	0.371	38	46	32	85	59	109	79	77	73	97	86	66	28
	High						0.081	-0.002	0.359	30	41	31	85	53	108	85	79	72	94	87	69	46
6.28	Low						0.081	-0.016	0.333	29	37	22	86	53	75	66	78	80	90	76	75	45
	High						0.081	-0.023	0.332	24	31	22	84	56	63	66	78	82	82	79	75	40

'Alala PHVA

Table 19. 'Alala Wild Population. Management Options. Disease Control, Predator Control and Double-Clutching.

Ind Dpr	EV in mort	Input Values					Results																TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years					
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
No Catastrophes																							
0.00	Low	65	3	34	10	10	0.175	0.156	0.099	0	178	40	90	0	199	6	87	0	200	6	83	--	
	High						0.175	0.155	0.110	0	171	45	90	0	198	17	87	0	199	7	84	--	
3.14	Low						0.175	0.124	0.091	0	156	55	89	0	200	7	87	0	200	5	84	--	
	High						0.175	0.124	0.103	0	155	51	90	0	197	14	88	0	198	6	84	--	
6.28	Low						0.175	0.099	0.087	0	130	53	90	0	198	18	89	0	197	19	86	--	
	High						0.175	0.097	0.095	0	127	59	90	1	195	25	88	2	198	6	84	--	
Catastrophes: Disease, Drought, Hurricane, Volcano																							
0.00	Low	65	3	34	10	10	0.148	0.094	0.382	21	137	71	88	27	159	67	82	38	143	76	74	--	
	High						0.148	0.098	0.375	16	138	72	88	21	160	68	81	35	159	71	76	--	
3.14	Low						0.148	0.054	0.368	17	124	65	88	27	140	75	82	47	131	81	76	--	
	High						0.148	0.050	0.384	20	106	67	87	34	138	77	81	51	134	81	74	98	
6.28	Low						0.148	0.033	0.361	21	94	62	88	39	132	80	85	53	127	84	78	92	
	High						0.148	0.030	0.362	29	98	66	87	42	127	84	81	59	128	85	79	69	

'Alala PHVA

Table 20. 'Alala Wild Population. Low supplementation from captive population (1 pair per year for 20 years).

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	HY Mor	Juv Mor	Ad Mor	Population Growth			20 years				50 years				100 years				TE
							Det r	Stoch r*	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	50	3	67	10	10	0.023	0.005	0.103	0	53	14	97	0	71	41	91	8	113	63	84	--
	High	50	3	67	10	10	0.023	0.003	0.101	0	52	17	97	0	73	48	91	9	106	70	83	--
3.12	Low	50	3	67	10	10	0.023	-0.013	0.102	0	51	13	97	1	60	39	91	21	50	52	79	--
	High	50	3	67	10	10	0.023	-0.012	0.107	0	51	16	97	1	59	39	91	18	50	51	79	--
6.28	Low	50	3	67	10	10	0.023	-0.024	0.160	0	51	13	97	1	60	39	91	21	50	52	79	--
	High	50	3	67	10	10	0.023	-0.039	0.187	0	51	16	97	1	59	39	91	18	50	51	79	--
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.0	Low	50	3	67	10	10	-0.002	-0.050	0.333	0	34	18	96	42	38	37	85	83	54	56	75	50
	High	50	3	67	10	10	-0.002	-0.047	0.340	0	41	22	96	38	37	36	84	78	46	46	71	63
3.12	Low	50	3	67	10	10	-0.002	-0.052	0.315	0	40	25	96	47	50	34	87	80	54	52	78	50
	High	50	3	67	10	10	-0.002	-0.049	0.295	0	40	20	96	42	37	30	86	82	34	34	81	54
6.28	Low	50	3	67	10	10	-0.002	-0.071	0.347	0	41	20	96	47	32	27	86	92	11	7	77	51
	High	50	3	67	10	10	-0.002	-0.060	0.320	0	37	21	96	44	35	31	85	86	30	35	79	51

*r for years of no supplementation; r for years with supplementation approximately 0.07 with no catastrophes, 0.05 with catastrophes.

'Alala PHVA

Table 21. 'Alala Wild Population. High supplementation from captive population (2 pairs per year for 20 years).

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	HY Mor	Juv Mor	Ad Mor	Population Growth			20 years				50 years				100 years				TE
							Det r	Stoch r*	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
No Catastrophes																						
0.00	Low	50	3	67	10	10	0.023	0.012	0.075	0	91	22	98	0	129	47	95	0	154	47	91	--
							0.023	0.009	0.085	0	90	21	98	0	121	51	95	1	141	50	91	--
3.12	Low						0.023	0.003	0.075	0	96	21	98	0	121	46	96	1	121	59	90	--
	High						0.023	0.002	0.086	0	96	23	98	0	123	48	96	1	115	62	90	--
6.28	Low						0.023	-0.008	0.085	0	94	19	98	0	104	46	95	10	85	59	89	--
	High						0.023	-0.004	0.083	0	95	22	98	0	113	45	96	2	82	55	89	--
Catastrophes: Disease, Drought, Hurricane, Volcano																						
0.00	Low	50	3	67	10	10	-0.002	-0.047	0.349	0	74	30	98	23	71	61	88	68	68	63	84	68
	High						-0.002	-0.047	0.355	0	75	34	98	27	72	63	89	74	68	65	84	71
3.12	Low						-0.002	-0.063	0.364	0	80	28	98	30	59	53	89	80	48	56	81	65
	High						-0.002	-0.049	0.330	0	70	31	98	23	76	62	91	73	56	63	82	74
6.28	Low						-0.002	-0.059	0.333	0	73	31	98	28	58	50	90	79	37	41	84	64
	High						-0.002	-0.055	0.322	0	71	28	98	31	60	55	90	76	62	54	84	62

*r for years of no supplementation; r for years with supplementation approximately 0.105 with no catastrophes, 0.09 with catastrophes.

'Alala PHVA

Table 22. Life lines and reproductive summaries for captive female 'Alala, 1979-1992.

Stbk. #	Name	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
9	Hiialo	$\frac{0^a}{0^b}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{10}$	$\frac{0}{4}$	$\frac{0}{2}$	$\frac{0}{2}$						
10	Iole-e	$\frac{0}{0}$													
14	Luukia	$\frac{0}{3}$	$\frac{0}{2}$	$\frac{3}{8}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{1}$	$\frac{0}{0}$	$\frac{0}{10}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{0}{2}$	$\frac{0}{0}$	$\frac{0}{0}$
15	Mana	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{2}$	$\frac{0}{2}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{1}{5}$	$\frac{0}{3}$		
16	Kulohe (imprinted)			$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$
20	Waalani				$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{1}{3}$	
21	Hooku							$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$				
24	Lanaki														

^a Figure above line represents the number of chicks hatched by each female in a given year.

^b Figure below line represents the number of eggs laid by each female in a given year.

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Table 23. Summary of production of captive female 'Alala, 1979-1992.

All eggs laid:

Eggs Laid			Chicks Hatched		
# Eggs	# Females	Percentage	# Chicks	# Females	Percentage
0	38	70.3%	0	49	90.7
1	2	3.7	1	3	5.6
2	4	7.4	2	3	1.8
3	2	3.7	3	1	1.8
4	2	3.7			
5	1	1.8			
6	0	0			
7	0	0			
8	3	5.6			
9	0	0			
10	2	3.7			

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Table 24. Reproductive and Mortality Schedules used in the Simulation Models.

Model Name	Table #	Percent of Females that Produce Clutches of Size:											Age-Specific Mortality		
		0	1	2	3	4	5	6	7	8	9	10	HY	Juv	Ad
Basic	Table 23	68	4	8	4	4	2	0	0	6	0	4	89	0	7.6
Improved Hatchability	Table 24	68	4	8	4	4	2	0	0	6	0	4	64	0	7.6
Decreased Breakage	Table 25	56.8	5.4	10.8	5.4	5.4	2.7	0	0	8.1	0	5.4	89	0	7.6
Supplement from Wild Low	Table 26	68	4	8	4	4	2	0	0	6	0	4	89	0	7.6
Supplement from Wild High	Table 27	68	4	8	4	4	2	0	0	6	0	4	89	0	7.6

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Table 25. 'Alala Captive Population. Current demographic parameters.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
Model: Carrying Capacity = 125																						
No Catastrophes																						
0.00	Mod	32	10	89	0	7.6	-0.005	-0.044	0.180	14	11	8	83	72	11	9	63	97	20	10	64	37
3.14	Mod						-0.005	-0.054	0.187	17	9	5	82	83	5	3	57	100	--	--	--	33
6.28	Mod						-0.005	-0.052	0.185	22	10	7	82	83	6	3	65	100	--	--	--	33
Catastrophes: Disease																						
0.00	Mod	32	10	89	0	7.6	-0.032	-0.078	0.270	51	49	9	6	94	8	5	44	100	--	--	--	20
3.14	Mod						-0.032	-0.085	0.258	52	7	5	79	95	4	3	53	100	--	--	--	20
6.28	Mod						-0.032	-0.089	0.267	50	5	4	77	100	--	--	--	100	--	--	--	20
Model: Carrying Capacity = 50																						
No Catastrophes:																						
0.00	Mod	32	10	89	0	7.6	-0.005	-0.039	0.180	11	10	7	83	69	9	5	70	92	16	16	43	36
3.14	Mod						-0.005	-0.047	0.182	17	11	6	83	74	9	7	68	92	4	4	2	37
6.28	Mod						-0.005	-0.055	0.185	20	9	6	82	86	4	1	65	100	--	--	--	34

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Catastrophes: Disease																						
0.00	Mod	32	10	89	0	7.6	-0.032	-0.075	0.249	51	8	7	78	95	16	5	63	99	2	--	--	19
3.14	Mod						-0.032	-0.085	0.262	45	7	6	79	98	10	4	74	100	--	--	--	21
6.28	Mod						-0.032	-0.092	0.271	54	7	6	81	97	5	3	73	100	--	--	--	19

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Table 26. 'Alala Captive Population. Improved hatchability--64% egg hatchability

Ind Dpr	EV in mort	Input Values					Results																TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years					
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
Model: Carrying Capacity = 125																							
No Catastrophes																							
0.00	Mod	32	10	64	0	7.6	0.141	0.118	0.138	1	92	37	90	1	122	5	83	1	123	7	77	--	
3.14	Mod						0.141	0.085	0.123	1	66	41	87	6	114	27	83	7	119	14	81	--	
6.28	Mod						0.141	0.061	0.117	2	55	37	87	3	97	39	83	9	104	34	79	--	
Catastrophes: Disease																							
0.00	Mod	32	10	89	0	7.6	0.112	0.073	0.232	13	64	42	83	17	102	34	76	17	104	31	68	--	
3.14	Mod						0.112	0.031	0.228	16	46	37	83	30	86	41	78	37	82	42	72	--	
6.28	Mod						0.112	0.006	0.227	14	45	34	84	31	68	46	79	55	61	45	74	85	
Model: Carrying Capacity = 50																							
No Catastrophes:																							
0.00	Mod	32	10	89	0	7.6	0.141	0.108	0.148	1	44	12	86	2	49	3	77	2	49	4	66	--	
3.14	Mod						0.141	0.069	0.132	1	43	11	87	1	47	7	79	3	46	5	71	--	
6.28	Mod						0.141	0.046	0.123	1	42	11	88	2	45	7	81	3	42	10	72	--	
Catastrophes: Disease																							
0.00	Mod	32	10	89	0	7.6	0.112	0.063	0.216	17	37	16	83	22	40	14	71	27	39	15	54	--	
3.14	Mod						0.112	0.017	0.242	23	33	16	84	36	32	17	76	60	30	16	63	83	
6.28	Mod						0.112	-0.033	0.235	14	32	17	84	30	29	17	76	68	20	15	66	76	

'Alala PHVA

Table 27. 'Alala Captive Population. Prevention of Egg Breakage.

Ind Dpr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years				TE
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
Model: Carrying Capacity = 125																						
No Catastrophes																						
0.00	Mod	32	10	89	0	7.6	-0.005	-0.041	0.182	20	11	7	83	74	15	12	71	95	17	12	49	34
3.14	Mod						-0.005	-0.049	0.189	15	9	5	82	84	9	5	69	99	5	--	--	33
6.28	Mod						-0.005	-0.050	0.178	16	10	6	82	84	5	3	69	100	--	--	--	35
Catastrophes: Disease																						
0.00	Mod	32	10	89	0	7.6	-0.032	-0.072	0.262	45	10	9	79	94	9	5	69	100	--	--	--	22
3.14	Mod						-0.032	-0.076	0.253	49	8	6	81	95	5	3	70	99	2	--	--	21
6.28	Mod						-0.032	-0.085	0.264	42	6	4	79	98	3	1	62	100	--	--	--	22
Model: Carrying Capacity = 50																						
No Catastrophes:																						
0.00	Mod	32	10	89	0	7.6	-0.005	-0.040	0.183	15	11	7	82	66	9	8	70	98	14	15	37	40
3.14	Mod						-0.005	-0.055	0.189	20	9	5	83	89	7	3	66	100	--	--	--	32
6.28	Mod						-0.005	-0.058	0.182	26	9	7	83	86	6	6	68	100	--	--	--	27
Catastrophes: Disease																						
0.00	Mod	32	10	89	0	7.6	-0.032	-0.072	0.262	42	8	5	81	90	9	8	61	100	--	--	--	22
3.14	Mod						-0.032	-0.080	0.260	44	7	6	80	95	6	2	59	100	--	--	--	22
6.28	Mod						-0.032	-0.087	0.266	44	7	4	80	97	4	0	69	100	--	--	--	21

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Table 28. 'Alala Captive Population. Combination of increased hatchability and decreased egg breakage.

Inbd Depr	EV in mort	Input Values					Results																TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years					
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
Model: Carrying Capacity = 125																							
No Catastrophes																							
0.00	Mod	43.2	10	64	0	7.6	0.195	0.168	0.138	0	119	17	89	0	125	5	84	0	125	5	77	--	
3.14	Mod						0.195	0.138	0.125	0	116	21	89	1	124	5	85	1	124	4	80	--	
6.28	Mod						0.195	0.111	0.118	0	110	25	89	0	124	4	86	0	123	4	81	--	
Catastrophes: Disease																							
0.00	Mod	43.2	10	64	0	7.6	0.165	0.127	0.226	3	95	37	86	3	114	24	80	4	1251	21	73	--	
3.14	Mod						0.165	0.083	0.217	3	82	43	86	6	102	34	82	8	1241	25	75	--	
6.28	Mod						0.165	0.058	0.213	6	82	41	88	10	96	37	84	17	1239	40	77	--	
Model: Carrying Capacity = 50																							
No Catastrophes:																							
0.00	Mod	43.2	10	64	0	7.6	0.195	0.161	0.152	0	49	4	86	0	50	3	77	0	49	3	61	--	
3.14	Mod						0.195	0.116	0.134	0	49	3	88	0	49	4	78	0	49	3	66	--	
6.28	Mod						0.195	0.084	0.126	2	41	12	91	2	49	3	82	3	47	5	74	--	
Catastrophes: Disease																							
0.00	Mod	43.2	10	64	0	7.6	0.165	0.118	0.238	4	42	13	84	6	45	10	74	8	46	9	58	--	
3.14	Mod						0.165	0.061	0.233	7	40	14	85	12	37	14	74	22	39	15	61	--	
6.28	Mod						0.165	0.031	0.232	12	40	13	87	15	38	15	77	41	29	17	66	--	

'Alala PHVA

Table 29. 'Alala Captive Population. Sustainability of Harvest from Captive Population with Improved Hatchability and Reduced Breakage.

Inbd Depr	EV in mort	Input Values					Results																TE
		% Brd	Max lit	Mortality			Population Growth		20 years				50 years				100 years						
				HY	Juv	Ad	Det r	Stoch r SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H			
Model: Carrying Capacity = 125																							
No Catastrophes																							
0.00	Mod	43.2	10	64	0	7.6	0.195	0.148	0.136	0	119	17	89	0	124	5	85	0	125	4	79	--	
3.14	Mod							0.148	0.161	0	113	24	89	1	124	4	86	1	123	6	80	--	
6.28	Mod							0.128	0.151	0	109	27	89	2	121	13	87	3	121	8	82	--	
Catastrophes: Disease																							
0.00	Mod	43.2	10	64	0	7.6	0.165	0.112	0.248	4	88	43	86	15	98	36	82	27	108	29	75	--	
3.14	Mod							0.090	0.250	8	81	43	86	23	92	42	81	49	88	43	77	--	
6.28	Mod							0.094	0.239	5	79	44	88	28	79	47	84	64	82	44	82	82	
Model: Carrying Capacity = 50																							
No Catastrophes:																							
0.00	Mod	43.2	10	64	0	7.6	0.195	0.163	0.172	0	48	4	87	0	47	7	80	1	48	5	68	--	
3.14	Mod							0.139	0.163	0	47	6	88	1	44	9	81	8	39	13	72	--	
6.28	Mod							0.129	0.161	1	48	4	88	1	38	12	83	51	20	15	72	99	
Catastrophes: Disease																							
0.00	Mod	43.2	10	64	0	7.6	0.165	0.113	0.255	6	43	12	85	19	36	16	75	61	28	18	61	91	
3.14	Mod						-0.032	0.084	0.267	5	36	16	84	47	28	17	76	95	22	23	65	52	
6.28	Mod						-0.032	0.071	0.256	10	35	16	85	48	20	17	78	96	14	14	70	51	

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Table 30. 'Alala Captive Population. Supplement from wild population--1 pair per year for 20 years.

Ind Dpr	EV in mort	Input Values					Results																TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years					
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
Model: Carrying Capacity = 125																							
No Catastrophes																							
0.00	Mod	32	10	89	0	7.6	-0.005	-0.036	0.142	0	49	17	97	2	29	21	89	64	18	18	72	91	
3.14	Mod						-0.005	-0.040	0.141	0	50	18	97	3	30	24	89	63	13	13	73	90	
6.28	Mod						-0.005	-0.045	0.144	0	50	17	97	3	33	35	90	74	10	8	76	83	
Catastrophes: Disease																							
0.00	Mod	32	10	89	0	7.6	-0.032	-0.069	0.243	0	34	17	97	37	13	16	81	95	15	21	69	56	
3.14	Mod						-0.032	-0.079	0.250	0	37	17	97	43	17	23	84	98	4	2	51	54	
6.28	Mod						-0.032	-0.081	0.234	0	37	17	97	39	14	16	84	98	4	3	72	53	
Model: Carrying Capacity = 50																							
No Catastrophes:																							
0.00	Mod	32	10	89	0	7.6	-0.005	-0.035	0.152	0	41	8	97	7	21	12	88	62	11	8	68	90	
3.14	Mod						-0.005	-0.043	0.154	0	42	8	97	10	19	10	88	80	8	6	61	81	
6.28	Mod						-0.005	-0.052	0.156	0	43	7	97	8	19	10	88	89	5	3	68	74	
Catastrophes: Disease																							
0.00	Mod	32	10	89	0	7.6	-0.032	-0.081	0.261	0	32	11	97	57	11	7	78	98	13	11	57	49	
3.14	Mod						-0.032	-0.082	0.244	0	34	11	97	38	12	9	82	99	20	--	--	54	
6.28	Mod						-0.032	-0.083	0.238	0	33	11	97	44	11	8	84	100	--	--	--	53	

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Table 31. 'Alala Captive Population. Supplement from wild population--2 pairs per year for 20 years.

Ind Dpr	EV in mort	Input Values					Results																TE
		% Brd	Max lit	Mortality			Population Growth			20 years				50 years				100 years					
				HY	Juv	Ad	Det r	Stoch r*	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
Model: Carrying Capacity = 125																							
No Catastrophes																							
0.00	Mod	32	10	89	0	7.6	-0.005	-0.029	0.130	0	51	9	98	0	56	33	94	34	29	27	82	--	
3.14	Mod						-0.005	-0.030	0.123	0	88	23	99	0	57	32	94	63	25	29	82	--	
6.28	Mod						-0.005	-0.039	0.129	0	88	20	99	0	51	28	98	49	16	17	80	--	
Catastrophes: Disease																							
0.00	Mod	32	10	89	0	7.6	-0.032	-0.073	0.237	0	69	26	98	22	21	18	87	95	20	18	74	69	
3.14	Mod						-0.032	-0.079	0.234	0	65	27	98	20	20	23	87	94	7	9	69	63	
6.28	Mod						-0.032	-0.072	0.226	0	65	25	98	20	21	17	89	94	13	15	69	66	
Model: Carrying Capacity = 50																							
No Catastrophes:																							
0.00	Mod	32	10	89	0	7.6	-0.005	-0.033	0.148	0	49	2	98	2	24	11	90	57	14	12	70	91	
3.14	Mod						-0.005	-0.043	0.148	0	49	2	98	3	23	11	90	68	8	9	69	81	
6.28	Mod						-0.005	-0.050	0.155	0	49	2	98	4	21	12	89	89	6	6	66	78	
Catastrophes: Disease																							
0.00	Mod	32	10	89	0	7.6	-0.032	-0.071	0.237	0	44	8	98	30	15	11	84	98	13	6	73	60	
3.14	Mod						-0.032	-0.072	0.224	0	44	10	98	29	16	12	86	98	7	6	73	59	
6.28	Mod						-0.032	-0.080	0.235	0	43	10	98	31	12	9	84	100	--	--	--	56	

r* growth rate for years of no supplementation. r for years with supplementation approximately equal to ; r with catastrophes approximately equal to .

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Table 32. 'Alala Captive and Wild Population. Metapopulation Model 1.

Inbd Depr	EV in mort	Input Values					Results													TE	
		% Brd	Max lit	Mortality			Population Growth		20 years				50 years				100 years				
				HY	Juv	Ad	Det r	Stoch r	SD	PE	N	SD	H	PE	N	SD	H	PE	N		SD
Model: Carrying Capacity = 125																					
No Catastrophes																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 8					0.091	0.085	0	137	54	92	0	315	20	91	0	319	12	89	--	
3.14						0.071	0.083	0	122	60	93	0	288	49	91	0	306	33	89	--	
6.28						0.056	0.083	0	103	51	93	1	235	75	91	1	287	50	89	--	
Catastrophes: As in Tables 24 and 8																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 8					0.054	0.169	1	78	56	90	7	208	83	83	8	257	79	79	--	
3.14						0.025	0.167	4	75	52	90	9	150	101	84	21	172	99	80	--	
6.28						0.002	0.170	2	78	70	87	15	105	93	84	43	125	95	82	--	
Model: Carrying Capacity = 50																					
No Catastrophes:																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 8					0.080	0.087	0	94	24	92	0	197	41	90	0	234	20	86	--	
3.14						0.060	0.087	0	82	28	92	0	152	44	89	0	184	45	86	--	
6.28						0.047	0.083	0	82	19	93	0	127	36	90	0	125	35	86	--	
Catastrophes: As in Tables 24 and 8																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 8					0.049	0.172	0	68	38	90	5	104	60	82	8	142	76	76	--	
3.14						0.020	0.169	0	55	34	89	13	85	45	84	24	84	54	77	--	
6.28						-0.006	0.181	1	51	30	90	17	60	37	84	50	48	44	75	100	

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Table 33. 'Alala Captive and Wild Populations. Metapopulation Model 2.

Inbd Depr	EV in mort	Input Values					Results													TE	
		% Brd	Max lit	Mortality			Population Growth		20 years				50 years				100 years				
				HY	Juv	Ad	Det r	Stoch r SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD		H
Model: Carrying Capacity = 125																					
No Catastrophes																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 17					0.105	0.083	0	160	60	93	0	322	9	91	0	322	8	90	--	
3.14						0.086	0.080	0	136	60	93	0	315	37	91	0	320	10	89	--	
6.28						0.069	0.79	0	123	64	93	0	297	64	91	0	308	48	89	--	
Catastrophes: As in Tables 24 and 17																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 17					0.068	0.161	1	64	64	89	5	233	96	86	5	272	67	83	--	
3.14						0.044	0.164	4	92	66	91	8	207	104	88	12	235	96	83	--	
6.28						0.019	0.167	2	54	54	90	11	159	112	85	31	180	103	84	--	
Model: Carrying Capacity = 50																					
No Catastrophes:																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 17					0.097	0.087	0	111	36	93	0	242	28	91	0	245	11	88	--	
3.14						0.081	0.082	0	106	25	93	0	226	33	91	0	238	17	88	--	
6.28						0.064	0.80	0	98	29	93	0	191	50	91	1	215	35	88	--	
Catastrophes: As in Tables 25 and 17																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 17					0.057	0.193	2	75	38	90	6	135	78	85	6	158	83	79	--	
3.14						0.038	0.172	0	75	69	91	5	124	71	85	8	116	79	78	--	
6.28						-0.014	0.171	5	66	37	91	14	104	71	86	33	79	62	79	--	

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Table 34. 'Alala Captive and Wild Populations. Metapopulation Model 3.

Inbd Depr	EV in mort	Input Values					Results															
		% Brd	Max lit	Mortality			Population Growth		20 years				50 years				100 years				TE	
				HY	Juv	Ad	Det r	Stoch r SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
Model: Carrying Capacity = 125																						
No Catastrophes																						
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 13		0.082	0.086	0	125	58	92	0	273	44	91	0	314	14	88	--					
3.14		0.063	0.085	0	103	53	92	0	263	60	89	0	299	25	88	--						
6.28		0.049	0.083	0	91	44	93	0	225	75	90	2	264	52	88	--						
Catastrophes: As in Tables 24 and 13																						
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 13		0.050	0.162	4	72	53	89	8	192	96	83	11	251	73	80	--					
3.14		0.023	0.169	2	71	56	90	14	147	89	84	25	184	96	82	--						
6.28		-0.004	0.178	6	55	46	90	22	94	86	82	51	113	79	81	--						
Model: Carrying Capacity = 50																						
No Catastrophes:																						
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 13		0.073	0.088	0	84	18	92	0	161	39	89	0	214	32	86	--					
3.14		0.053	0.086	1	77	23	92	1	133	39	88	1	137	38	84	--						
6.28		0.039	0.087	0	74	21	93	0	101	24	89	1	93	19	85	--						
Catastrophes: As in Tables 24 and 13																						
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 13		0.038	0.178	6	55	29	89	11	97	55	82	16	119	67	74	--					
3.14		0.013	0.170	3	55	27	91	12	76	38	85	29	68	44	76	--						
6.28		-0.012	0.181	7	45	28	89	29	54	35	82	61	42	29	74	88						

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Table 35. 'Alala Captive and Wild Populations. Metapopulation Model 4.

Inbd Depr	EV in mort	Input Values					Results													TE	
		% Brd	Max lit	Mortality			Population Growth		20 years				50 years				100 years				
				HY	Juv	Ad	Det r	Stoch r SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD		H
Model: Carrying Capacity = 125																					
No Catastrophes																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 18						0.142	0.086	0	260	71	94	0	323	8	92	0	324	8	90	--
3.14		0.127	0.081	0	257	71	94	0	323	7	92	0	323	8	90	--					
6.28		0.110	0.080	0	237	79	94	0	323	11	93	0	322	8	91	--					
Catastrophes: As in Tables 24 and 18																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 18						0.109	0.169	0	185	94	92	1	292	60	89	1	288	64	85	--
3.14		0.082	0.172	2	172	99	92	4	260	88	90	6	285	62	87	--					
6.28		0.055	0.178	3	136	97	92	10	226	106	89	14	247	95	86	--					
Model: Carrying Capacity = 50																					
No Catastrophes:																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 18						0.147	0.090	0	200	51	93	0	249	6	91	0	249	8	87	--
3.14		0.128	0.085	0	198	47	94	0	247	8	92	0	248	8	89	--					
6.28		0.108	0.082	0	178	46	94	0	247	9	92	0	246	9	89	--					
Catastrophes: Disease																					
0.00	Input Parameters: Captive Population: See Table 24 Wild Population: See Table 18						0.101	0.209	1	139	76	91	2	202	71	87	2	201	71	82	--
3.14		0.073	0.193	2	127	71	91	4	167	85	87	10	184	84	82	--					
6.28		0.049	0.193	2	118	65	91	5	156	85	88	10	140	92	81	--					

'Alala PHVA

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APPENDIX I.

HAWAI'IAN FOREST BIRDS CAMP TAXON REPORT

SPECIES: *Corvus hawaiiensis* - 'Alala

STATUS:

Mace-Lande: Critical
USFWS: Endangered
CITES: Not listed
State of Hawai'i: Endangered
IUCN: Endangered

Taxonomic status: Species

Distribution: Hawai'i, central Kona Coast on McCandless Ranch;
range less than 200 km²; possibly Hualala'i; occasional unconfirmed reports in Kau and
Kapapala forests.

Elevation: 1,000-8,000 ft. historically; 3,500-5,500 ft. presently

Wild Population: 12 in one population (Mauna Loa); 1 in another
(Hualalai)

Field Studies: see PHVA

Threats: Predation ('Io, Pueo), and predation by exotics (mongoose, rats, cats), disease,
catastrophes (fire, hurricanes, tsunami), genetics, human interference (shooting), loss of habitat,
catastrophes, (possibly interspecific competition for food from gamebirds and
introduced passerines).

Comments: The Hawai'ian crow is at such low numbers that any threat or loss of adults or
chicks would result in a significant population decline. Six chicks hatched via artificial
incubation eggs collected during 1993 season.

Recommendations:

Research Management: Monitoring; Limiting factors research; Limiting factors
management; Life history studies; Habitat management
PHVA: Yes; December 1992

Captive Population: 11 (plus 7 chicks hatched via artificial incubation during the 1993 season).

Captive Programs: Ongoing program should be increased; Emergency program should be
implemented for 90/100 level of management immediately (within 0-3 years).

APPENDIX II.

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SECTION 2.

AKOHEKOHE (CRESTED HONEYCREEPER)

Palmeria dolei

**POPULATION AND HABITAT
VIABILITY ASSESSMENT REPORT**

Compiled and Edited by

Ulysses Seal, Susie Ellis, Robert Lacy, Kimberly Hughes, and Cynthia Kuehler

in conjunction with the participants
of PHVA workshops held in
Hilo, Hawaii
10-12 December 1992

A Publication of the
CAPTIVE BREEDING SPECIALIST GROUP
SPECIES SURVIVAL COMMISSION, IUCN-THE WORLD CONSERVATION UNION

in partial fulfillment of
USFWS Grant No. 14-48-0001-925926



CBSG



AKOHEKOHE (CRESTED HONEYCREEPER)
Palmeri dolei
POPULATION AND HABITAT VIABILITY ASSESSMENT

Working Group: Ulysses Seal (Chairperson), Paul Conry, Fern Duvall, Jack Jeffrey

1. GENERAL BIOLOGY

1.1 Limiting Factors.

The Akohekohe or Crested Honeycreeper (*Palmeria dolei*) is thought to be limited in its population size because of the effects of avian disease, habitat degradation, fragmentation, and loss due to effects of human activities, alien mammal, bird, and plant invasions in its habitat, as well as predation by introduced birds (e.g., Common Barn Owl), rodents (e.g., Black Rat) and feral cats. The clearly demarcated and truncated population distribution at the 4,500' elevation on Haleakala is thought to be related to presence of avian diseases at lower elevations. Wet Ohi'a forests that seem adequate for the Akohekohe clearly extend far lower than the 4500' zone. Feral pigs, cattle, and goats all exist in Crested Honeycreeper habitat. The birds occur mainly in forests with good fern and subcanopy strata, and low levels of ungulate disturbance. Van Gelder (pers. comm.) reported the presence of, and trapped, the Black Rat (*Rattus rattus*) and feral cats (*Felis domesticus*) near nesting birds in the Waikamoi preserve. Wittemann (pers. comm.) suspects that Red-billed Leiothrix (*Leiothrix lutea*) may directly impact the Crested Honeycreeper by harassing foraging activities and possible nest predation. Short-eared Owls (*Asio flammeus sandwichensis*) were observed by Van Gelder only 60' and 80' from two different nests, respectively, lost to predation the following day.

1.2 Life History.

The Crested Honeycreeper is approximately 7" (18 cm) in length; weights for 6 birds ranged from 23-31 grams (Wittemann, pers. comm.). Plumage of adults is basically dull blackish gray with contour feathers tipped with white, cream-buff, red or orange. The nape and ocular ring is orange-red, and the distinctive brush-like crest is white or yellow and often covered with pollen. The tail is square and widely banded with white tips. Juveniles are gray-brown and non-descript, lacking a crest and colors except for the white tipped tail feathers. Voice is clear tonal whistle calls given singularly or in couplets; and song is characterized by unmusical guttural croaks, rasps, and clucking and clicks.

Foods taken seem to be primarily nectars of Ohi'a (*Metrisideros polymorpha*), Akala (*Rubus hawaiiensis*), Ohelo (*Vaccinium calycinum*), and mints (*Stenogyne spp.*), and perhaps fruit (or insects on the fruits) of Olapa (*Cheirodendron spp.*) and Kawa'u (*Ilex anomala*). Akohekohe forage for insects in terminal clusters of Ohi'a and other forest trees of upper and mid-canopies.

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Most foraging, and general activities too, take place in the high canopy layer of the forest. Long distance flights (> 1m) between foraging areas, for non-breeders, at approximately 100 m over the canopy, is commonplace. Wittemann (pers. comm.) reported such behavior started in late September, during his study.

Nests remained undiscovered until Van Gelder was able to locate 11 in 1992 in the Waikamoi Preserve. She found they were twig moss and lichen constructions, all in terminal clusters of Ohi'a 65' to 85' above ground level, and often over streams or steep ridges. One nest had been built over a previous nest. The vegetation at the nesting sites was comprised of endemics only; it remained unclear if the birds cued in on such floral pristine conditions as requisites for nesting. Van Gelder found the birds to be monogamous, and observed one pair in her study beginning a new nest together on the day after two, still dependent, fledglings of a first clutch successfully fledged. It is unclear how many clutches are produced in each annual nesting cycle. Clutch size appears to be two eggs on the average; Van Gelder observed nine nests with two chicks and two nests with one chick. Duvall (pers. comm.), however, observed one case in which three very recently fledged adult-dependent chicks were resting side-by-side. Nests were found between the first week of February and the 3rd-4th week in May. Incubation duration appeared to be 12-15 days, and nestlings fledged at 20-25 days of age. Fledgling food-begging calls appear to be soft whistles similar to, but not as loud as, adult whistles. Fledglings remained for up to 30 days in the immediate vicinity of the nest and nest tree attended by both parents. Parents mostly foraged in adjacent or nearby trees when procuring foods for dependent offspring.

Two nests were collected after fledging occurred and will soon be characterized. Perhaps most important was the discovery that all nests were within 100' to approximately 300' proximity to each other. Van Gelder felt that Akohekohe perhaps were loose colony nesters, especially since she did not observe intra-specific aggression even when conspecifics foraged in nest trees near active nests.

Akohekohe have been observed to fly high up above the canopy and also to fly in tight circles while vocalizing (approximately 200 m detection distance), often in small groups of three to four birds. This behavior often attracts other conspecifics. The function and significance of such behavior is unknown. Other social behaviors and detailed studies at the nest are currently underway by Van Gelder and Smith. Pimm and Conant have initiated a three-year banding, demography, and life history research project which began in the summer of 1992. Plans have been made to collect several pairs of Crested Honeycreepers for captive propagation research at the Olinda Endangered Species Captive Propagation Facility during 1993.

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2. POPULATION BIOLOGY

2.1 Introduction.

Historically, the Akohekohe was found in wet forests of East and West Maui and Moloka'i. By 1980 the population was reduced to a single wild population on East Maui, and was estimated at 3800 ± 700 birds (Scott et al., 1986). The most recent survey conducted in 1984 found a 30%

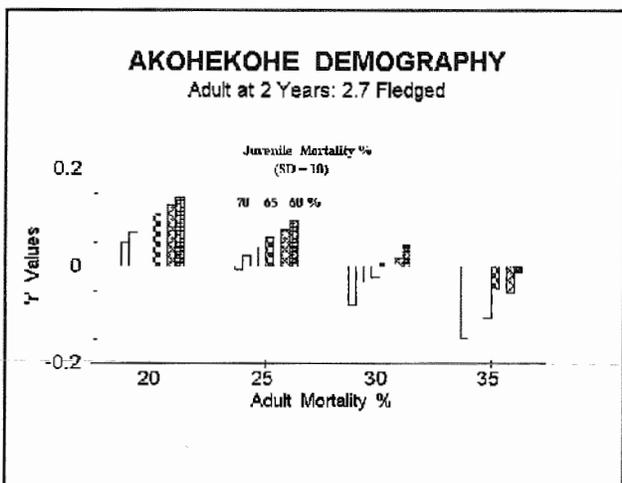


Figure 1. Effects of adult and juvenile mortality on population growth rate expressed as 'r'; the first bar represents the stochastic 'r' value and the second the deterministic 'r'.

reduction in the number of survey stations at which the bird was detected, suggesting a possible decrease in the population of this species. The range of the species (northeast slope of Haleakala, Makawao forest reserve to Kaupo) also appears to have constricted over the past 10-15 years. A field study on the breeding biology of the species by van Gelder and Smith is the only demographic information on nesting success. There is no captive population of this species. The Hawai'ian Forest Birds CAMP review (Ellis et al., 1993) recommended that a captive population be established within three years. The species is classified as Endangered by the USFWS and the State of Hawaii. The IUCN lists it as Rare. A review of the status of this species (Ellis et al., 1993), classified the species as Endangered based upon application of the Mace/Lande criteria (Mace and Lande, 1991).

2.2 General Southern Hemisphere Temperate Passerine Models.

The only data available on the demography of the Akohekohe are the historic loss of the Moloka'i and West Maui populations, the possible continuing decline of the remaining East Maui population based upon two censuses, and the one recent season of field data on nesting and production of fledglings (see below). This one season of reproductive data suggest that the reproductive strategy of the Akohekohe is similar to that of the southern hemisphere passerines summarized by Rowley and Russell (1991). We have used the information they presented to construct a matrix of models to encompass the range of reproductive and mortality data found in these species. Sensitivity analyses in this series of models, coupled with the information now available on the Akohekohe and that being collected in ongoing studies, may allow identification of high priority information needed to formulate a more accurate picture of the demography of

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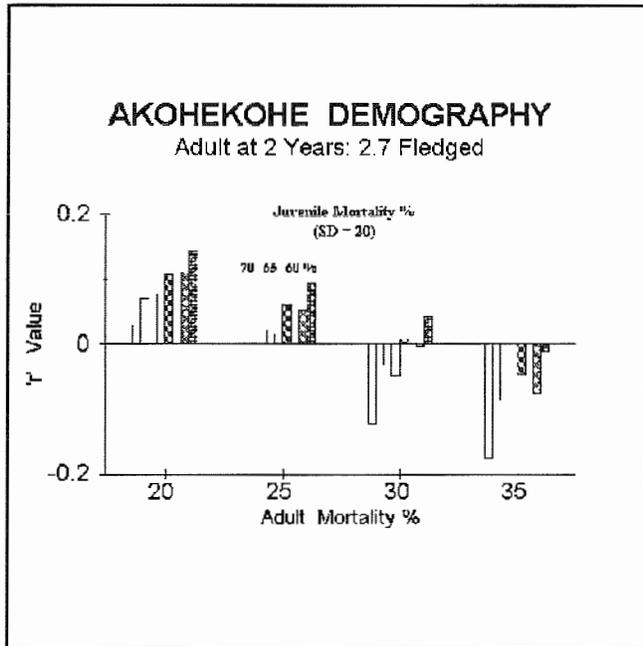


Figure 2. The EV of juvenile mortality was increased to 20% with all other conditions the same as in Fig. 1.

Juvenile survival from fledging to one year ranged from 28-41% yielding mortality rates of 59-72% from fledging to one year. Adult survival rates ranged from 58-87% (mortality rates of 13-42% per year). Fifteen of the 22 southern temperate species had survival rates of better than 70% (mortality rates of less than 30%). These survival rates are substantially higher than those reported for northern temperate species in Europe and North America where few species reach annual survival rates better than 70% and most are below 60%.

These demographic characteristics, and the sparse data available on the Akohekohe led us to examine the interactions of: 1) juvenile mortality (from fledging) of 60, 65, and 70%;

the wild Akohekohe population and to assist selection of targeted management priorities.

Detailed demographic information on wild populations of southern hemisphere temperate passerine species has been summarized by Rowley and Russell (1991). Pertinent data for 21 similar sized passerine species of Australia and New Guinea are reproduced in Table 1. Rowley and Russell stated that most or all of these species could breed at age one but that generally the age of first reproduction was two years. They noted that 16 of 21 species produced multiple clutches in a season, mean clutch size varied from 1.9 to 4.4 and that the number of chicks fledged per year varied from 1.1 to 4.0 with the values below 2 for those species that did not multiple clutch. Longevities ranged from 7-10 years with some birds living longer.

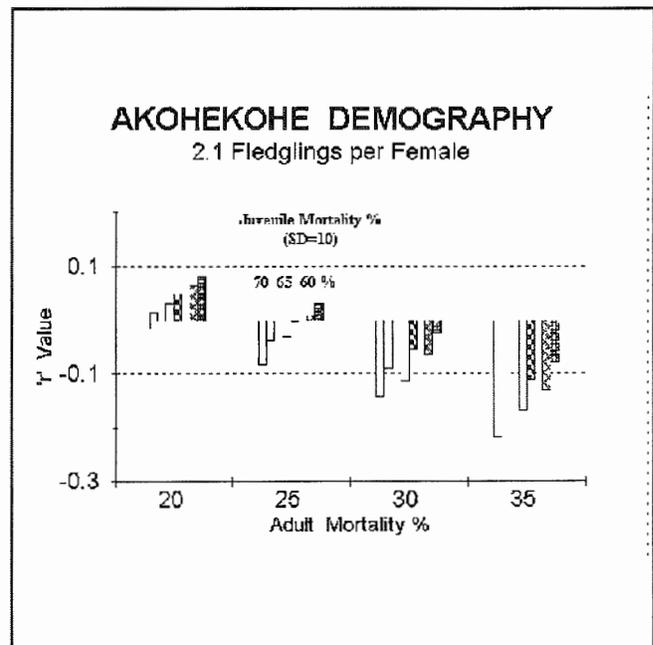


Figure 3. Reduction in annual productivity from 2.7 to 2.1 fledglings with other conditions same as Fig. 1.

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mortality (from fledging) of 60, 65, and 70%;

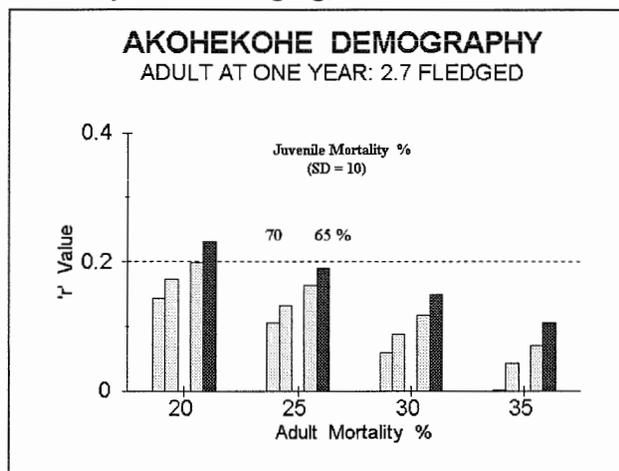


Figure 4. Age of first reproduction at one rather than 2 years, other conditions as in Fig. 1.

2) adult mortality of 20, 25, 30, and 35%; 3) productivity of 3 or 4 fledglings per year for 90% and 70% of adult females (this is equivalent to 2.70 or 3.60 fledglings per female when 90% of females successfully produce and 2.1 or 2.8 fledglings per female when 70% of females successfully produce fledglings in a given year); and 4) ages of first reproduction for both sexes of 1 or 2 years. The species was assumed to be monogamous in a season, all adult males were considered to be in the breeding pool, the sex ratio at hatching was taken as equal or 0.5, and the age of senescence was set at 10 years. No density dependence of either breeding or mortality was included. The carrying capacity was set at either 3000 or 5000 and the population truncated across age classes

and sexes when it reached this level in a given year. The results from the interactions of the combinations of these parameter values are tabulated in Tables 2-12 and are illustrated in Figures 1-16. The Tables are arranged such that each table is for a single value of juvenile mortality, age of first reproduction, and carrying capacity. Each Table presents the results from four levels of adult mortality, two levels of reproductive success (generally 2.1 and 2.7 fledglings per female) for each adult mortality level, and then two levels of variation in juvenile mortality (EV = environmental variation as standard deviation in annual mortality rates) for number of fledglings. The Figures present the interaction of the adult and juvenile mortality rates, across the range of selected values, upon the selected parameter ('r', population size, risk of extinction).

The baseline model was initialized with the conditions that breeding does not usually begin until year two, an average of two successful nests per year with a mean productivity of 2.7 or 2.1 fledglings, and a starting population of 2600 birds in a stable age distribution. The sets of mortality and reproductive values that are necessary for the population to maintain itself, under the specified conditions, can be quickly surveyed by scanning Tables 4-6 and Figures 1-3 for values of r that are positive under deterministic and stochastic scenarios. The first column of each pair of bars is the stochastic value of r and the second is the deterministic value. Each pair of bars is for a specified level of juvenile mortality and each grouping is for a level of adult mortality. The results, in terms of population growth rates, for 2.7 fledglings and two levels of EV in juvenile mortality suggest that the upper limits for adult mortality are 20-25% at juvenile mortality rates of 60-65% (Figures 1 & 2). Increased levels of year to year variation in juvenile mortality, such as might occur with a recurring disease process, reduce the levels of adult mortality that can be tolerated if the population is to remain stable or grow (Figure 6 and 8). Populations with a positive r can decline over the long term or appear to stabilize at lower

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numbers than the initial population of 2600. The risk of extinction is high for all levels of juvenile mortality with adult mortalities of 30 and 35% (Figures 7 & 9).

If productivity is 2.1 fledglings per year per adult female in the population then with 70% juvenile mortality from fledging to one year of age, the average annual mortality for birds of more than one year of age must be 20% (deterministic) or less (stochastic) for the population to survive (Figure 3, Table 4). If the juvenile mortality is reduced to 60% then the population can sustain about 20% adult mortality under a conservative stochastic scenario and have a positive r and have less than 5% probability of extinction in 100 years. However at the 25% adult mortality level the average population size declined about 50% in 100 years (Table 6).

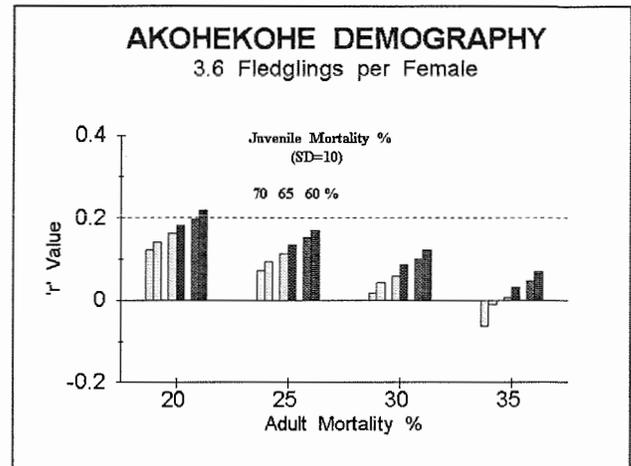


Figure 5. Mean annual productivity 3.6 fledglings rather than 2.7 with other conditions as in Fig. 1.

If productivity averages 3.6 fledglings per year per adult female in the population (three successful nests per year) then with 70% juvenile mortality to one year of age, the average annual mortality for birds of more than one year of age must be 30% (deterministic) or less (stochastic) for the population to have a positive r (Figure 5, Table 12). However a stable population for 100 years was only achieved with 25% adult mortality and low levels of EV. If the juvenile mortality is reduced to 60% then the population can sustain 35% adult mortality and maintain a stable population for 100 years with near 0 probability of extinction under conservative conditions of environmental variation (EV). Higher levels of EV result in a gradually declining population on average and about a 12% probability of extinction in 100 years (Table 12).

If the species usually breeds at one year of age, and produces 2.7 chicks per adult female in the population then it can sustain 70% juvenile mortality and about 20-25% adult mortality and maintain a stable or slowly declining population (higher EV) with a low probability of extinction in 100 years (Figure 4, Table 2). Reduction of juvenile mortality to 65% provides a stable or growing population under these conditions (Table 3).

2.3 Akohekohe Wild Population Variables.

2.3.1 Habitat Capacity. The Akohekohe was reported to occur at densities greater than 200 per km² in some locations at elevations above 1500 m (Scott et al., 1986). However, given the

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possible range constriction at present, the possible 30% reduction in population size from 1980 to 1992, and the uncertainty about the factors responsible for the decline of the bird on West Maui and Moloka'i, two carrying capacity values were evaluated in the model. One was 3000 and the other 5000 birds. If additional suitable habitat is available to the species but it is not maintaining or expanding its range, this provides an indication of limiting factors in its environment and a continuing decline.

Comparisons of effects of K on P(E) (Figures 13 & 15) and population size (Figures 12 & 14) were done with age of first reproduction of two years, production of 2.1 or 2.7 fledglings per female in the population, and other conditions as set for all of the Tables. The deterministic r values are not affected by simply changing K from 3000 to 5000 (for example compare files 74-77 in Table 4 with files 109-112 in Table 7). The differences in the

stochastic r values are also minimal in the same comparisons and probably reflect chance differences. Extinction probabilities in most of the simulations were not affected by the choice of K as either 3000 (Figures 7 & 9, Tables 4-6) or 5000 (Figures 13 & 15, Tables 7-9). Those

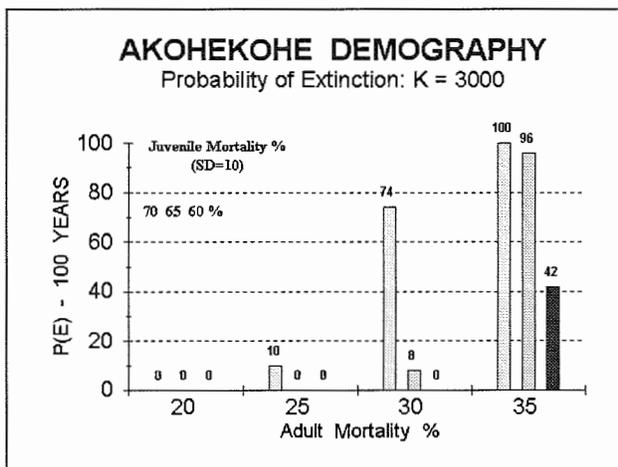


Figure 7. Effects of levels and stochasticity in adult and juvenile mortality on P(E) under the conditions of Fig. 1. Compare with Figs. 5 & 6.

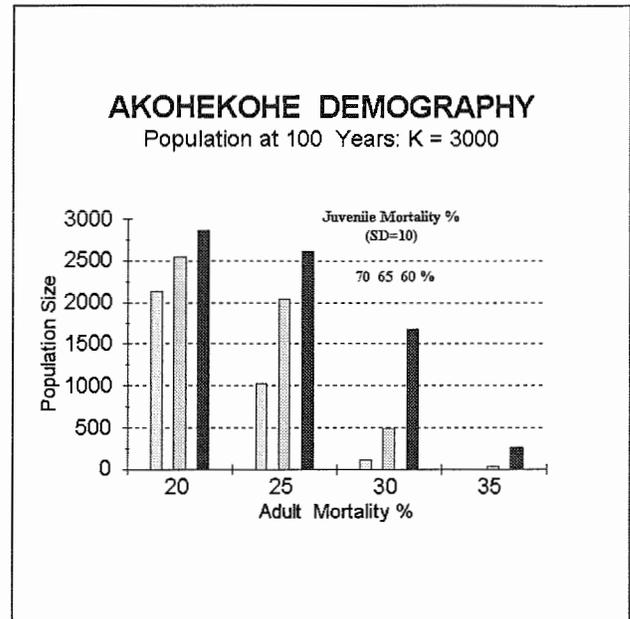


Figure 6. Simulated effects of stochasticity in mortality on population sizes at 100 years with conditions the same as in Fig. 1. Compare with the 'r' values in Fig.5.

scenarios that included increased levels of EV in juvenile mortality resulted in lower population sizes at 100 years (Figures 12 & 14), but they were still higher than with the carrying capacity set at 3000 (Figures 6 & 8).

2.3.2 Mortality. There is no information on mortality rates or life expectancy for the akohekohe either in the wild or captivity. We have drawn upon life history information from similar passerine species in Hawai'i and other regions of the Southern hemisphere temperate tropics to estimate the boundary conditions for juvenile and adult mortality for the reproductive scenarios. These scenarios for the Akohekohe are based upon the set of nesting data in the

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next section and options based upon between one and three successful nests in a year by the breeding birds as occurs in other species in this region. Juvenile mortalities are estimated from the time of fledging to the age of one year. Juvenile mortality rates of 60, 65, and 70% per year were used in a matrix of combinations with adult mortality rates of 20, 25, 30, and 35% as described above. These values are in the range that has been reported from studies of temperate southern passerines. Mortality rates for the 1-2 year age class, for the scenarios based upon two years as the age of first reproduction, are set as the same as adult mortality rates. Since there are no data on the sex ratio of the adult population, male and female mortality rates are set the same.

We examined two levels of variation in juvenile rates (10 and 20%) as expressed in the standard deviation of the mortality rates. The higher level (20%) provides an indication of possible fluctuating effects of disease upon juvenile survival rates. Possible epidemics, with larger mortalities, have not been included in these scenarios but might be considered as possible catastrophic events. Their impact would be to further increase the risk of extinction and decrease population sizes. Also no consideration has been given to possible trends in mortality or reproduction imposed by environmental events such as long term habitat management effects or global warming.

2.3.3 Reproduction. The available data are from one breeding season and are tabulated here. This is the only life history information available for this species, although additional field studies are now under way. It is planned to bring some birds into captivity in the near future. Assuming that husbandry will be successful, additional useful information on reproduction can be obtained from the captive studies.

Data of Van Gelder:

Nest	Eggs	Chicks (Assumed)	Fledged
1	2	2	2
2	2	2	2
3	2	2	0
4	2	2	1
5	2	2	2
6	2	2	0
7	2	2	2
8	2	2	1
9	2	2	2
10	2	1	1
11	2	1	1
13		2	

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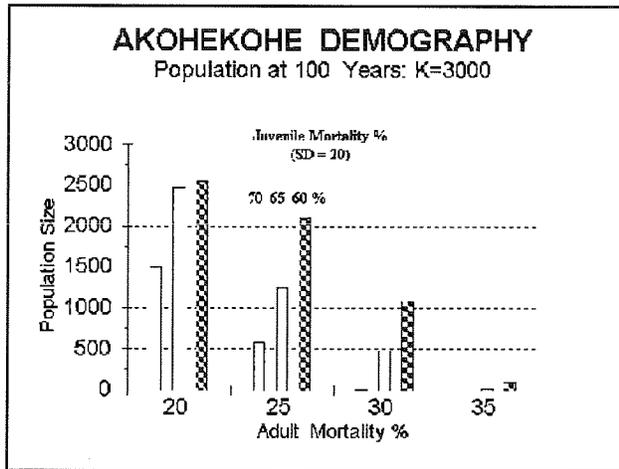


Figure 8. Simulation of effects on increased EV (SD as a measure of environmental stochasticity) in juvenile mortality on projected population size at 100 years.

Year-to-year variation in mortality rates of juvenile Akohekohe may be influenced by variations in available food resources, rainfall, predation (avian and mammalian), and disease (malaria and avian pox).

These data served as the basis for estimation of average clutch size (2.0 per nest), hatching rate (1.82 per nest) and fledging rate (1.27 per nest) for the 11 nests observed from the beginning) - recognizing the small sample size and that only one year of data are available. Another active nest has been found in the Hawai'i Natural Area Reserve (P. Conry, pers. comm.) and contained two chicks. However, the nest was not monitored and its outcome is unknown.

Another observation was made of three equal sized fledglings roosting side-by-side on a branch (F. Duvall, pers. comm.). It was assumed they were from the same nest. These data were not used in the estimates. However, they do suggest that occasional nests with three eggs may be found.

2.3.4 Inbreeding Depression. Inbreeding depression was not included in the model since there is no indication that this population has been through a recent bottleneck (low hundreds or less) and the census numbers have been in the low thousands. The model does indicate the rates of loss of genetic heterozygosity through time based upon random drift effects. Estimates of effective population size, as a fraction of the total population size, have not been made. There are not any molecular genetic data on levels of genetic heterozygosity in the population.

2.3.5 Census and Distribution. The species formerly was more widely distributed on Maui and on Moloka'i. It is now restricted to a single population estimated at 3800 ± 700 in 1980. The last census was done in 1992 and the population may have declined further at that time based upon its detection at fewer of the census stations. Given this possibility, we chose to initialize the models with a population of 2600 distributed across the age classes

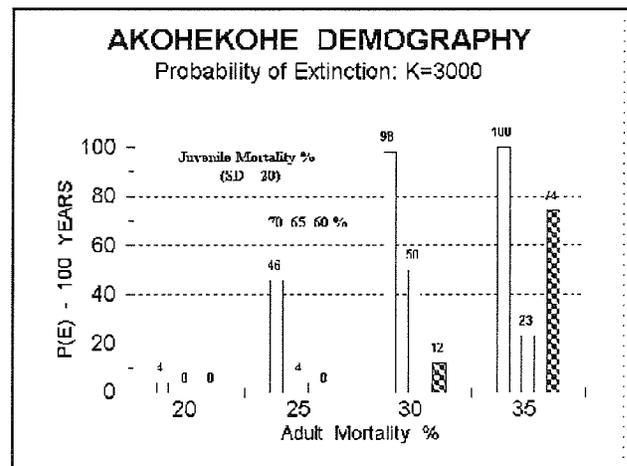


Figure 9. Effects of increased EV in juvenile mortality on P(E) over 100 years. Compare with Fig. 8. Other conditions as in Fig. 1.

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according to a stable age distribution and with an even sex ratio.

Trends of rates of change of 1-2% per year are very difficult to detect with current census methodology, even over a 10-20 period and year to year variations and short-term fluctuations further complicate detection of long-term trends. However, the shrinkage of range of the species which has occurred during the past 50 years appears to have continued and the census of 1980 suggests an interpretation of a declining population.

2.3.6 Catastrophes. Events evaluated as possible catastrophes for the Akohekohe included hurricanes, reduced rainfall, fire, predation by exotics, and disease epidemics. Habitat alteration by exotic plants would likely not be a sudden pulse event but would be reflected by a decline in range and numbers over time. Pulses in predation might occur depending upon increases in other food resources for the predators supporting an increase in their population. Disease may be having a continuing impact upon the juvenile survival rates, with year to year variation but there is no evidence for (or against) periodic epidemics causing substantial mortality over a short period of time in the Akohekohe. This may change with the continued spread of mosquitos and carrier species to higher altitudes. There are no recent records of hurricanes through the habitat of the akohekohe, but examination of historical data (Armstrong, 1991) suggested that one per century might pass over the island. Rainfall is high and periodic decreases still do not result in droughts in the usual sense and there does not appear to be clear evidence of adverse effects of observed fluctuations in rainfall. We included two low- probability events at a frequency of 1% (1 per century on average) with minimal

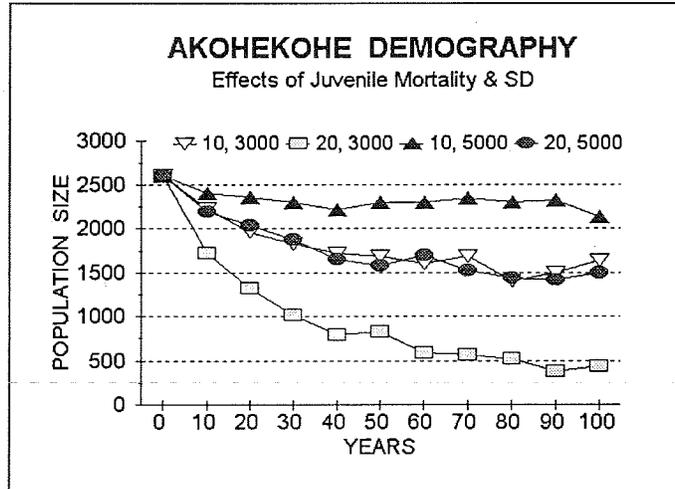


Figure 10. Sizes of surviving population and their SDs with identical conditions and 'r' values except for increased EV of juvenile mortality.

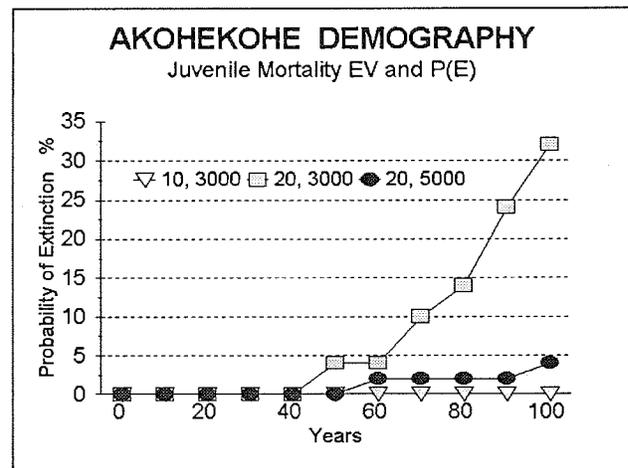


Figure 11. Progressive effects of increased environmental variance in juvenile mortality on the risk of extinction. The deterministic 'r' values are the same. See Fig. 11.

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We included two low- probability events at a frequency of 1% (1 per century on average) with minimal effects upon survival (20% reduction in the year of the event). One event was modelled to have no effect upon reproduction and the other reduced reproduction 90% for one year.

2.3.7 Time Span of the Simulations. All scenarios were simulated for 100 years with reports at 10 year intervals to provide trend information on rates of extinction and population change. Given an approximate generation time of about four years this provides a span of about 25 Akohekohe generations. This time span allows the demonstration of subtle long term effects that may result in a declining population.. The number of runs per scenario ranged from 100 to 250 depending upon the statistical reliability wanted for the estimates of population size, P(E) and the stochastic r value.

2.4 Assumptions and General Conditions of the Simulations.

The minimal population and life history data available for this species necessitated use of general information from other tropical passerine species from Hawai'i (Van Riper, 1987; Morin, 1992; Pletschet and Kelly, 1990; and Palila data summarized in this report), Australia, and New Guinea (Rowley and Russell, 1991) in the modelling process as well as information on southern hemisphere temperate region passerines.

One population was simulated since there is only one remaining wild population. The sex ratio at hatching was taken as 0.500 and no differential mortality was applied to the sexes since there are no data on the sex ratio in the population. The age of senescence was taken as 10 years although data from other wild passerines suggests they might live as long as 12 years. However, given the typical adult mortality rates of other species in the wild, few birds will live beyond this time. Monogamous mating within a given season was assumed and all adult males were assumed to be potentially in the breeding pool so that availability of males would not limit the number of females that breed in a given season. Reproduction was assumed to be density-independent since it was felt that there is contiguous unoccupied habitat available. Also there is little persuasive evidence for density-dependence in southern hemisphere temperate passerines (Rowley and Russell, 1991).

Each scenario was run 200 times for 100 years for the one population. Data reports were taken at ten year intervals for analysis of trends. Extracts of the data from the individual scenarios are presented in the Tables and Figures. The VORTEX input and output files from all the scenarios are available as MSDOS ASCII files on disk. Details concerning use and the algorithms of the VORTEX program are provided in the VORTEX User Manual available from the CBSG Office.

3. RESULTS FOR THE AKOHEKOHE POPULATION

The results of the simulation models are summarized in Tables 1-12 and Figures 1-15. Some of

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the results from 192 scenarios are presented. The outputs from each of the scenarios are available as ASCII computer files on 3 1/2 inch disks in MSDOS format. Simulations were run with VORTEX version 5.1, dated May 7, 1992. A copy of the input file and the output for one scenario is attached as an appendix to this report.

All of the scenarios were formulated in terms of a 4-way matrix of juvenile and adult mortality rates, productivity, and variation in juvenile mortality (Tables 2-12). Each Table is for a single juvenile mortality rate (60, 65, or 70%) and each Table includes a set of four scenarios for each of four adult mortality rates (20, 25, 30, and 35%). Each of these sets includes two levels of productivity or fledglings per female and two levels of variation - 10 & 20% - of juvenile mortality for each level of productivity for a total of 16 scenarios in each Table.

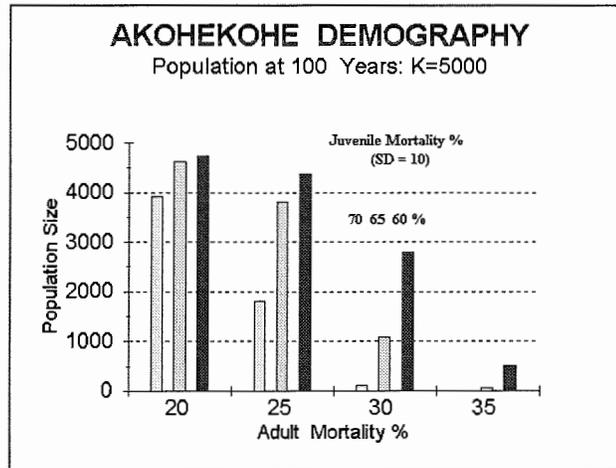


Figure 12. Effects of increasing K to 5000 on the projected population sizes at 100 years. Other conditions same as Figs. 1 and 6.

The effects of three additional variables upon projected risk of extinction and population size estimates in the four-way matrix were evaluated. The age of first reproduction (as one year rather than two years in Tables 2 & 3 and Figure 4), carrying capacity (5000 rather than 3000 in Tables 7-9), and increased productivity (three nests per year rather than one or two) (Tables 10-12). The baseline scenarios, Tables 4-6, were with values of two years for age of first reproduction, 3000 for carrying capacity, and either 2.7 or 2.1 fledglings per year per female (90 and 70% times three fledglings per nest rows in all Tables).

The output data presented in each Table for each scenario (a code number for the scenario is in the first column of the Tables) include:

- (1) the calculated deterministic 'r' (based upon females with no limitations of mates and no inbreeding depression),
- (2) the mean stochastic 'r' and its standard deviation (r is calculated for each run or population over the 100 years of the simulation for each run and then the statistics are calculated over the number of populations ranging 100 to 250 depending upon the number of runs made),

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and at 20, 50, and 100 years

(3) the probability of extinction, PE, as a per cent,

(4) the mean population size with its standard deviation,

(5) the expected per cent heterozygosity remaining in the population (this figure is calculated to two decimal places so that a value of 99 might actually be between 98.6 and 99.9%).

and finally at 100 years

(6) the mean or median time to extinction, T(E), in years. Medians are reported when half or more of the populations had gone extinct during the 100 year time period of the projections otherwise the number is the mean for the populations that went extinct.

3.1 Age of First Reproduction.

Species similar to the Akohekohe are usually physiologically able to breed at one year especially if maintained in captivity. However few of the southern temperate passerine species breed before the age of two years in the wild. If the Akohekohe regularly begins breeding at the age of one with two nests per year and an average of 2.7 fledglings per female per year, then the population could maintain a positive growth rate with an adult mortality rate no higher than 20% with a juvenile rate of 70% (Table 2 and Figure 1). If the juvenile rate is decreased to 65% with an EV of 10% (standard deviation) then an adult rate of 30% could be sustained. If the EV of the juvenile rate was increased to 20% then a long term decline in the population occurred with a 10% probability of extinction by 100 years. Deterministic calculations of 'r' yielded positive or zero values for seven scenarios with negative stochastic 'r' values.

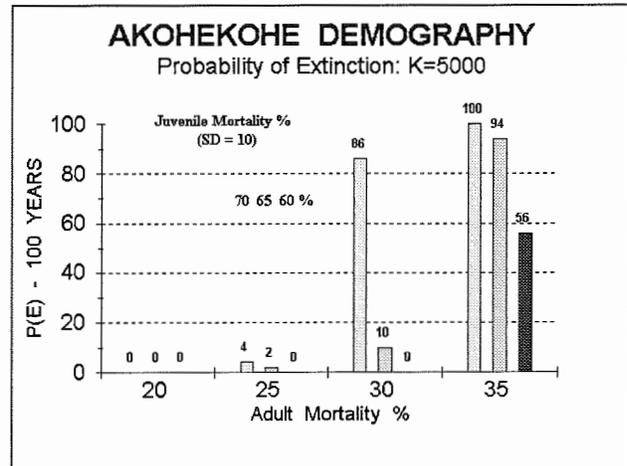


Figure 13. Effects of increasing K to 5000 from 3000 on P(E) at 100 years. Other conditions same as Figs. 1 and 7.

Most of the sets of simulation scenarios were run with 2 years taken as the age of first reproduction. This choice was based upon the reported studies of other southern temperate and

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tropical passerine species (Rowley and Russell, 1991). Until field studies of the Akohekohe provide data, this assumption would be the most conservative choice.

3.2 Mortality.

No mortality data are available for the Akohekohe. Estimates are available for about 22 southern hemisphere species, Table 1 (adapted from Rowley and Russell, 1991) and for tropical passerines which indicate a different life history strategy for these species when compared to the Northern temperate species. Annual mortality rates ranged from 13 to 45% with a mean of 27%. These small passerines of the southern hemisphere are longer lived and have lower annual mortality rates than the species of the northern hemisphere (North America and Europe) which are reported to have annual adult mortality rates of 30-60%.

Simulations of the interaction of juvenile mortality (from fledging to age one year), adult mortality, and number of fledglings on the deterministic and stochastic 'r' (population rate of increase) were done (Figures 1,4, and 5) using ranges of values based upon the Akohekohe fledging data and from the published data on other southern hemisphere passerines (Table 1). If the Akohekohe nests only once in a season (Figure 5), then juvenile mortality would need to be less than 60% and adult mortality less than 20% per year. Two nests per year (Figure 1) would

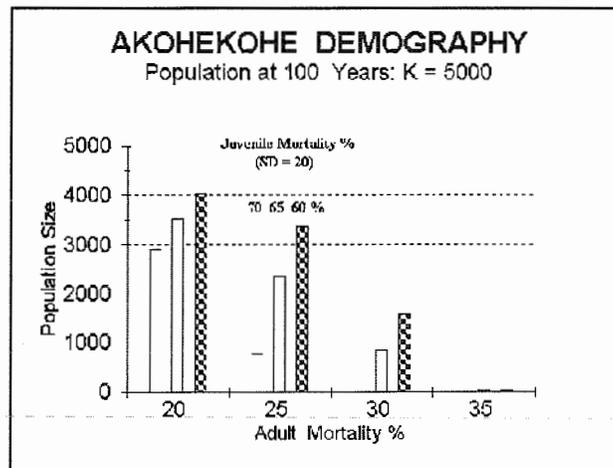


Figure 14. Effects of increasing K to 5000 from 3000 and higher $EV=20$ in juvenile mortality on projected population at 100 years. Compare Fig. 13.

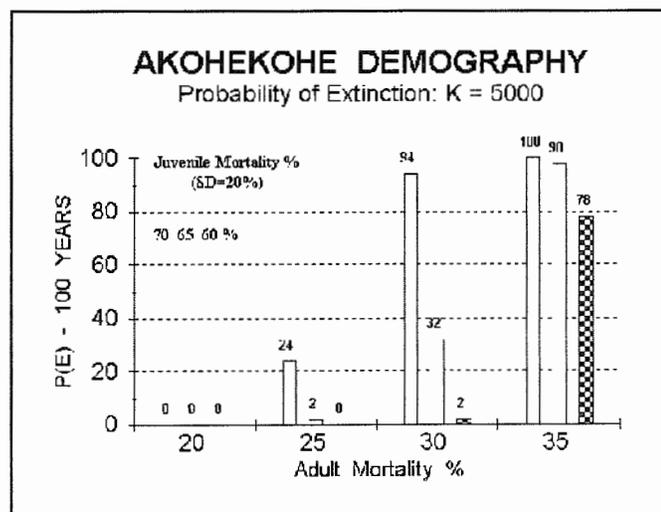


Figure 15. Effects of increasing K to 5000 from 3000 on P(E) at 100 years. Other conditions same as Fig. 1.

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allow a positive growth rate at about 65% juvenile mortality and 25% adult mortality with a wide range of environmental variance (Figures 1 and 2). However the recovery of the population after losses would be marginal and slow at these limiting values (Figure 6) particularly if the environmental variance in juvenile mortality is high (Figure 8). The probability of extinction in 100 years is less than 5% under these conditions (Figure 7 and 9). Expansion of carrying capacity to 5000, with this mortality scenario, indicates that the population size would be larger at 100 years (Figure 10 and 12).

3.3 Life Span, Sex Ratio, and Mating.

The age of senescence was set at 10 years. This may be an underestimate since many of the Australian passerine species have a few individuals living to 11 or 12 years. Given the adult mortality rates, the demographic effect on 'r' or final population sizes of choosing 10 years will be minimal. There is no information on the adult sex ratio of the Akohekohe population. For these simulations it was assumed that the species is monogamous in a season and that all adult males were available as breeders.

3.4 Catastrophes.

Catastrophes were estimated to occur at such a low rate (one per century) that they had little impact upon the outcome averaged over 100-250 simulated populations.

3.5 Carrying Capacity.

Population size was estimated at 3800 ± 700 in 1979 and based on a 30% decline in stations occupied by 1992, was assumed to be about 2600 for these simulations. It was estimated at 3800 ± 700 in 1979. We chose to compare scenarios in which population growth was limited by habitat resources and scenarios for which population size may be limited by factors such as predation or disease but not habitat resources. This distinction is important for developing and testing alternative management strategies for which are designed to reverse the decline of the Akohekohe. However, density dependent variation in reproductive rate or adult survival has not been demonstrated for any of the Australian passerines so far studied (Rowley and Russell, 1991). The starting population size for all of the scenarios was set at 2600. In VORTEX when the population size reaches the carrying capacity in a given year of the simulation, the population is truncated by removal of animals from all of the age and sex classes.

The effect, on population size at 100 years and on P(E), of setting carrying capacity at 3000 (Figures 6-9) and 5000 (Figures 10-13) was compared at the two levels of EV in juvenile mortality.

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When the EV of juvenile mortality was simulated at SD=10%, the population sizes of surviving populations were almost doubled when K was set at 5000 rather than 3000 under all of the conditions tested (12 scenarios) that yielded survivors at 100 years (Figures 6 and 10). However, the probability of extinction was not significantly affected in any of these scenarios (Figures 7 and 11). The mean or median times to extinction were also similar.

When the EV of juvenile mortality was simulated at SD=20%, the population sizes of surviving populations at 100 years were consistently lower than those observed with EV=10% (Figures 8 and 12). Setting K at 5000 compared to 3000 again resulted in higher population sizes under all of the conditions tested that yielded survivors at 100 years (Figures 8 and 12). The probability of extinction was less, for K=5000, in some of these scenarios (Figures 9 and 13) with intermediate P(E) values. The mean or median times to extinction were similar.

4. CAPTIVE POPULATION

A decision has been made to begin establishing a captive population of the Akohekohe. The CAMP review of all of the Hawai'ian forest birds supported this decision with the recommendation that a breeding population be established over the next three years. The current IUCN policy on captive breeding for conservation of species advocates the establishment of captive populations early in the decline of a species while the numbers are in the thousands. This allows collection of sufficient numbers of founders, over a time period suitable for the species and the rate of the decline, to accomplish the learning process for husbandry and reproduction and to establish sufficient facilities and expertise to manage a population of the size and productivity needed to meet program goals.

There are at least three sets of considerations to evaluate in the process of developing program goals for this species. They include: 1) the effort required to establish the husbandry requirements of the species and the requirements for successful or maximal reproduction; 2) the biology of the species of which little is known but much can be guessed; and 3) the resources for the tasks, including facilities and personnel.

The first factor is of importance because: a) there is no direct experience with this species; b) the small passerines have received relatively little attention for their husbandry requirements; c) this group of passerines has specialized nutritional requirements which require experienced expertise to identify and provide a balanced captive diet; and d) there will be a need for ongoing veterinary attention to minimize the occurrence of disease and to manage illness and failure to thrive as it occurs. All of these factors emphasize the importance of resource commitment to provide a fair opportunity for success in the program. These factors are discussed in detail in the CAMP Report on the Hawai'ian Forest Birds.

The second factor, limited knowledge of the biology of the species, suggests the importance of

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organizing the captive management program to collect high priority biological information on the species during the establishment of the program and as a goal of the program. Some characteristics can already be inferred from the studies underway. Informed guesses can be made on other traits of importance for a captive breeding program. Thus it is likely that in captivity the birds can breed at the age of one year and that they can produce two or three clutches per year. The nest studies done the past year indicate high fertility and hatchability with the greatest losses occurring between hatching and fledging. These losses may be due to either predation or disease both of which should be reduced in the captive population. The life span of the Akohekohe under optimal conditions may be 10-12 years and its reproductive life span at least 5-7 years. These provide some indicators of goals to achieve with captive husbandry. However this must be tempered with the observation that 30% annual mortality rates are the current norm for such species in captivity. (It will be useful to do a breakdown into northern and southern temperate species and tropical species to see if there is a differential in captivity as in the wild.)

The third factor of resource requirements will include the need to use expertise from around the world to assist the program for this species and to bring together the highly dispersed information that is already available. The actual scope of the physical facility requirements will evolve on an experimental basis depending upon the husbandry needs of the species.

All of these problems characterized the black-footed ferret (*Mustela nigripes*) program at its initiation. They included a similar level of ignorance of the captive requirements of the species, a similar demographic pattern of reproduction and mortality (although only one litter per season), and a similar need for resources. Once the husbandry and needs were identified and conditions providing maximum reproductive output were established, the population rapidly expanded and subpopulations are being established in a number of locations while an active reintroduction program is underway.

5. SUMMARY

Understanding of the dynamics of the wild population Akohekohe will depend upon collection of some very fundamental demographic information. High priority items are the average age of first reproduction and the average number of successful nests each year. Estimates of adult mortality rates and of mortality between fledging and age of first reproduction are also essential. It would be useful to have information on the adult sex ratio of the population given the apparent monogamy of these species. This information would provide a basis for seeking the factors that may be limiting the expansion of the population or are producing a continuing decline in range. Each piece of information would allow a stronger focus on management research that is needed to maintain the wild population and support its expansion into favorable habitat. The lack of much of this information further supports the decision to establish a captive population as a research tool for the species as well as providing a backup if there is a further precipitous decline as a result of disease or unexpected events.

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TABLE 1. REPRODUCTION AND MORTALITY IN SOME SOUTHERN HEMISPHERE PASSERINES (Adapted from Rowley and Russell, 1991)					
SPECIES	Weight - g	Repeats	Fledges/ Egg Laid	Fledged	Adult Mortality
<i>Eopsaltria georgiana</i>	17	+	.81	3.1	22
<i>Eopsaltria australis</i>	22	+	.28	2.1	25
<i>Pomatostomus temporalis</i>	40	+	.60	2.3	
<i>Malurus splendens</i>	10	+	.47	2.8	28
<i>Malurus cyaneus</i>	10	+	.53	3.9	34
<i>Malurus elegans</i>	9	+	.52	2.5	19
<i>Acanthiza reguloides</i>	8	-	.20	1.1	42
<i>Acanthiza pusilla</i>	7	-	.19	1.0	13
<i>Acanthiza chrysorrhea</i>	7	+	.53	3.7	
<i>Manorina melanophrys</i>	32	+	.33	3.7	37
<i>Phylidonyris novaehollandiae</i>	22	+	.76	2.8	45
<i>Zosterops lateralis</i>	11	+	.44	3.1	40
<i>Corvus mellori</i>	541	-	.36	1.5	15
<i>Corvus coronoides</i>	645	-	.35	1.5	23
<i>Petroica australis</i>	22	+	.27	2.5	20
<i>Gerygone igata</i>	6	+	.38	4.0	18
<i>Mohoua albicilla</i>	18	+	.35	1.1	
<i>Hirundo spilodera</i>	21	+	.57	1.8	
<i>Pogonocichla stellata</i>	21	-	.51	1.5	20
<i>Motacilla clara</i>	20	+		1.7	25
<i>Myrmecocichla formicivora</i>	46	+		3.2	

Data on juvenile mortality (i.e., from fledging to one year) was limited to three species (*Malurus splendens*, *M. elegans*, *Eopsaltria georgiana*) and was 47,59, and 72%, respectively.

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Table 1. AKOHEKOHE - VARIABLE AGE FIRST BREEDING AND JUVENILE AND ADULT MORTALITY

FILE	MORTALITY			Results															TE Yr	
	0-1	>1	>1 SD	Population Growth			20 years				50 years				100 years					
				Deter r	Stochastic r	SD	PE %	N	SD	H	PE %	N	SD	H	PE %	N	SD	H		
Age First Breeding = 1 Year																				
008	80	30	3	-.049	.099	.22	0	777	576	99	10	127	167	92	93	15	10	70	68	
009	77.5			-.012	-.050	.19	0	1275	791	99	4	582	676	97	41	265	402	84	79	
007	75			.023	-.001	.16	0	1870	702	99	0	1482	836	99	0	1146	941	96	-	
010	72.5			.056	.038	.16	0	2254	631	99	0	2295	658	99	0	2264	672	98	-	
Age First Breeding = 1 Year																				
012	80	35	3	-.100	-.155	.24	0	320	280	99	68	12	11	73	100	0	0		45	
013	77.5			-.062	-.120	.22	0	533	419	99	27	68	118	85	98	58	13	75	58	
011	75			-.025	-.068	.20	0	1110	686	99	2	451	559	95	62	164	414	82	89	
014	72.5			-.009	-.022	.18	0	1758	759	99	1	1056	751	98	13	619	681	94	85	
Age First Breeding = 2 Year																				
016	80	30	3	-.125	-.172	.22	0	183	147	99	84	6	6	72	100	0	0		41	
017	77.5			-.099	-.144	.21	0	327	203	99	53	13	23	81	100	0	0		50	
015	75			-.074	-.115	.20	0	536	273	99	15	35	33	89	99	4		66	61	
018	72.5			-.052	-.092	.19	0	757	440	99	1	110	105	94	99	6		79	76	

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Age First Breeding = 2 Years																		
020	80	35	3	-.183	-.228	.23	2	59	40	96	100	0			100	0		31
021	77.5			-.156	-.205	.24	0	100	66	98	99	3		72	100	0		35
019	75			-.131	-.177	.23	0	167	110	98	95	5	3	69	100	0		41
022	72.5			-.108	-.156	.22	0	263	152	99	71	10	10	68	100	0		45

Male and female age of first reproduction set at **1 or 2 years**. Juvenile mortality from time of fledging, varied from 72.5 to 80% with 10% SD as estimate of environmental variation effects. **Three fledglings** per female per season with 10% of females not successful. Carrying capacity set at **3000** with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding in a season with all adult males in the potential breeding pool. No density dependence except for truncation at K. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction for 1 year and a 20% decrease in survival.

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Table 2. AKOHEKOHE - K=3000, ADULT AT 1 YEAR, 70% JUVENILE MORTALITY

File	Input Values			Results															TE Yr	
	%F Br	<1 Mt	SD Mt	Population Growth			20 years				50 years				100 years					
				Deter r	Stochastic r	SD	PE %	N	SD	H	PE %	N	SD	H	PE %	N	SD	H		
Adult mortality = 20 ± 10 %																				
204	90	70	10	.173	.144	.22	0	2612	586	99	0	2666	506	99	0	2683	553	99		
205			20	.173	.109	.33	0	2192	816	99	0	2201	741	99	0	2356	944	98		
206	70		10	.091	.062	.20	0	2458	636	99	0	2222	766	99	0	2493	760	99		
207			20	.091	.034	.30	0	1682	828	99	0	1629	919	99	0	1418	998	96		
Adult mortality = 25 ± 10 %																				
044	90	70	10	.132	.106	.22	0	2650	499	99	0	2602	558	99	0	2583	521	99	-	
045	90	70	20	.132	.069	.35	0	2032	883	99	0	1705	954	99	2	1868	1024	97	-	
046	70	70	10	.046	.014	.22	0	1817	744	99	0	1490	950	99	2	1511	1070	95	-	
047	70	70	20	.046	-.020	.32	0	1503	1002	99	4	974	971	96	28	638	932	90	74	
Adult mortality = 30 ± 10 %																				
040	90	70	10	.088	.059	.23	0	2330	729	99	0	2277	752	99	0	2190	750	98	-	
041	90	70	20	.088	.0007	.38	0	1469	1030	99	6	1087	1008	96	32	1168	976	92	65	
042	70	70	10	-.000	-.048	.24	0	1346	789	99	0	612	610	96	30	177	353	84	78	
043	70	70	20	-.000	-.090	.34	2	772	644	99	32	467	640	92	84	100	131	72	68	

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Adult mortality = 35 ± 10 %																			
048	90	70	10	.043	.001	.25	0	1897	776	99	2	1425	1032	99	8	1158	1005	93	75
049	90	70	20	.043	-.069	.39	0	871	899	98	26	590	933	91	76	514	887	86	71
050	70	70	10	-.049	-.111	.27	0	623	668	99	38	129	177	89	90	18	16	74	59
051	70	70	20	-.049	-.154	.37	0	553	634	97	64	39	60	83	99	0			44

Male and female age of first reproduction, **1 year**. Juvenile mortality from time of fledging set at **70%** with 10% and 20% SD as estimate of environmental variation effects. **Three fledglings** per female per season with 10 or 30% of females not successful. Carrying capacity **3000** with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 3. AKOHEKOHE - K=3000, ADULT AT 1 YEAR, 65% JUVENILE MORTALITY

File	Input Values			Results															TE	
	%F Br	<1 Mt	<1 Mt SD	Population Growth			20 years				50 years				100 years					
				Det r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
Adult mortality = 20 ± 10 %																				
204	90	65	10	.230	.198	.21	0	2923	353	99	0	2759	497	99	0	2919	337	99		
205	90	65	20	.230	.179	.31	0	2559	638	99	0	2608	619	99	0	2697	650	98		
206	70	65	10	.140	.122	.19	0	2787	371	99	0	2770	323	99	0	2705	500	99		
207	70	65	20	.140	.091	.28	0	2258	855	99	0	2413	762	99	0	2450	793	98		
Adult mortality = 25 ± 10 %																				
056	90	65	10	.190	.164	.21	0	2805	545	99	0	2726	467	99	0	2730	425	99		
057	90	65	20	.190	.136	.33	0	2481	852	99	0	2359	736	99	0	2404	725	98		
058	70	65	10	.097	.073	.20	0	2617	579	99	0	2467	763	99	0	2323	708	99		
059	70	65	20	.097	.048	.29	0	2049	847	99	0	1839	972	99	0	1642	995	97		
Adult mortality = 30 ± 10 %																				
052	90	65	10	.149	.117	.23	0	2767	423	99	0	2609	632	99	0	2615	591	99		
053	90	65	20	.149	.084	.34	0	2012	826	99	0	2047	866	99	0	2000	943	97		
054	70	65	10	.053	.022	.22	2	2034	786	99	2	1608	912	99	2	1636	897	97	20	
055	70	65	20	.053	-.016	.32	0	1473	953	99	4	992	981	97	32	854	859	93	69	

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Adult mortality = 35 ± 10 %																			
060	90	65	10	.106	.071	.23	0	2418	734	99	0	2351	770	99	0	2330	772	98	
061	90	65	20	.106	.034	.36	0	1658	843	99	0	1540	1009	98	10	1491	952	95	84
062	70	65	10	.006	-.050	.25	0	1333	750	99	4	600	697	97	52	364	502	86	97
063	70	65	20	.006	-.074	.35	0	972	853	99	22	496	727	91	72	205	244	87	68

Male and female age of first reproduction, 1 year. Juvenile mortality from time of fledging set at 65% with 10% and 20% SD as estimate of environmental variation effects. Three fledglings per female per season with 10 or 30% of females not successful. Carrying capacity 3000 with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 4. AKOHEKOHE - K=3000, ADULT AT 2 YEARS, 70% JUVENILE MORTALITY

File	Input Values			Results															
	%F Br	0-1 Mt	SD Mt	Population Growth			20 years				50 years				100 years				TE
				Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
>1 Year Mortality = 20 ± 10%																			
208	90	70	10	.071	.049	.20	0	2355	704	99	0	2303	619	99	0	2133	761	99	
209			20	.071	.030	.30	0	2044	911	99	0	1584	1010	99	4	1497	1022	97	80
210	70		10	.013	-.016	.20	0	1735	743	99	2	1368	935	99	12	810	873	96	79
211			20	.013	-.037	.28	0	1166	854	99	0	699	808	97	28	427	748	88	79
>1 Year Mortality = 25 ± 10%																			
74	90	70	10	.022	-.005	.21	0	1907	875	99	0	1436	1035	99	10	1026	780	97	75
75			20	.022	-.039	.32	0	1276	934	99	6	740	851	95	46	583	669	91	73
76	70		10	-.037	-.084	.23	0	847	666	99	8	208	296	94	76	19	23	77	80
77			20	-.037	-.107	.31	0	655	703	99	32	132	187	92	94	12	6	57	61
>1 Year Mortality = 30 ± 10%																			
70	90	70	10	-.031	-.079	.25	0	950	734	99	6	258	406	94	74	109	203	80	84
71			20	-.031	-.123	.33	2	540	583	98	40	117	247	90	98	4		56	60
72	70		10	-.090	-.142	.26	0	365	332	98	60	36	34	85	99	0			47
73			20	-.090	-.156	.32	0	358	553	98	70	56	96	85	99	0			39

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>1 Year Mortality = 35 ± 10%																		
78	90	70	10	-.086	-.149	.28	0	363	388	98	58	29	41	79	99	0		48
79			20	-.086	-.176	.38	6	271	335	97	78	95	139	84	10	0		39
80	70		10	-.147	-.217	.29	2	87	106	95	94	11	14	72	99	0		34
81			20	-.147	-.225	.36	8	87	90	94	96	3	1	55	99	0		31

Male and female age of first reproduction, 2 years. Juvenile mortality from time of fledging set at 70% with 10% and 20% SD as estimate of environmental variation effects. Three fledglings per female per season with 10 or 30% of females not successful. Carrying capacity 3000 with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 5. AKOHEKOHE - K=3000, ADULT AT 2 YEARS, 65% JUVENILE MORTALITY

File	Input Values			Results															TE	
	%F Br	0-1 Mt	SD Mt	Population Growth			20 years				50 years				100 years					
				Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
>1 Year Mortality = 20 ± 10%																				
212	90	65	10	.108	.085	.19	0	2688	511	99	0	2515	559	99	0	2544	558	99		
213			20	.108	.077	.28	0	2067	771	99	0	2213	778	99	0	2478	682	99		
214	70		10	.048	.031	.18	0	2042	616	99	0	2109	746	99	0	2154	708	99		
215			20	.048	.009	.26	0	1723	777	99	0	1688	1032	99	0	1285	940	97		
>1 Year Mortality = 25 ± 10%																				
86	90	65	10	.060	.040	.20	0	2448	711	99	0	2379	742	99	0	2046	819	99		
87			20	.060	.016	.29	0	1870	960	99	0	1422	985	99	4	1239	935	95	65	
88	70		10	-.002	-.031	.21	0	1329	661	98	0	889	753	98	20	568	778	90	78	
89			20	-.002	-.054	.28	0	1176	678	97	6	575	663	97	48	308	529	88	78	
>1 Year Mortality = 30 ± 10%																				
82	90	65	10	.008	-.021	.22	0	1471	779	98	0	1051	846	98	8	484	581	92	75	
83			20	.008	-.048	.32	0	1429	1067	96	6	743	884	96	50	477	659	88	99	
84	70		10	-.054	-.112	.24	0	655	466	91	24	92	172	91	98	9		75	61	
85			20	-.054	-.127	.32	0	539	563	87	44	92	197	87	100	0			52	

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>1 Year Mortality = 35 ± 10%																			
90	90	65	10	-.047	-.106	.26	0	648	515	90	20	145	265	90	96	36	2	87	62
91			20	-.047	-.113	.34	0	761	715	88	28	157	403	88	96	20	23	81	58
92	70		10	-.110	-.167	.27	0	240	273	72	84	9	7	72	100	0			43
93			20	-.110	-.178	.34	0	200	226	81	88	19	17	81	100	0			39

Male and female age of first reproduction, 2 years. Juvenile mortality from time of fledging set at 65% with 10% and 20% SD as estimate of environmental variation effects. Three fledglings per female per season with 10 or 30% of females not successful. Carrying capacity 3000 with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 6. AKOHEKOHE - K=3000, ADULT AT 2 YEARS, 60% JUVENILE MORTALITY

File	Input Values			Results															TE	
	%F Br	0- 1 Mt	SD	Population Growth			20 years				50 years				100 years					
				Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
>1 Year Mortality = 20 ± 10%																				
216	90	60	10	.142	.126	.18	0	2777	357	99	0	2905	341	99	0	2860	392	99		
217			20	.142	.111	.27	0	2532	676	99	0	2530	525	99	0	2553	688	99		
218	70		10	.079	.063	.18	0	2554	565	99	0	2307	629	99	2	2317	595	99		
219			20	.079	.046	.26	0	2114	727	99	0	2143	844	99	0	2021	907	99		
>1 Year Mortality = 25 ± 10%																				
98	90	60	10	.094	.075	.19	0	2540	545	99	0	2414	647	99	0	2616	534	99		
99			20	.094	.053	.29	0	2162	850	99	0	2087	887	99	0	2094	896	97		
100	70		10	.030	.009	.19	0	2080	727	99	0	1450	840	99	2	1497	917	97	58	
101			20	.030	-.016	.27	0	1420	815	99	0	1089	923	98	12	756	1010	90	76	
>1 Year Mortality = 30 ± 10%																				
94	90	60	10	.043	.019	.20	0	2153	784	99	0	1953	897	99	0	1678	946	98		
95			20	.043	-.003	.30	0	1543	1014	99	4	1145	983	98	12	1083	1091	93	71	
96	70		10	-.022	-.063	.22	0	1174	701	99	0	346	430	96	60	208	346	81	90	
97			20	-.022	-.081	.30	0	849	702	99	18	343	505	94	76	88	110	76	80	

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>1 Year Mortality = 35 ± 10%																			
102	90	60	10	-.011	-.052	.24	0	1193	681	99	2	561	658	96	42	255	424	86	78
103			20	-.011	-.075	.32	0	757	676	99	10	392	645	92	74	105	115	84	78
104	70		10	-.077	-.129	.26	0	487	397	99	28	42	72	85	100	0			56
105			20	-.077	-.154	.33	0	350	466	98	68	24	32	79	100	0			44

Male and female age of first reproduction, **2 years**. Juvenile mortality from time of fledging set at **60%** with 10% and 20% SD as estimate of environmental variation effects. **Three fledglings** per female per season with 10 or 30% of females not successful. Carrying capacity **3000** with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 7. AKOHEKOHE - K 5000, ADULT AT 2 YEARS, 70% JUVENILE MORTALITY

File	Input Values			Results															TE	
	%F Br	0-1 Mt	SD	Population Growth			20 years				50 years				100 years					
				Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H		
>1 Year Mortality = 20 ± 10%																				
220	90	70	10	.071	.052	.20	0	3799	1228	99	0	3850	1090	99	0	3928	966	99		
221			20	.071	.034	.29	0	3078	1385	99	0	2753	1599	99	0	2899	1680	98		
222	70		10	.013	-.009	.19	0	2440	1364	99	0	1547	1321	99	2	1283	1343	95	92	
223			20	.013	-.033	.28	0	1978	1437	99	4	1410	1470	98	36	1045	1265	94	80	
>1 Year Mortality = 25 ± 10%																				
109	90	70	10	.022	-.005	.21	0	2422	1353	99	0	2443	1702	99	4	1804	1568	96	96	
110			20	.022	-.028	.31	0	1712	1309	99	2	1335	1464	97	24	768	1129	94	72	
111	70		10	-.037	-.078	.23	0	1223	1044	99	2	353	583	93	70	75	113	77	81	
112			20	-.037	-.092	.31	0	1104	984	99	14	389	641	94	84	70	109	75	71	
>1 Year Mortality = 30 ± 10%																				
105	90	70	10	-.031	-.089	.26	0	920	906	99	6	192	344	92	86	107	90	87	71	
106			20	-.031	-.108	.33	0	1176	1438	98	38	252	331	89	94	67	33	90	64	
107	70		10	-.090	-.148	.26	0	285	254	99	68	18	16	77	100	0			46	
108			20	-.090	-.165	.34	0	672	928	97	72	80	185	86	100	0			42	

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>1 Year Mortality = 35 ± 10%																		
113	90	70	10	-.086	-.146	.27	0	394	516	99	68	46	37	87	100	0		47
114			20	-.086	-.176	.38	2	307	409	98	80	46	67	86	100	0		42
115	70		10	-.147	-.199	.28	2	115	109	97	94	3	1	50	100	0		36
116			20	-.147	-.216	.37	6	144	165	96	96	5	1	70	100	0		33

Male and female age of first reproduction, **2 years**. Juvenile mortality from time of fledging set at **70%** with 10% and 20% SD as estimate of environmental variation effects. **Three fledglings** per female per season with 10 or 30% of females not successful. Carrying capacity **5000** with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 8. AKOHEKOHE - K=5000, ADULT 2 YEARS, 65% JUVENILE MORTALITY

File	Input Values			Results															TE
	%F	0-1 Mt	SD	Population Growth			20 years				50 years				100 years				
	Br			Deter r	Stochastic r	SD	PE %	N	SD	H	PE %	N	SD	H	PE %	N	SD	H	
>1 Year Mortality = 20 ± 10%																			
224	90	65	10	.108	.090	.19	0	4425	950	99	0	4386	957	99	0	4619	669	99	
225			20	.108	.065	.28	0	3621	1403	99	0	3644	1193	99	0	3536	1527	99	
226	70		10	.048	.030	.19	0	3510	1219	99	0	3597	1359	99	0	3539	1326	99	
227			20	.048	.009	.26	0	2743	1470	99	0	2018	1561	99	2	2062	1678	99	
>1 Year Mortality = 25 ± 10%																			
121	90	65	10	.060	.041	.20	0	3984	1132	99	0	3725	1296	99	2	3812	1294	99	64
122			20	.060	.018	.29	0	2978	1680	99	0	2525	1622	99	2	2359	1764	97	100
123	70		10	-.002	-.030	.20	0	1920	1232	99	0	987	944	98	12	782	1214	91	80
124			20	-.002	-.053	.28	0	1612	1400	99	2	953	1248	97	38	303	952	86	80
>1 Year Mortality = 30 ± 10%																			
117	90	65	10	.008	-.017	.21	0	2545	1368	99	0	1670	1400	99	10	1083	1213	95	78
118			20	.008	-.036	.30	0	1625	1383	99	10	1328	1481	97	32	875	1256	90	66
119	70		10	-.054	-.103	.25	0	822	735	99	22	137	198	91	94	35	38	72	67
120			20	-.054	-.118	.32	0	741	865	99	30	125	195	90	94	43	37	83	60

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>1 Year Mortality = 35 ± 10%																			
125	90	65	10	-.047	-.110	.27	0	710	680	99	18	126	209	88	94	54	69	78	62
126			20	-.047	-.124	.35	0	528	610	99	42	166	319	87	98	22			56
127	70		10	-.110	-.170	.27	0	297	460	98	74	14	14	77	100	0			44
128			20	-.110	-.198	.34	4	151	193	97	90	5	1	74	100	0			37

Male and female age of first reproduction, **2 years**. Juvenile mortality from time of fledging set at **65%** with 10% and 20% SD as estimate of environmental variation effects. **Three fledglings** per female per season with 10 or 30% of females not successful. Carrying capacity **5000** with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 9. AKOHEKOHE - K=5000, ADULT AT 2 YEARS, 60% JUVENILE MORTALITY

File	Input Values			Results																
	%F	0-1% Mt	SD	Population Growth			20 years				50 years				100 years				TE Yr	
	Br			Deter r	Stochastic r	SD	PE %	N	SD	H	PE %	N	SD	H	PE %	N	SD	H		
>1 Year Mortality = 20 ± 10%																				
228	90	60	10	.142	.122	.19	0	4656	499	99	0	4718	678	99	0	4744	593	99		
229			20	.142	.111	.28	0	4220	1129	99	2	4521	819	99	2	4042	1291	99	50	
230	70		10	.079	.058	.18	0	4173	1014	99	0	4196	923	99	0	4247	1121	99		
231			20	.079	.049	.25	0	3600	1488	99	0	3467	1405	99	0	3447	1478	99		
>1 Year Mortality = 25 ± 10%																				
133	90	60	10	.094	.075	.19	0	4365	985	99	0	4290	914	99	0	4376	802	99		
134			20	.094	.060	.29	0	3769	1310	99	0	3609	1518	99	0	3363	1440	99		
135	70		10	.030	.012	.19	0	3129	1496	99	0	2798	1659	98	0	2473	1480	98		
136			20	.030	-.005	.26	0	2673	1608	99	0	2083	1555	96	6	1675	1777	96	78	
>1 Year Mortality = 30 ± 10%																				
129	90	60	10	.043	.020	.20	0	3331	1260	99	0	3018	1393	99	0	2801	1501	99		
130			20	.043	.005	.20	0	2286	1452	99	0	2559	1710	96	2	1589	1556	96	81	
131	70		10	-.022	-.061	.22	0	1554	1072	99	0	579	602	97	48	212	261	83	77	
132			20	-.022	-.076	.30	0	1263	1225	99	0	469	708	93	64	248	570	77	85	

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>1 Year Mortality = 35 ± 10%																			
137	90	60	10	-.011	-.061	.24	0	1495	1224	99	0	497	679	96	56	504	737	86	95
138			20	-.011	-.082	.34	0	1303	1240	99	6	422	644	93	78	38	54	77	82
139	70		10	-.077	-.133	.26	0	520	408	99	46	61	145	85	100	0			52
140			20	-.077	-.142	.32	0	417	380	98	58	78	129	85	100	0			46

Male and female age of first reproduction, 2 years. Juvenile mortality from time of fledging set at 60% with 10% and 20% SD as estimates of environmental variation effects. Three fledglings per female per season with 10 or 30% of females not successful. Carrying capacity 5000 with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 10. AKOHEKOHE - 4 FLEDGLINGS, K=3000, ADULT AT 2 YEARS, 70% JUVENILE MORTALITY

File	Input Values			Results															TE Yr
	%F	0-1% Mt	SD	Population Growth			20 years				50 years				100 years				
	Br			Deter r	Stochastic r	SD	PE %	N	SD	H	PE %	N	SD	H	PE %	N	SD	H	
>1 Year Mortality = 20 ± 10%																			
232	90	70	10	.142	.123	.21	0	2795	450	99	0	2697	512	99	0	2820	319	99	
233			20	.142	.095	.34	0	2327	804	99	0	2211	794	99	0	2172	839	98	
234	70		10	.079	.055	.21	0	2443	659	99	0	2272	738	99	0	2252	767	99	
235			20	.079	.033	.31	0	1850	857	99	0	1636	910	99	4	1864	1049	97	75
>1 Year Mortality = 25 ± 10%																			
145	90	70	10	.094	.072	.22	0	2366	674	99	0	2486	651	99	0	2383	596	99	
146			20	.094	.043	.35	0	1851	841	99	0	1929	1012	99	4	1560	1004	98	64
147	70		10	.030	.003	.21	0	1625	796	99	0	1335	858	99	0	1214	1006	96	
148			20	.030	-.022	.33	0	1548	905	99	2	930	909	98	28	789	960	94	78
>1 Year Mortality = 30 ± 10%																			
141	90	70	10	.043	.018	.23	0	1964	806	99	0	1682	872	99	0	1643	1094	97	
142			20	.043	-.035	.32	0	1317	831	99	4	823	931	95	32	439	732	83	77
143	70		10	-.022	-.069	.25	0	1106	734	99	2	455	696	95	66	153	252	84	92
144			20	-.022	-.094	.35	0	736	699	99	18	380	720	90	86	161	173	88	66

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>1 Year Mortality = 35 ± 10%																			
149	90	70	10	-.011	-.062	.27	0	1234	894	99	6	440	551	95	58	231	414	86	93
150			20	-.011	-.108	.41	0	652	723	97	36	222	417	88	94	119	150	85	54
151	70		10	-.077	-.134	.29	0	500	486	99	46	57	93	88	100	0			52
152			20	-.077	-.158	.38	0	224	273	97	68	107	204	83	98	17			40

Male and female age of first reproduction, 2 years. Juvenile mortality from time of fledging set at 70% with 10% and 20% SD as estimate of environmental variation effects. Four fledglings per female per season with 10 or 30% of females not successful. Carrying capacity 3000 with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 11. AKOHEKOHE - 4 FLEDGLINGS, K=3000, ADULT AT 2 YEARS, 65% JUVENILE MORTALITY

File	Input Values			Results															TE Yr
	%F	0-1% Mt	SD	Population Growth			20 years				50 years				100 years				
	Br			Deter r	Stochastic r	SD	PE %	N	SD	H	PE %	N	SD	H	PE %	N	SD	H	
>1 Year Mortality = 20 ± 10%																			
236	90	65	10	.182	.163	.20	0	2835	415	99	0	2814	383	99	0	2881	328	99	
237			20	.182	.147	.30	0	2660	622	99	0	2681	590	99	0	2533	718	99	
238	70		10	.117	.094	.20	0	2681	512	99	0	2740	450	99	0	2571	506	99	
239			20	.117	.081	.28	0	2336	757	99	0	2368	774	99	0	2302	793	99	
>1 Year Mortality = 25 ± 10%																			
157	90	65	10	.135	.113	.21	0	2741	463	99	0	2598	539	99	0	2729	510	99	
158			20	.135	.096	.32	0	2417	693	99	0	2268	777	99	0	2327	782	99	
159	70		10	.069	.050	.20	0	2382	650	99	0	2174	620	99	0	2331	681	99	
160			20	.069	.028	.29	0	1904	847	99	0	1712	867	99	0	1226	840	96	
>1 Year Mortality = 30 ± 10%																			
153	90	65	10	.085	.058	.22	0	2171	724	99	0	2470	605	99	0	2307	796	98	
154			20	.085	.036	.34	0	1818	937	99	0	1612	1023	99	2	1524	985	97	99
155	70		10	.017	-.012	.22	0	1878	858	99	0	1162	846	99	6	644	744	94	79
156			20	.017	-.043	.32	0	1468	850	99	0	797	962	96	42	417	721	86	75

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>1 Year Mortality = 35 ± 10%																			
161	90	65	10	.031	.006	.23	0	1838	845	99	0	1397	852	99	0	1181	878	95	
162			20	.031	-.025	.36	0	1352	864	99	4	1011	906	96	30	704	921	89	73
163	70		10	-.037	-.094	.27	0	633	458	99	10	197	376	89	86	22	22	62	69
164			20	-.037	-.106	.35	0	719	821	99	36	168	252	91	90	136	268	78	60

Male and female age of first reproduction, **2 years**. Juvenile mortality from time of fledging set at **65%** with 10% and 20% SD as estimate of environmental variation effects. **Four fledglings** per female per season with 10 or 30% of females not successful. Carrying capacity **3000** with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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Table 12. AKOHEKOHE - 4 FLEDGLINGS, K=3000, ADULT AT 2 YEARS, 60% JUVENILE MORTALITY

File	Input Values			Results															TE Yr
	%F	0- 1% Mt	SD	Population Growth			20 years				50 years				100 years				
	Br			Deter r	Stochastic r	SD	PE %	N	SD	H	PE %	N	SD	H	PE %	N	SD	H	
>1 Year Mortality = 20 ± 10%																			
240	90	60	10	.218	.197	.20	0	2893	386	99	0	2877	377	99	2	2827	365	99	40
241			20	.218	.181	.30	0	2722	465	99	0	2684	502	99	2	2614	625	99	68
242	70		10	.151	.131	.19	0	2832	467	99	0	2764	343	99	0	2812	399	99	
243			20	.151	.114	.28	0	2513	658	99	0	2496	621	99	0	2530	511	99	
>1 Year Mortality = 25 ± 10%																			
169	90	60	10	.172	.152	.20	0	2846	351	99	0	2849	438	99	0	2765	471	99	
170			20	.172	.134	.31	0	2551	650	99	0	2624	566	99	0	2617	571	99	
171	70		10	.103	.083	.20	0	2697	474	99	0	2653	577	99	0	2626	556	99	
172			20	.103	.059	.29	0	2448	766	99	0	2070	855	99	2	2030	892	98	62
>1 Year Mortality = 30 ± 10%																			
165	90	60	10	.122	.100	.21	0	2799	499	99	0	2702	370	99	0	2554	411	99	
166			20	.122	.083	.32	0	2315	681	99	0	2216	857	99	0	2239	881	98	
167	70		10	.053	.028	.21	0	2128	776	99	0	2057	788	99	0	1887	857	98	
168			20	.053	.006	.31	0	1556	844	99	2	1343	1002	98	16	1354	934	97	76

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>1 Year Mortality = 35 ± 10%																			
173	90	60	10	.070	.047	.22	0	2105	631	99	0	2302	748	99	0	2267	728	98	
174			20	.070	.017	.34	0	1697	899	99	0	1746	1118	98	12	1466	1181	83	83
175	70		10	-.001	-.038	.23	0	1331	777	99	6	747	724	97	28	450	655	90	68
176			20	-.001	-.068	.34	0	1151	825	99	14	542	699	95	66	221	374	78	86

Male and female age of first reproduction, 2 years. Juvenile mortality from time of fledging set at 60% with 10% and 20% SD as estimate of environmental variation effects. Four fledglings per female per season with 10 or 30% of females not successful. Carrying capacity 3000 with no trends and a starting population of 2600 set at a stable age distribution. Monogamous breeding with all adult males in the breeding pool. Age of senescence set at 10 years and the sex ratio at hatching at 0.50. No inbreeding effects. Two catastrophes at 1% frequency with one having no effect on reproduction and a 20% reduction in survival and the second producing a 90% reduction in reproduction and a 20% decrease in survival.

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**APPENDIX I.
HAWAIIAN FOREST BIRDS CAMP TAXON REPORT**

SPECIES: *Palmeria dolei* - Crested Honeycreeper

STATUS:

Mace-Lande: Endangered
USFWS: Endangered
CITES: Not listed
State of Hawaii: Endangered
IUCN: Rare

Taxonomic status: Species

Distribution: Northeast slope of Haleakala, Makawao forest reserve to Kaupo. Area - AA-2.
Elevation: 4,000 - >7,000 ft.

Wild Population: + 3,800

Population estimated based on Scott et al. (1986) report on 1981 survey.
1992: pending 1993 report however - there is a decline both in distribution and frequency of the species. No subpopulations.

Field Studies: Nesting biology and life biology studies (foraging) beginning in 1991 by Ellen VanGelder and Tom Smith.

Threats: Disease, interspecific competition with exotics, predation by exotics, habitat loss because of exotic plants and animals, habitat loss (fragmentation), catastrophes/hurricanes.

Comments: This species was formerly found on Moloka'i and west Maui. They can fly extremely high and have aerial displays. May be colonial nesters.

Recommendations:

Research Management: Surveys; Life history; Limiting factors research
PHVA: Yes (Done in December 1992)
Other: More intensive wild management for alien species control. Interspecific competition, disease, predation research.

Captive Population: None

Captive Programs: Immediate (within 0-3 years) captive program with management at the 90/100 level

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APPENDIX II

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SECTION 3.

PALILA
Loxoides bailleui
POPULATION AND HABITAT
VIABILITY ASSESSMENT REPORT

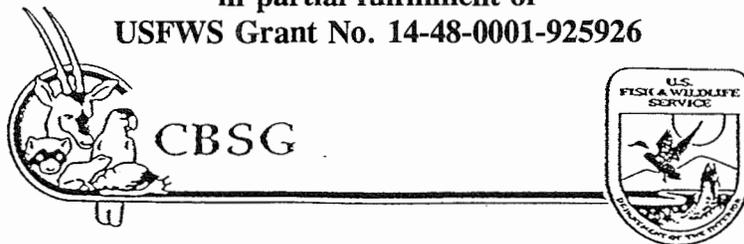
Compiled and Edited by

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in conjunction with the participants
of PHVA workshops held in
Hilo, Hawaii
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PALILA
Loxiodes bailleui
POPULATION AND HABITAT VIABILITY ASSESSMENT

Working Group: Robert Lacy (Chairperson), Steve Fancy, Gerald Lindsey, Thane Pratt

INTRODUCTION

The Palila, *Loxiodes bailleui*, is a Hawai'ian finch (Fringillidae: Drepanidinae) whose life history depends upon the mamane tree (*Sophora chrysophylla*). Palila feed principally on the unripe seeds and flowers of mamane and on insects in mamane seeds and foliage. This dietary specialization restricted Palila historically to mamane forests on the western flanks of the volcanos Mauna Loa and Hualalai and on all slopes of the extinct volcano Mauna Kea, Island of Hawai'i. The fossil record also documents Palila from O'ahu, where mamane forests no longer exist. In the late 1800's, Palila disappeared from Mauna Loa and Hualalai for unknown causes, but survived on Mauna Kea, between elevations of 1800 to 2800 m, where they inhabit savanna or closed woodland dominated by mamane, or mamane and naio (*Myoporum sandwichensis*). Estimates of population numbers for Palila on Mauna Kea range from 1,300 to 6,400 for the period 1980-1993, with large fluctuations but no obvious trend.

Concern for the Palila developed concurrently with efforts to protect the mamane/naio forests on Mauna Kea. Large populations of feral ungulates, mostly sheep, had browsed the woodland for more than a century, removing the understory and preventing regeneration of mamane. Death of older trees caused the forest to thin out and timberline to recede by greater than 150 m elevation. Most lands now supporting the mamane forest lie within the State-owned Mauna Kea Forest Reserve and Kaohe Game Management Area managed under conflicting mandates to protect native forest and wildlife and to sustain populations of feral ungulates for hunting. To reduce the impact of browsing by ungulates, the State reduced feral sheep herds and introduced a new ungulate, Mouflon (*Ovis musimon*), the foraging behavior of which was hoped to have less impact on the forest.

The U.S. Department of Interior listed the Palila as an Endangered Species in 1966, as did the Hawai'i Department of Land and Natural Resources in 1975. The species is also classified as Endangered by the State of Hawaii, and is listed as Rare by IUCN-The World Conservation Union. A recent review of the status of Hawai'ian forest bird species (Ellis et al., 1993) classified the Palila as Endangered based upon application of the Mace/Lande criteria (Mace and Lande, 1991) (Appendix I).

Research conducted in the 1970s showed that ungulate herds still prevented mamane regeneration (Giffin 1976, 1981; Scowcroft and Giffin, 1983). Two law suits brought against the State in 1980 and 1986 for take of Palila under the federal Endangered Species Act resulted in a ruling that feral goat, feral sheep, and mouflon populations be removed from

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the forest reserve and game management areas. These ungulate populations have since been reduced to small numbers, though complete removal has not been achieved. Recovery of the ecosystem has begun but may be slowed by spread of exotic grasses formerly suppressed by sheep. Grasses also pose a serious hazard as a fuel base for fire.

To assist in the recovery of the Palila on Mauna Kea, several research projects have been undertaken since the mid-1970's. Van Riper for his graduate thesis studied the reproductive biology of the Palila and Common 'Amakihi (*Hemignathus virens*) at Pu'u La'au. Systematic surveys of the Palila population have been conducted annually since 1980 by the U.S. Fish and Wildlife Service (USFWS) and Hawai'i Division of Forestry and Wildlife. In 1987, the Hawai'i Research Group of the Patuxent Wildlife Research Center, USFWS, initiated a research program, still ongoing, investigating the ecology of Palila and factors limiting its population. These studies formed the principal source of data for the population viability analysis.

1. POPULATION BIOLOGY PARAMETERS

Population and habitat viability assessment is an approach for utilizing available data to determine the likely fate, or range of plausible fates, of a biological population, in order to help inform conservation and management. The value of the analysis is critically dependent upon the quality of information available to the analysis. The Palila PHVA benefitted greatly from the wealth of increasingly detailed data that have been collected and analyzed by a number of researchers. The numbers used in this analysis were derived from published sources (primarily Van Riper 1978, 1980; Scott et al. 1984, 1986; Pletschet and Kelly, 1990), from unpublished research results by the U.S. Fish and Wildlife Service, and from the collective expertise of members of the Palila PHVA Working Group and other participants of the Hawai'ian Forest Bird Conservation Assessment meeting. The primary participants in the Palila Working Group are listed in Appendix II. Many other participants in the broader Hawaiian Forest Bird PHVA workshop assisted with particular aspects of the analyses and this summary report. Where field data were not available to provide accurate estimates of potentially important parameters, the working group examined a range of plausible parameters. The computer program VORTEX was used to model the Palila population, in order to understand better the factors controlling its dynamics and likely fate.

1.1 Current Population Size and Recent Trends.

Annual estimates of total size of the Palila population are available for the past 13 years beginning in 1980, and continuing through the January 1993 count conducted subsequent to the PHVA workshop (Figure 1). Surveys were conducted each January or February throughout their range using the variable circular plot method along transects established during the

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Hawaiian forest bird surveys (Scott et al., 1986). Population size has varied considerably during the 14-year period, with means ranging from 1317 to 6410 Palila, and annual estimates have had wide confidence intervals. The deterministic growth rate for the population between 1980-1992 was $r = -0.07$ with a standard deviation of 0.48, indicating a highly variable and perhaps slowly decreasing population. The most intensive studies of the Palila population, that have provided our best estimates of population parameters, have been conducted during the past five years by the U.S. Fish and Wildlife Service during a period of apparent population decline.

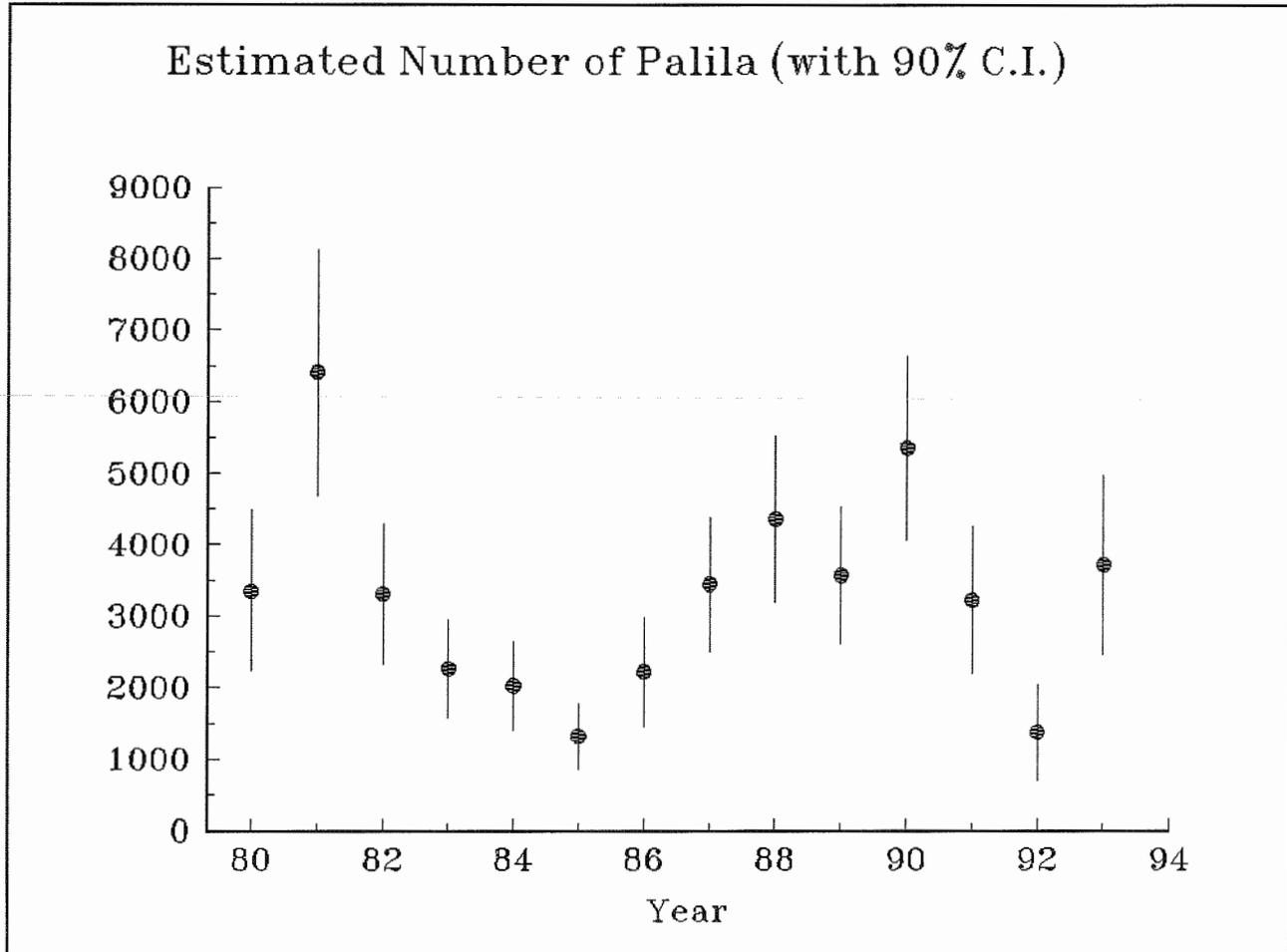


Figure 1. Estimated number of Palila (\pm 90% C.I.)

Although most of the data used in this report were the most recent numbers available at the December 1992 PHVA workshop, an additional count was conducted in January 1993. This count estimated the population to be 3719 Palila. The increase relative to the 1992 count (estimated $N = 1371$) is too great to be accounted for solely by reproduction, especially considering the very low rate of nesting observed during the 1992 drought. The 1992 count seems now to have been an underestimate, hampered by winds and possibly by low activity

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levels of the birds during the 1992 drought. With the inclusion of the recent 1993 census estimates, the data suggest that the Palila population has fluctuated widely but has shown little net increase or decrease since 1980 (mean $r = 0.008$, $SD = 0.57$). Although there is certainly still reason for management concern and action, the decline may not have been as great as had been believed at the workshop in 1992.

1.2 Carrying Capacity.

Palila currently occupy only 5% of their historical range (Scott et al. 1984). Their 139 km² of designated critical habitat on Mauna Kea is bounded at upper elevations by treeline and at lower elevations by pastures and a military training area. Mamane forests are slowly regenerating in some areas after removal of most of the feral ungulates from mamane forests, but some stands of mamane forest within their designated critical habitat may be unable to sustain a viable population because of their small size, narrow elevational range, degree of fragmentation, and the low dispersal potential of Palila.

Current carrying capacity of Palila habitat on Mauna Kea is unknown. The population was estimated at 6410 Palila in 1981, but it is uncertain whether current habitat could sustain a population of that size given high environmental variability such as annual changes in mamane pod production. For purposes of modeling the population, the Palila working group decided not to limit population growth by arbitrarily assigning a carrying capacity. A cap of 8000 was entered into Vortex primarily to prevent memory overflows and excessive computer time required for runs using optimistic data.

1.3 Sex and Age Structure of the Palila Population.

Sex and age structure was determined using capture data from four mist-net stations established over the elevational range of the Palila. Ten mist nets per station were operated three days per month, primarily during the non-breeding season (October to March) during 1987-1990 and from January to November of 1991 and 1992.

Sex ratio for adult (> one year old) birds was 68% male : 32% female (2.1 M : 1 F). Inability to accurately determine the sex of juvenile Palila (< one year old) prevented an estimate of the sex ratio of this age class. The birds caught in the mist nets were distributed as 38% juveniles : 62% adults (1:1.7). The ratio of juveniles (young from the preceding breeding season) to adult females was 1.9:1.

The adult sex ratio suggests differential mortality between the sexes, but data on sex-specific mortality rates will not be available until current banding studies are completed and analyzed. The mortality estimates used in the modeling (see below) assume no sex-difference in mortality,

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but it is recognized that the females are the limiting sex in this monogamous species and that the population projections can be accurate only if the mortality rates used are appropriate for females.

1.4 Reproduction.

Nesting by Palila follows the cycle of seasonal changes on Mauna Kea. Most nesting by Palila takes place between April and September. Peak production of ripening mamane seeds occurs in March and April. Age at first breeding is one year or later for female Palila and two years or more for males. Palila keep the same mate within and among seasons and re-nest within a few hundred meters of their previous nests. Males are monogamous and defend their mates and nest sites, but both parents forage over a radius of several kilometers from the nest, overlapping broadly with the home ranges of many other Palila. In years of high nesting rates, nearly all pairs re-nest at least once, whether successful in their attempts or not. The nesting season is long enough to accommodate three or more nesting attempts per pair, especially when early nests fail. The probability of detecting three nesting attempts, even if it occurs regularly, is extremely small, and no cases of three nesting attempts in one year have been documented. Modal clutch size is two eggs, and females can fledge four (perhaps six) young per season. Eggs and chicks can die for a variety of reasons including: wind or rain storms; predation by black rats (*Rattus rattus*), feral cats (*Felis sylvestris*), and Short-eared Owls (*Asio flammeus*); poor condition of females; or poorly constructed nests. Hatching and fledging rates showed little variability between years. Nesting effort varied greatly in response to availability of mamane seeds and to weather. Numbers of nesting attempts varied from 52 to 86 active nests found in the same sampling effort in 1989-1991; only 5 nests were found in the severe drought year 1992.

For the PHVA modelling, it was assumed that either 80% (with environmental variation of 15% SD) or 90% (10% SD) of the adult females attempt to nest each year. Catastrophic droughts were assumed to greatly depress nesting attempts (see below). Scenarios were examined with either two or three nesting attempts per year per breeding female, and all clutches were assumed to consist of two eggs.

1.5 Mortality.

Pre-fledging survivorship (nest success) has been estimated by several researchers. Productivity of chicks produced per female can also be estimated from the ratio of juveniles to adult females caught in mist nets. Van Riper (1980) estimated fledging rate (chicks fledged per egg laid) at 52% (65% hatching success and 80% fledging success), but he observed only 12 nests, and he reduced predators at the study site by trapping feral cats and rats. Pletschet and Kelly (1990) estimated just 24% chicks fledged per egg. Nest observations between 1989-1992 have yielded a preliminary fledging rate of about 30% (T. Pratt, unpubl. data).

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Mist-netting during the non-breeding seasons of 1987-1991 yielded 189 young produced during the previous breeding season ("after hatch year" birds) and 85 adult females. Assuming that the young were, on average, six months past fledging when netted, and assuming that juvenile survival between fledging and one year is 41% (see below) and constant, the number of fledgling birds that would have given rise to the 189 six-month old (on average) birds that were captured would have been very approximately $189 / \sqrt{.41} = 295$. Assuming that annual adult survival is 75% (see below), the number of adult females alive during the breeding season that would have given rise to the 85 adult females netted 6 months later would have been very approximately $85 / \sqrt{.75} = 98$. Therefore, the production rate would be approximately $295 / 98 = 3.0$ fledglings per female. To achieve this number of fledglings would require a 75% egg-to-fledging survival if females are producing two nests (4 eggs) per year, or 50% egg-to-fledging survival if females are producing three nests (6 eggs) per year. These results may have been biased by higher capture probabilities for unwary juveniles than for the more vigilant adults.

Because young birds undergoing their prebasic molt in the fall months cannot be aged accurately, the 189 "after hatch year" birds observed during 1987-1991 might include some second-year birds, produced two breeding seasons earlier. If so, the number of fledglings would be overestimated from these data, and egg-to-fledging survival could be less than calculated immediately above. This could account for the discrepancy between the 50% to 75% fledging success estimated from the number of captures of "after hatch year" birds and the 24%, 30%, and 52% fledging rates determined from nest observations.

Age-specific post-fledging mortality was determined with the Jolly-Seber model, using capture-recapture data obtained during mist-netting and re-sighting of individually marked Palila during the years 1987-1992. All nestling Palila and birds captured at mist nets were individually marked with three colored, plastic legbands and one USFWS aluminum band. Mean annual adult (> 1 year old) mortality was $36\% \pm 6\%$ (SE). Mean annual juvenile (fledging to 1 year) mortality was $69\% \pm 10\%$ (SE).

Several years of the data were thought by the working group to be unrepresentative of the Palila demography over time. In 1987, the first year of the mist-netting, few birds (23) were banded, and few of these were recaptured later. Beginning in 1990, the population declined markedly for two years, and the survival estimates for 1990 (the last year estimated with the Jolly-Seber method, which requires data from recaptures during two subsequent years to estimate an annual mortality) were very low. To estimate survival rates more representative of "typical" years, Jolly-Seber estimates from the two years (1988 and 1989) prior to the recent decline were averaged. Mortality in these years averaged 59% for juveniles (fledging to 1 year) and 25% for adults.

Following from the above calculations and considerations, analyses were conducted with two levels of adult mortality and three levels of juvenile (egg to 1 year) mortality. Adult mortality was set at either 35% (approximate rate estimated from birds banded from 1987 to 1990) or

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25% (mean rate estimated from birds banded in 1988 and 1989). Juvenile mortality was set at one of three rates: 88%, 79%, or 69%. The highest of the mortality rates tested, 88%, was estimated by compounding the 30% egg-to-fledging survival (T. Pratt, unpubl. data) and the 41% fledging-to-one year survival estimated from birds banded in 1988 and 1989. The middle mortality rate, 79%, was estimated by compounding the 52% egg-to-fledging survival estimated by Van Riper (1980) and 41% fledging-to-one year survival. This estimate of 79% egg-to-one year survival can also be obtained by compounding the 50% egg-to-fledging survival estimated from the ratio of juveniles to adult females caught in the mist nets (with an assumption of three nesting attempts per year; see above) and 41% fledging-to-one year survival. The best mortality rate, 69%, was estimated by compounding the (very optimistic) 75% egg-to-fledging survival estimated from the ratio of juveniles to adult females caught in the mist nets (with an assumption of two nesting attempts per year; see above) and 41% fledging-to-one year survival.

A maximum age was set at 10 years in the simulation, although the mortality rates estimated above project that very few Palila would live to that age.

1.6 Environmental Variation in Mortality.

Annual mortality rates for Palila banded from 1987 through 1992 showed considerable inter-year variation, which could be attributed to the combined effects of fluctuations in the annual survival probabilities due to environmental variation, demographic variation around the annual survival probabilities, and sampling error. The population of Palila is large enough (1370 to 5354 during the mark-recapture study) that demographic variation would have contributed insignificantly to the observed between-year variation in mortality. The expected binomial sampling variance was calculated for each estimate of annual mortality and this source of variation was subtracted from the total between-year variation to yield estimates of 6% (SD) and 10% (SD) for the environmentally caused variation in fledging-to-1 year and adult mortality. The total environmental variation in egg-to-1 year mortality would be augmented by an unknown amount of variation in the egg-to-fledging mortality yielding, perhaps, environmental variation in the egg-to-one year survival on the same order as the annual variation (10% SD) in adult survival.

Recognizing the considerable uncertainty in these estimates, the PHVA modelling examined three levels of environmental variation in mortality rates: a high rate of 15% SD both for year one and for adult mortality; a mid rate of 10% SD for year one and adult mortality; and, because mortality estimates from two of the four years of data were thought to be anomalous (1987 and 1990, see above), a lower rate of 5% SD for both year 1 and adult mortality.

1.7 Catastrophes.

Although many types of catastrophes might befall the geographically very restricted population

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of Palila (including disease epidemic, arrival of brown tree snakes or other exotic predators on the island, or large-scale forest fires), the only type of catastrophe for which the probability of occurrence and severity of impacts could be even approximated was severe drought. The 1992 drought, apparently a consequence of "El Niño" shifts in ocean temperatures and currents, is a striking example of the potentially devastating impact of drought on the Palila population. Only five active nests were observed along transects in 1992, in contrast to the mean of 80.5 nests observed in the previous three years. Population estimates over the past 13 years seem to be correlated with rainfall patterns.

In six of the last 60 years the rainfall recorded at Pu'u La'au was less than half the long-term mean. Several more years had rainfall just slightly above this threshold. El Niño years are expected to occur about once in seven years, or 14% of the time. The PHVA modeling examined the effects of droughts occurring at frequencies of 10% or 15%. It was guessed that during drought years, the proportion of the adult females nesting would be depressed to just 6.2% ($5 / 80.5$) of the normal nesting rate. It was assumed that droughts would have no impact on the mortality rate of the adult population or of the nestlings that were produced.

1.8 Inbreeding Depression.

The Palila population is sufficiently large that close inbreeding would be extremely rare unless both sexes stayed near their natal sites for breeding. The population could decline to such low numbers that inbreeding became common, but only if the population were extremely unstable demographically even in the absence of, or prior to, any inbreeding. Genetic studies of Palila using DNA fingerprinting show a level of genetic variability comparable to that of continental passerines with large populations. These studies also present evidence that the Palila population on Mauna Kea is a panmictic one, without differentiation between breeding groups on the western and eastern sides of the mountain. The mating system of Palila and results from genetic studies suggest low levels of inbreeding for this species.

Because the dynamics of the presently moderate sized population will be driven much more by demographic factors (including annual environmental variation and sporadic catastrophes) than by genetic factors, initially PHVA modelling was conducted under the simplifying assumption that inbreeding (to the small extent that it might occur in the models) would not affect survival or other components of fitness. Secondly, scenarios were also tested, with fewer simulations, under the assumption that each individual at the start of each simulation carried a single, unique, recessive lethal allele (the Recessive Lethals model of inbreeding depression in the simulation program VORTEX). This would cause a relatively modest effect of inbreeding on survival, killing, for example, 12.5% of the offspring of any matings between full siblings. The median effect of inbreeding on mammals is about three-fold stronger than this (survey of 40 mammalian species: Ralls et al. 1988). No comparable survey of inbreeding effects exists for bird species. Stronger effects of inbreeding, with the Heterosis model of inbreeding depression in the

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VORTEX PHVA simulation program, could not be tested for Palila because of the very large memory (about 70 MB of available RAM for a population with a carrying capacity of 8000 birds) and computer time requirements of such analyses.

1.9 Time Period and Numbers of Population Projections.

Simulations were run for 100 years, with population parameters reported at 20 years, 50 years, and 100 years. Each set of parameters was tested with 250 iterations, in cases with no inbreeding effects, or 100 iterations, in cases of inbreeding depression of juvenile survival.

2. POPULATION VIABILITY RESULTS

The results of the population and habitat viability analyses for the Palila are summarized in Tables 1-4. In each table are given input parameters and statistics summarizing various aspects of population viability for 36 scenarios that model population dynamics that might describe the Palila population presently on the Island of Hawai'i. Columns 2-5 of the tables, together with the table headings, indicate the values of the input parameters that were varied among scenarios. Tables 1 and 2 list results for scenarios in which female Palila were assumed to attempt two nests (of two eggs each) per year. Tables 3 and 4 show results from comparable scenarios with females attempting three nests each year. Tables 1 and 3 show results from scenarios in which the probability of catastrophic drought (one that almost eliminates breeding for the year) is 10%. Tables 2 and 4 are the comparable scenarios with a 15% frequency of droughts.

Columns 2-5 of each table indicate the percent of adult females breeding each year (**%Brd**), the mean mortality from egg to 1 year (**0-1 mort**), the mean percent annual adult mortality (**Ad. mort**), and the environmental variation in the mortality rates (**EV mort**) expressed as a standard deviation around the mean percent mortality. The next column (**Deter r**) gives the deterministic population growth rate (the exponential rate, r) as determined from life table analysis for the specified fecundity and mortality rates. Next is given the mean and SD of the population growth rate (prior to any carrying capacity truncation) experienced by the simulated populations in the stochastic model. In the three sets of four columns that follow are given the probability (or frequency) of extinction (**PE**), the mean population size of those simulated populations not extinct (**N**), the standard deviation in the population size (of those not extinct) among simulations (**SD**), and the expected heterozygosity or gene diversity (**H**) of those simulated populations not extinct, expressed as a percent of the initial gene diversity. These results are given for 20 years, 50 years, and 100 years in the future. In the last column is given the median time to extinction (**TE**) for those scenarios in which at least 50% (125 of 250) of the simulated populations went extinct within 100 years.

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2.1 Life Table Determinations of Population Growth Rates.

Standard life table analysis of average age-specific birth and death rates was used to estimate the expected long-term population growth rate (**Deter r** in the tables). Such analyses assume that birth and death rates are constant (no annual variation nor stochastic fluctuations), there is no limitation of mates, and inbreeding has no impact on fecundity or viability. If the population parameters are as estimated from nest monitoring, mist-netting, and other observations over recent years, then the Palila population is projected to be in a moderate to rapid deterministic decline. For example, the deterministic decline calculated from the life table would be $r = -.22$ ($\lambda = .80$, a 20% annual decline) if 80% of females breed, those that breed nest twice per year, nest success (30% fledging rate, followed by a 41% fledging-to-1 year survival) is as observed in recent nest observations, mortality rates for adults (35%) is as estimated from banding studies since 1987, and droughts occur, on average, once a decade (see Scenario 1 of Table 1a). An assumption of 90% nesting by adult females (Scenario 19, Table 1b) slightly improves the deterministic projection (to $r = -.19$), while an assumption of a 15% drought frequency yields a population decline that is very slightly faster ($r = -.23$ or $r = -.20$, with 80% or 90% breeding; see Table 2a and 2b). Although the average decline estimated from 1980 through 1992 was about 7% (mean $r = -.07$), the population declined rapidly from 1990 through 1992, during which time many of the demographic data were collected.

Although there are no observations of Palila nesting three times in a year, the breeding season is long enough for allow three nest attempts, especially if birds re-nest after nest failures. If Palila regularly attempt three nests per year, then the deterministic projections of population decline (under the other assumptions described above) range from $r = -.07$ to $r = -.12$, depending on the percent of females breeding and the frequency of droughts (Tables 3 and 4).

The Palila Working Group recognized that mortality rates estimated from data collected during the recent population decline may be anomalous or biased. If adult mortality is more typically like that estimated from mist-net studies during 1988 and 1989 (25%), and/or if nest success is more typically like that estimated by Van Riper (1980) or as estimated from the ratio of juveniles to adults caught in mist nests, then the deterministic population projections are much less negative or even strongly positive. For example, if there are two nest attempts per year (Tables 1 and 2), then population growth is projected by life table analysis to be positive if first year mortality is at the lowest level tested (69%), or first year mortality is at the intermediate level (79%) and adult mortality is low (25%). With three nest attempts per year, low or middle first year mortality leads to projections of positive population growth, regardless of whether adult mortality is 25% or 35% (Tables 3 and 4).

2.2 Stochastic Simulations of Population Dynamics.

Calculations of population growth rates from average birth and death rates in a life table will

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over-estimate long-term population growth if there are fluctuations in demographic parameters for any reasons (even random sampling variation). For the Palila, field data make clear that the population undergoes significant year-to-year fluctuations in size, reproductive rate, and perhaps mortality rates. Since 1980, the population has varied almost five-fold in size. The annual changes from 1980 through 1993 in estimated numbers yield a mean $r = 0.008$, with large annual fluctuations: $SD(r) = 0.57$. After adjustment for a change in the number of transects, the numbers of active nests along the nest-observation transects over the past four years have varied between just five (in 1992) to 113 (in 1988). Although confidence intervals around estimates from the mist-netting studies are large, estimates of first year survival have varied from 14% to 53%, and estimates of adult survival have varied from 46% to 76% over four years (1987-1990).

The impact of this variability on the viability of the Palila population was explored using the VORTEX computer program to simulate population changes when subjected to fluctuating and probabilistic processes. The mean population growth rate (r) resulting from the simulations was lower in every model tested than the deterministic growth rate calculated from the mean life table parameters. The magnitude of the difference between the deterministic growth rate calculation and the growth rate in the stochastic model was always large and was greater when the year-to-year variation in the stochastic model growth rate ($SD(r)$) was larger, demonstrating how strongly a life table (deterministic) analysis can over-estimate long-term mean population growth in a highly variable system.

The 144 scenarios tested with stochastic PHVA modelling represent a complete 6-way factorial design. In order to examine the relative impacts on Palila population viability of the six parameters varied in the stochastic modelling (number of nest attempts per year, frequency of drought catastrophe, percent of adult females breeding annually, first-year mortality, adult mortality, and environmental variation in mortality), the mean effect of each level tested on population performance statistics was calculated. For example, the effect of each of three levels of first-year mortality (69%, 79%, and 88%) on mean population growth was calculated as the mean growth rate averaged across those scenarios in which first-year mortality was set at that level. This calculation summarizes the average effects of the levels **for the range of parameters tested in the modelling**, under the assumption that the various parameters are acting independently. A more complete analysis-of-variance of the sensitivity of the simulation results to the varied parameters is probably not appropriate or useful given the present uncertainty in the selection of the range of values to be modelled in the scenarios.

Figures 2-5 show the mean effects of the varied parameters on mean population growth (Figure 2), fluctuations in population growth (Figure 3), probability of extinction within 50 years (Figure 4), and median time to extinction (Figure 5). The 50-year criteria for examining the probability of extinction was chosen because that time frame provides the best discrimination among scenarios (many scenarios had no extinctions at 20 years, and many scenarios had 100% extinction at 100 years). The median time to extinction could only be calculated for those

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scenarios in which at least 50% of the simulated populations went extinct, so the effects of parameters on that statistic were calculated from a subset of the scenarios tested.

2.3 Mean and variation in growth rates.

Mean population growth rate was most strongly determined by mortality rates (69%, 79%, or 88% first-year mortality; 25% vs. 35% annual adult mortality) and the numbers of nesting attempts per year (2 vs. 3) (see Figure 2). The more pessimistic scenarios projected precipitous declines (up to 30% per year, $r = -0.36$), not unlike the decline that was observed from 1990 through 1992. Annual variation in mortality (SD of 5%, 10%, or 15% in first-year and in adult mortality rates), the percent of females breeding (80% vs. 90%), and the frequency of droughts (10% vs. 15%) had significant but much lesser effects on the mean growth rates of the simulated populations.

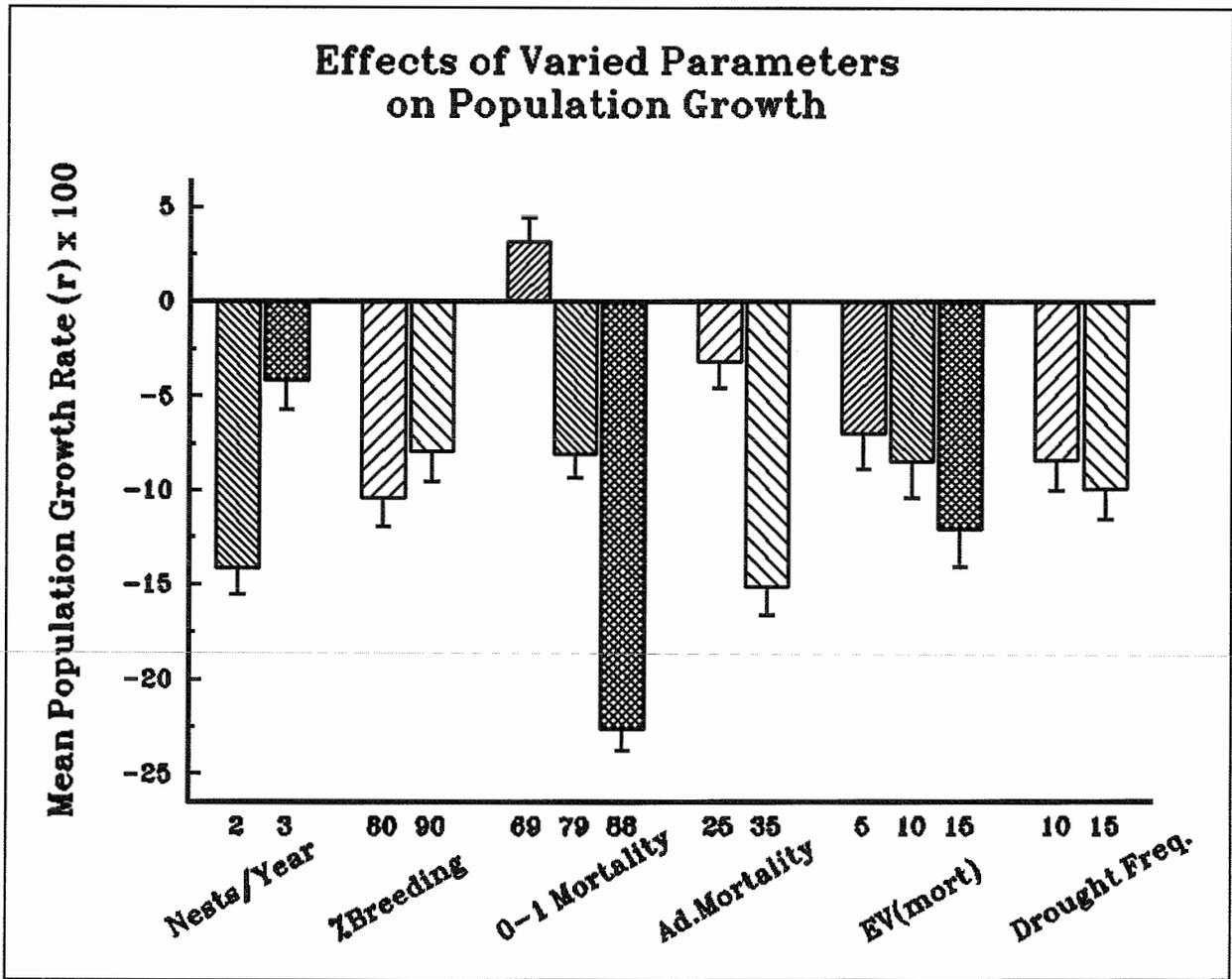


Figure 2. Mean effects averaged over scenarios tested.

The size of the annual fluctuations in population growth was strongly determined by the level of environmental variation in mortality (see Figure 3). In addition, the variation in growth rate was somewhat greater in those scenarios in which the population quickly declined toward extinction (relative to cases with lower mortality and more stable or growing populations), and in scenarios in which there were three nesting attempts per year (rather than two). Within the ranges tested, the frequency of droughts (10% vs. 15%) and the percent of females breeding (80% vs. 90%) had very weak (though still statistically significant) effects on population fluctuations. Those scenarios in which there was high environmental variation in mortality and three nesting attempts per year showed fluctuations in the population growth rate that approached that observed over the past 13 years ($SD(r) = 0.57$).

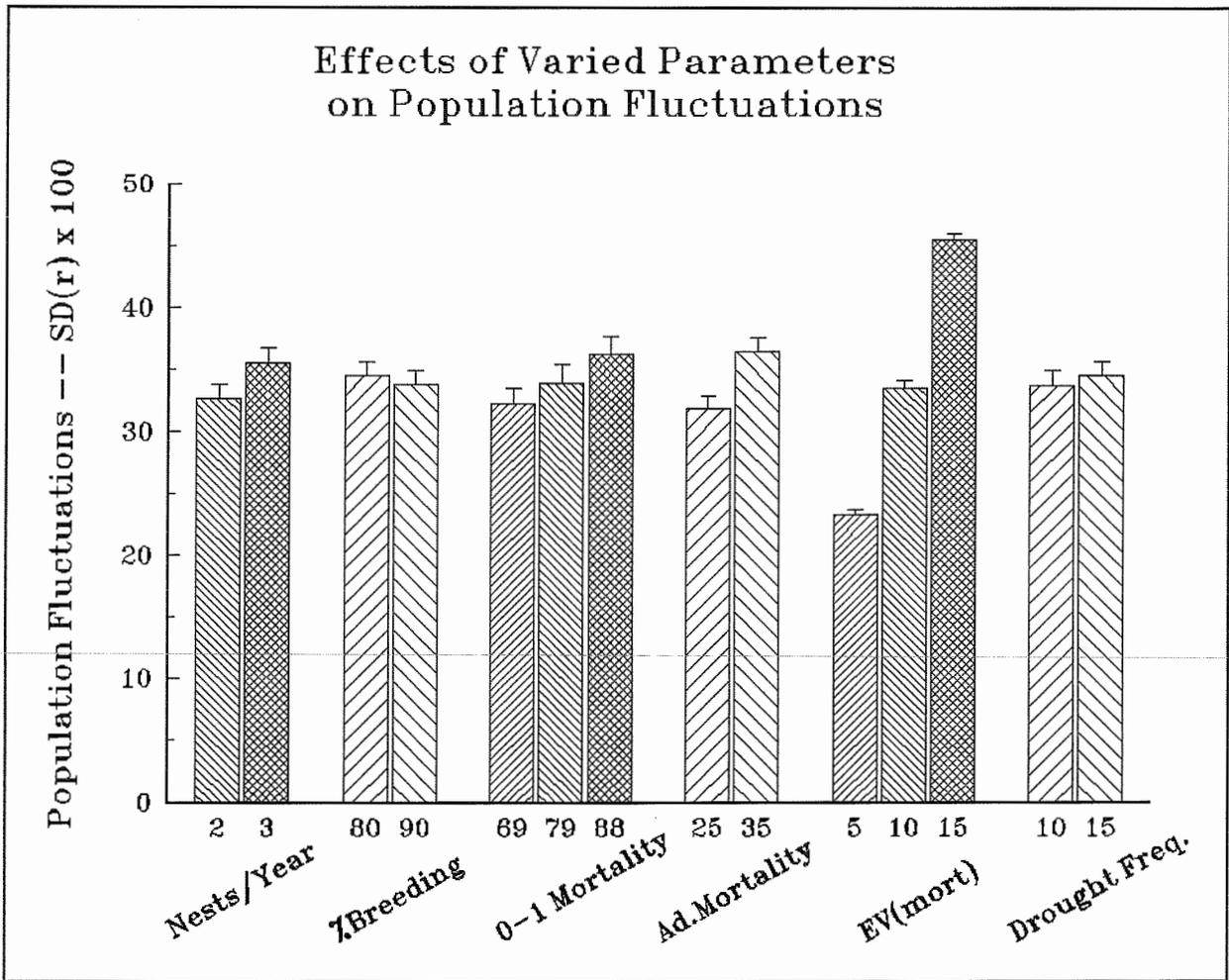


Figure 3. Mean effects averaged over scenarios tested.

2.4 Probabilities of and times to extinction.

Not surprisingly, the simulated populations almost always went extinct in those scenarios in which the life table analyses projected deterministic population decline. In addition, many cases with deterministically projected positive population growth showed high probabilities of extinction in the simulation model incorporating stochastic processes. Overall, mortality rates and, to a lesser extent, the number of nesting attempts per year and the

environmental variation in mortality, were the primary determinants of the probabilities of extinction (Figure 4), just as these factors had the strongest impacts on the mean population growth rates. With two nesting attempts per year, the population appeared to be fairly safe from extinction only when both first-year and adult mortality were estimated to be low and

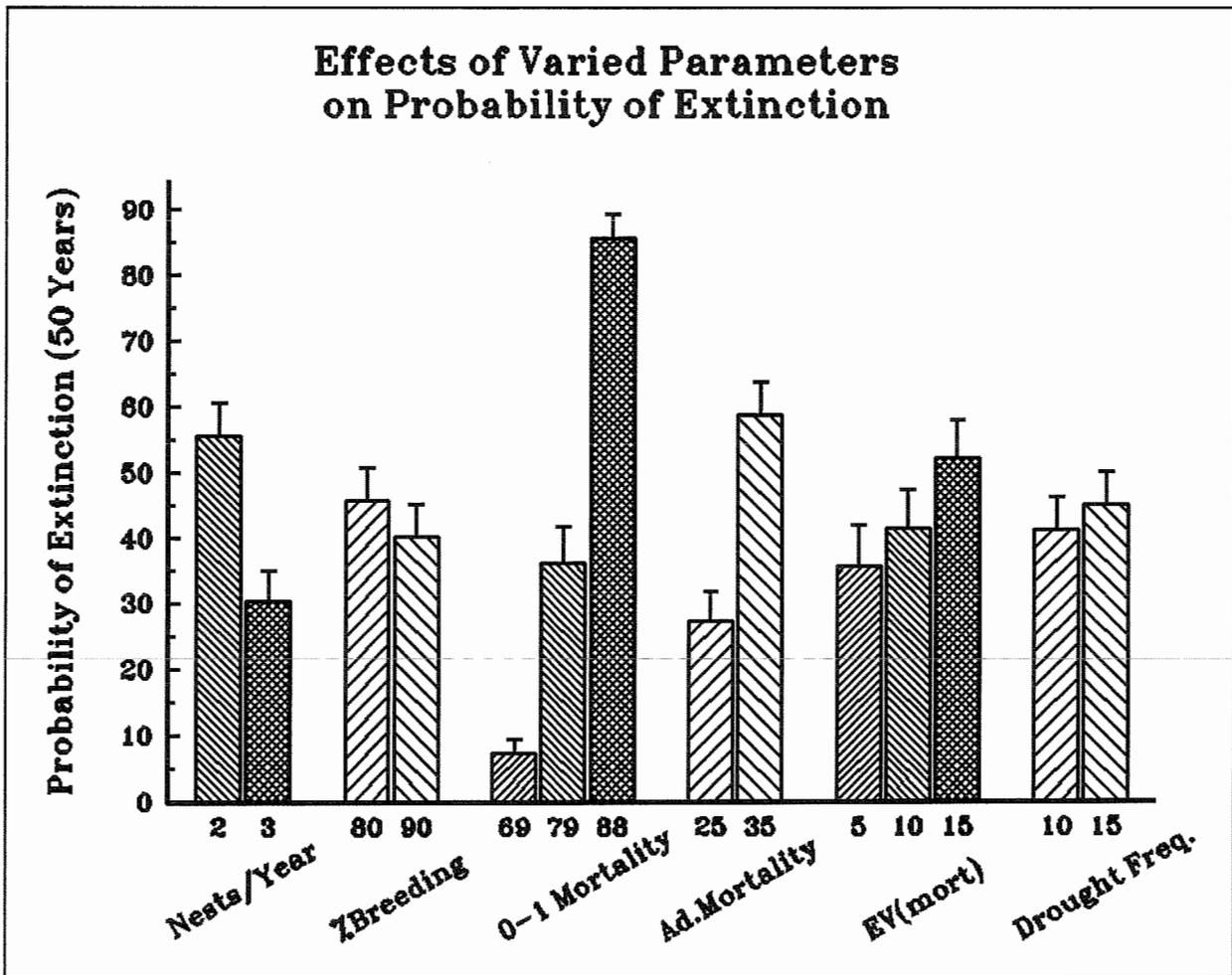


Figure 4. Mean effects averaged over scenarios tested.

environmental variation in mortality was not high (last two Scenarios on each of Tables 1a, 1b, 2a, and 2b). With three nesting attempts per year (Tables 3 and 4), the simulated populations rarely or never went extinct when environmental variation in mortality was below 15% and either first-year or adult mortality was low. In all of these cases, the fluctuations in the population growth rate were smaller than has been observed over the past 13 years; thus, these more optimistic scenarios may represent cases that are unrealistically stable. Depending on the model examined, the median times to extinction of the simulated populations ranged from a low of 18 years to beyond 100 years. The times to extinction were impacted significantly by each of the variables tested, except for the two levels of drought frequency (Figure 5). Reflecting the role of stochastic variation in population viability, median times to extinction were shorter when environmental variation in mortality was greater, especially in those scenarios in which the deterministic population growth rate was estimated to be positive but small.

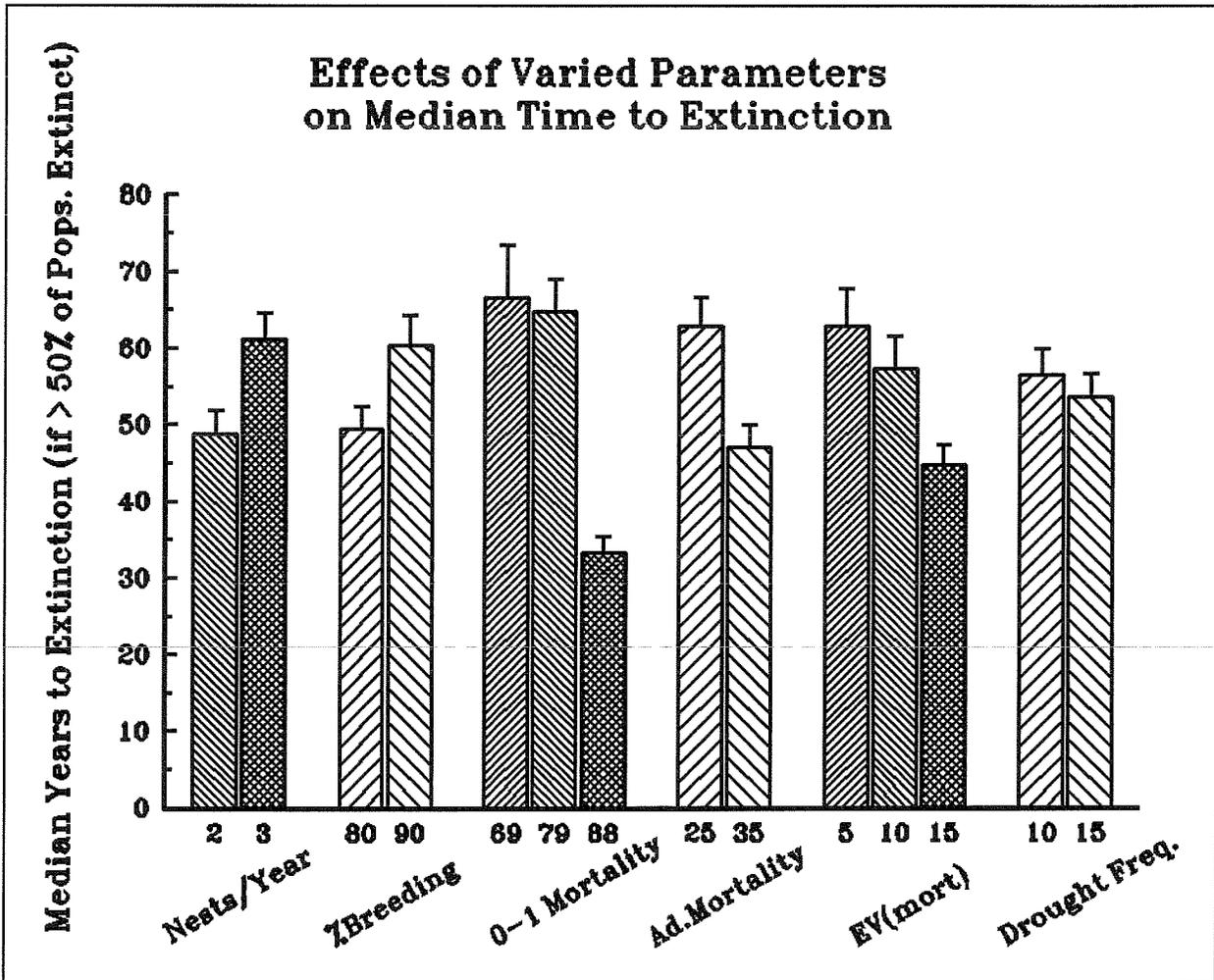


Figure 5. Mean effects averaged over scenarios in which at least 50% of the simulated populations went extinct within 100 years.

2.5 Losses of genetic variation and the effects of inbreeding.

Although the simulated populations lost considerable genetic variation (H , heterozygosity) and hence became quite inbred in some scenarios in which extinctions were common, extinctions of the simulated populations began occurring **before** much genetic variability was lost. Of those populations not yet extinct, population sizes were small and declining rapidly in those populations in which genetic variability dropped below about 90% of the initial level. Therefore, the presumption that demographic processes, rather than genetic processes, are controlling the population dynamics seems justified. Further supporting this interpretation, scenarios tested with a modest impact of inbreeding had dynamics (population sizes, probabilities

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and to times extinction, percents of heterozygosity retained) trivially or not at all different from scenarios in which inbreeding was assumed not to impact fitness. For example, the median times to extinction and stochastic population growth rates were not statistically different between scenarios without inbreeding depression and otherwise identical scenarios in which inbreeding was assumed to cause a moderate loss of fitness. Because they do not differ meaningfully from Tables 1-4, the tables of data for the tests with inbreeding depression are not presented in this report.

3. DISCUSSION: MANAGEMENT AND CONSERVATION RECOMMENDATIONS

Studies of Palila over the past 15 years suggest that population dynamics and dispersal may be driven more by fluctuations in climate and mamane pod production than by other factors. Palila respond to periods of food scarcity by making fewer nesting attempts and by moving greater distances in search of mamane pods. Juvenile and adult survival also appear to be lower during poor food years. Scott et al. (1984) noted that highest densities occur where the elevational range of mamane forests is greatest. More recent work suggests that there is a phenological gradient in mamane pod availability at various elevations, and a wide elevational range may be necessary to sustain a viable population given large annual variation in climate and mamane pod production.

The PHVA modelling conducted at the workshop supports this view of high variability in the Palila population. Moreover, the large fluctuations in population size, resulting from large fluctuations in reproduction and survival, apparently make the Palila population extremely vulnerable to extinction. Although the Palila is presently at greater numbers than are many other Hawaiian bird species, a few consecutive years with declines as great as observed in some recent years could lead to extinction. Given the very large fluctuations experienced by the Palila population, the present population is not sufficiently large to assure persistence over even a few decades. Although the situation is much more grave if mortality rates are high, the population was found to be unstable and subject to extinction even in many scenarios in which the mean birth rate is significantly greater than the mean death rate (deterministic $r > 0$). The probability of extinction appears strongly dependent on the average mortality rates, the fluctuations in mortality rates, and the number of nesting attempts per year. Within the ranges of parameters examined, population stability and viability was less sensitive to the proportion of females breeding (80% or 90%), the frequency of droughts (10% or 15%), and the severity of the impact of any inbreeding on survival.

Much of the currently designated critical habitat for Palila may not be able to support a Palila population during poor years because of the narrow elevational range of mamane forests, particularly on the eastern and northern slopes of Mauna Kea. Here the mamane forest is bounded at high elevation by treeline, and at the lower boundary by lands managed for cattle grazing. Perhaps the most important management action that could be undertaken would be to

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broaden the belt of mamane forest on the north and east slopes of the mountain by rehabilitating to mamane forest certain grazing lands presently under lease. Expansion of the elevational extent of the mamane forest would provide additional area over which the Palila can forage during periods of food shortage, particularly in the fall. This would be expected to increase survivorship of fledged young and adults. Without such actions, it is unlikely that a viable population of Palila could be maintained for more than a few decades, and extinction may come much sooner.

3.1 Research and Monitoring Recommendations.

The Palila population declined markedly from 1990 through 1992. Although the estimated population size rebounded substantially in the early 1993 census, it is not known at this time whether the decline reflected a few unlucky years in a highly stochastic system, or whether researchers and managers documented the beginning of a long-term decline. This uncertainty makes it difficult to determine appropriate management actions, or to determine what field data might be used as indicators of successful management. The analyses and discussions of the PHVA workshop helped to identify some important needs for data to assist the management and conservation of the Palila. The modeling results were found to be sensitive to the frequency of nest attempts (two or three per year), the mortality rates of nestlings and adults, and the annual fluctuations in these parameters. Better data on these variables would provide better understanding of the factors controlling the population dynamics, and therefore would indicate which factors might be manipulated or managed to best effect for the population survival.

Monitoring of nest success should continue. However, collecting data on the exact causes of nest failures may not, at this time, be as important as documenting better the frequency of nesting and the probability of success. This might be accomplished by focusing observations on fewer females, or minimizing encounters with females at nests, while increasing the duration and continuity of observation of nests in a restricted area. To avoid biasing data, or causing more rapid population decline, care should continue to be taken to use observational methods that are unlikely to cause nest failure. Because nest initiation varies so dramatically between years, observations will have to continue for a number of years to allow adequate characterization of trends and patterns of variation. If the frequency of nesting and/or the probability of nest success is found to be lower than needed for long-term population viability, then future research and management can focus on identifying and correcting the reasons for limited reproduction.

Model outputs were extremely sensitive to the preliminary mortality estimates for adults and juveniles obtained from banding and resighting studies. The values used in these simulations were preliminary estimates through 1990; better mortality estimates will be available after ongoing banding and resighting studies are completed in October 1993. Furthermore, because sex-specific mortality rates were not yet available at the time of the PHVA workshop, we assumed equal mortality for males and females in each age class, which is unlikely given the

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uneven sex ratio observed for adults. Similarly, ongoing studies of nesting success will yield better data than were available at the workshop. As better estimates of basic demographic parameters become available, PHVA modelling could be repeated to refine and re-assess the preliminary conclusions of this report.

During March 1993, subsequent to the PHVA workshop, Palila were translocated by the U.S. Fish and Wildlife Service to the eastern slope of Mauna Kea near Kanakaleonui, in order to determine the feasibility of translocation for speeding recovery of this species. The fate of the translocated birds should be monitored closely, and if the translocation is successful, translocation of Palila to additional areas such as near Puu Kole on the northern slope or the Pohakuloa Flats on the southern slope of Mauna Kea should be considered. Additional research will be needed at potential translocation sites to determine the availability of food resources, nesting sites, potential for disease, and numbers of predators before translocations are undertaken.

3.2 Additional Management Recommendations

As discussed above, the Palila population is subject to large variation in numbers across years, apparently driven by very large fluctuations in breeding productivity (reflected in first-year mortality). Therefore, the most critical management action is probably to assure that the available, suitable, and utilized nesting habitat is increased. Expansion of the breeding range would increase the probability that good nesting success occurred somewhere within the range each year. Larger population size would also reduce the probability that short-term population decline would lead to extinction.

Long-term protection of Palila nesting habitat must also involve fire management. Following removal of ungulates from Mauna Kea, the extensive spread of grasses has created an extremely hazardous fuel base. A fire plan should be developed that will identify agencies willing to respond to fire on Mauna Kea; find sources of and storage for fire-fighting equipment; and insure the establishment and maintenance of additional roads or firebreaks.

In addition to restoration of nesting habitat, measures that increase nest success might be undertaken or increased. Reduction or removal of predators (cats, rats, and mongooses) could be implemented as part of an adaptive management strategy: Management efforts could be taken and results closely monitored in order to provide information on the effects of such predators on nest success while simultaneously furthering recovery (if the predators are a significant factor).

Table 1a. Two Nesting Attempts per Year, 10% Droughts, No Inbreeding Effects

Scenario	Input Values				Results															
	%Brd	0-1 mort	Ad. mort	EV mort	Population Growth			20 years				50 years				100 years				TE
					Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
1	80	88	35	15	-.22	-.35	.47	64	23	38	87	100	--	--	--	100	--	--	--	18
2				10	-.22	-.32	.37	51	12	16	85	100	--	--	--	100	--	--	--	20
3				5	-.22	-.30	.26	32	9	8	83	100	--	--	--	100	--	--	--	22
4			25	15	-.11	-.24	.43	26	161	602	93	97	39	44	84	100	--	--	--	26
5				10	-.11	-.21	.32	8	90	146	95	98	11	8	81	100	--	--	--	32
6				5	-.11	-.18	.22	0	74	68	97	97	5	2	67	100	--	--	--	36
7		79	35	15	-.05	-.21	.46	14	120	252	92	96	46	59	85	100	--	--	--	29
8				10	-.05	-.20	.35	7	112	151	95	94	10	8	67	100	--	--	--	31
9				5	-.05	-.18	.26	0	74	61	96	97	8	10	65	100	--	--	--	35
10			25	15	.04	-.10	.41	3	967	1603	98	37	391	1083	89	85	197	520	82	58
11				10	.04	-.07	.29	0	876	1094	99	11	542	1208	92	66	365	1023	86	81
12				5	.04	-.06	.20	0	760	574	99	2	309	443	96	53	82	156	82	98
13		69	35	15	.09	-.12	.44	4	539	945	97	46	269	724	87	96	311	456	78	52
14				10	.09	-.09	.33	0	561	688	98	27	227	647	89	85	44	52	72	67
15				5	.09	-.08	.24	0	502	484	99	9	129	198	91	82	45	63	75	76
16			25	15	.18	.01	.38	0	2820	2511	99	0	2681	2588	98	8	2846	2692	95	--
17				10	.18	.04	.27	0	3679	2516	100	0	4489	2548	99	1	4936	2604	99	--
18				5	.18	.04	.18	0	3944	2129	100	0	6234	1896	100	0	6497	1679	99	--

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Table 1b. Two Nesting Attempts per Year, 10% Droughts, No Inbreeding Effects

Scenario	Input Values				Results														TE	
	%Brd	0-1 mort	Ad. mort	EV mort	Population Growth			20 years				50 years				100 years				
					Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD		H
19	90	88	35	15	-.19	-.35	.47	64	53	207	88	100	--	--	--	100	--	--	--	19
20				10	-.19	-.31	.37	44	13	15	85	100	--	--	--	100	--	--	--	21
21				5	-.19	-.28	.26	26	11	9	87	100	--	--	--	100	--	--	--	23
22			25	15	-.08	-.23	.43	25	131	327	93	97	55	80	83	100	--	--	--	27
23				10	-.08	-.18	.32	6	155	312	96	88	26	46	79	100	--	--	--	35
24				5	-.08	-.17	.22	0	102	84	97	88	8	8	69	100	--	--	--	38
25		79	35	15	-.01	-.20	.47	16	208	511	95	89	16	24	71	100	--	--	--	31
26				10	-.01	-.17	.34	3	162	236	96	84	35	81	80	100	--	--	--	37
27				5	-.01	-.16	.25	0	137	109	98	86	12	13	75	100	--	--	--	41
28			25	15	.08	-.08	.42	1	939	1483	98	30	605	1262	90	79	752	1697	80	67
29				10	.08	-.04	.28	0	1222	1189	99	5	837	1262	96	34	473	889	87	--
30				5	.08	-.02	.17	0	1237	849	100	0	899	1105	98	10	536	784	92	--
31		69	35	15	.14	-.09	.43	2	984	1587	97	34	490	1101	89	81	339	850	79	61
32				10	.14	-.05	.31	0	967	1147	99	10	689	1174	93	50	261	394	84	100
33				5	.14	-.04	.21	0	904	613	99	1	513	657	96	25	210	373	83	--
34			25	15	.23	.03	.38	0	3105	2541	99	2	3968	2863	98	3	3497	2695	97	--
35				10	.23	.06	.26	0	4552	2568	100	0	5996	1976	100	0	6302	1790	99	--
36				5	.23	.07	.17	0	5548	2048	100	0	7295	1125	100	0	7630	605	100	--

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Table 2a. Two Nesting Attempts per Year, 15% Droughts, No Inbreeding Effects

Scenario	Input Values				Results															
	%Brd	0-1 mort	Ad. mort	EV mort	Population Growth			20 years				50 years				100 years				TE
					Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
37	80	88	35	15	-.23	-.36	.47	62	29	58	86	100	--	--	--	100	--	--	--	18
38				10	-.23	-.33	.37	58	18	26	87	100	--	--	--	100	--	--	--	20
39				5	-.23	-.31	.27	47	9	10	83	100	--	--	--	100	--	--	--	21
40			25	15	-.13	-.25	.43	27	123	462	93	99	5	3	82	100	--	--	--	26
41				10	-.13	-.21	.32	9	96	263	94	96	9	7	79	100	--	--	--	29
42				5	-.13	-.20	.23	1	59	51	96	98	4	2	61	100	--	--	--	33
43		79	35	15	-.07	-.24	.46	22	117	315	92	97	32	58	79	100	--	--	--	26
44				10	-.07	-.21	.36	10	90	153	93	97	20	15	73	100	--	--	--	31
45				5	-.07	-.20	.26	2	64	63	95	99	8	4	79	100	--	--	--	33
46			25	15	.03	-.12	.42	3	694	1428	97	54	236	527	88	92	214	501	79	48
47				10	.03	-.08	.30	0	749	963	99	19	323	661	92	73	129	333	91	75
48				5	.03	-.08	.21	0	603	684	99	8	156	229	93	78	43	54	78	78
49		69	35	15	.07	-.14	.45	7	463	769	96	61	224	863	83	98	155	243	77	44
50				10	.07	-.11	.34	1	463	748	98	41	109	263	85	98	41	53	79	56
51				5	.07	-.10	.26	0	348	291	98	26	78	123	86	96	32	66	56	63
52			25	15	.16	.00	.39	0	2771	2630	99	3	2408	2586	97	17	2352	2611	94	--
53				10	.16	.02	.28	0	2976	2511	100	0	3536	2552	99	2	3825	2823	97	--
54				5	.16	.03	.19	0	2877	1959	100	0	4666	2434	99	0	5662	2221	99	--

Paila PHVA

Table 2b. Two Nesting Attempts per Year, 15% Droughts, No Inbreeding Effects

Scenario	Input Values				Results															
	%Brd	0-1 mort	Ad. mort	EV mort	Population Growth			20 years				50 years				100 years				TE
					Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
55	90	88	35	15	-.20	-.36	.48	68	26	50	85	100	--	--	--	100	--	--	--	18
56				10	-.20	-.31	.36	49	19	28	88	100	--	--	--	100	--	--	--	21
57				5	-.20	-.30	.26	34	11	9	87	100	--	--	--	100	--	--	--	22
58			25	15	-.10	-.24	.43	26	112	230	92	97	17	23	64	100	--	--	--	26
59				10	-.10	-.20	.32	9	111	205	95	95	20	28	80	100	--	--	--	33
60				5	-.10	-.18	.23	0	85	83	97	94	6	2	66	100	--	--	--	36
61		79	35	15	-.03	-.21	.46	15	185	494	93	94	13	9	78	100	--	--	--	29
62				10	-.03	-.19	.35	5	99	137	94	92	12	11	64	100	--	--	--	33
63				5	-.03	-.17	.26	0	99	79	97	92	7	6	68	100	--	--	--	38
64			25	15	.06	-.10	.42	3	881	1522	98	40	456	1231	90	88	216	310	87	59
65				10	.06	-.06	.29	0	1072	1396	99	8	534	984	94	56	280	637	85	94
66				5	.06	-.04	.19	0	902	660	99	2	429	536	96	28	219	486	85	--
67		69	35	15	.12	-.11	.43	2	799	1279	97	44	324	731	87	87	144	347	79	54
68				10	.12	-.07	.32	0	723	938	99	17	330	652	90	70	291	569	79	76
69				5	.12	-.06	.24	0	667	482	99	4	242	308	93	59	172	680	78	93
70			25	15	.20	.02	.38	0	3002	2566	99	1	2995	2693	98	6	3530	2835	96	--
71				10	.20	.05	.27	0	3923	2610	100	0	4974	2506	99	0	5361	2361	99	--
72				5	.20	.06	.19	0	4972	2290	100	0	6807	1576	100	0	6903	1460	99	--

Palila PHVA

Table 3a. Three Nesting Attempts per Year, 10% Droughts, No Inbreeding Effects

Scenario	Input Values				Results															
	%Brd	0-1 mort	Ad. mort	EV mort	Population Growth			20 years				50 years				100 years				TE
					Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
73	80	88	35	15	-.10	-.29	.53	45	121	319	90	99	15	20	71	100	--	--	--	22
74				10	-.10	-.24	.40	27	74	151	92	99	7	2	70	100	--	--	--	26
75				5	-.10	-.22	.28	6	42	44	93	99	3	0	67	100	--	--	--	29
76			25	15	0	-.18	.48	16	577	1405	95	82	237	537	90	100	--	--	--	34
77				10	0	-.12	.35	2	590	1106	97	50	209	539	87	95	77	101	76	51
78				5	0	-.10	.23	0	408	392	99	22	71	118	89	97	35	51	71	64
79		79	35	15	.10	-.13	.51	7	697	1395	96	60	392	969	84	96	974	2629	71	43
80				10	.10	-.09	.37	1	658	1023	98	33	366	806	90	84	245	570	78	63
81				5	.10	-.08	.25	0	637	565	99	7	155	219	91	79	52	77	74	81
82			25	15	.19	.01	.45	0	2787	2732	99	4	2508	2566	97	17	2300	2739	93	--
83				10	.19	.04	.32	0	3588	2599	100	1	4208	2646	99	3	4464	2576	98	--
84				5	.19	.05	.20	0	4347	2145	100	0	6238	1960	100	0	6463	1621	99	--
85		69	35	15	.28	.01	.46	0	2667	2577	99	4	2628	2737	97	18	2195	2489	92	--
86				10	.28	.03	.34	0	3399	2559	100	0	4065	2820	99	3	4350	2753	97	--
87				5	.28	.05	.24	0	3919	2268	100	0	5932	2096	99	0	6269	1822	99	--
88			25	15	.35	.12	.43	0	5410	2579	100	0	5837	2491	99	0	5588	2553	99	--
89				10	.35	.14	.34	0	6479	1977	100	0	6852	1665	100	0	6714	1668	99	--
90				5	.35	.15	.22	0	7502	905	100	0	7619	808	100	0	7699	699	100	--

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Table 3b. Three Nesting Attempts per Year, 10% Droughts, No Inbreeding Effects

Scenario	Input Values				Results															
	%Brd	0-1 mort	Ad. mort	EV mort	Population Growth			20 years				50 years				100 years				TE
					Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
91	90	88	35	15	-.07	-.27	.52	39	228	859	92	98	127	235	86	100	--	--	--	22
92				10	-.07	-.23	.40	17	96	265	92	97	26	51	67	100	--	--	--	28
93				5	-.07	-.20	.28	1	53	53	95	99	9	7	64	100	--	--	--	32
94			25	15	.03	-.15	.48	12	632	1244	96	72	287	871	88	98	61	56	87	38
95				10	.03	-.10	.35	0	594	975	98	38	210	512	89	88	131	406	79	58
96				5	.03	-.07	.22	0	607	589	99	6	181	318	92	72	72	122	78	83
97		79	35	15	.15	-.10	.51	3	924	1543	97	45	611	1426	89	88	477	845	77	54
98				10	.15	-.06	.35	0	1054	1200	99	12	668	1323	92	61	421	991	82	87
99				5	.15	-.03	.23	0	944	790	99	2	728	1092	96	24	411	949	87	--
100			25	15	.23	.03	.45	0	2996	2674	99	2	3152	2934	97	10	3161	2836	95	--
101				10	.23	.06	.31	0	4499	2584	100	0	5434	2368	99	0	5723	2310	99	--
102				5	.23	.08	.19	0	5714	2034	100	0	7130	1182	100	0	7253	1127	100	--
103		69	35	15	.34	.03	.45	0	3429	2860	99	2	3160	2624	97	8	3416	2885	95	--
104				10	.34	.07	.33	0	4616	2562	100	0	5505	2391	99	0	5835	2215	99	--
105				5	.34	.08	.23	0	5907	2094	100	0	7324	1156	100	0	7167	1251	99	--
106			25	15	.41	.15	.42	0	6069	2277	100	0	6418	2037	100	0	6180	2209	99	--
107				10	.41	.17	.30	0	7200	1221	100	0	7261	1291	100	0	7338	1176	99	--
108				5	.41	.18	.21	0	7781	561	100	0	7786	637	100	0	7736	672	100	--

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Table 4a. Three Nesting Attempts per Year, 15% Droughts, No Inbreeding Effects

Scenario	Input Values				Results															
	%Brd	0-1 mort	Ad. mort	EV mort	Population Growth			20 years				50 years				100 years				TE
					Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
109	80	88	35	15	-.12	-.30	.52	45	70	165	90	99	17	16	62	100	--	--	--	22
110				10	-.12	-.25	.40	26	71	202	91	100	--	--	--	100	--	--	--	26
111				5	-.12	-.23	.28	6	39	44	93	100	--	--	--	100	--	--	--	28
112			25	15	-.02	-.18	.48	16	398	981	95	81	251	835	86	99	350	423	76	32
113				10	-.02	-.13	.35	1	387	704	97	58	82	179	84	98	29	27	67	46
114				5	-.02	-.11	.24	0	338	314	99	33	62	168	86	98	31	28	65	57
115		79	35	15	.08	-.14	.51	9	612	1214	96	70	390	1053	85	97	1111	2573	74	41
116				10	.08	-.11	.38	0	519	960	98	45	160	356	85	93	237	695	80	53
117				5	.08	-.10	.27	0	427	485	99	22	88	141	86	90	29	47	63	61
118			25	15	.16	-.01	.45	1	2398	2483	99	10	2128	2540	95	32	2011	2559	91	--
119				10	.16	.02	.32	0	3053	2526	100	1	3381	2735	98	6	3407	2759	96	--
120				5	.16	.03	.21	0	3461	2235	100	0	5102	2442	99	0	5676	2135	99	--
121		69	35	15	.25	-.01	.47	2	2123	2325	98	10	1939	2317	95	32	2074	2529	91	--
122				10	.25	.02	.36	0	3070	2671	99	1	3066	2677	97	5	3036	2663	95	--
123				5	.25	.03	.26	0	3270	2162	100	0	4425	2485	99	1	4831	2543	98	--
124			25	15	.33	.10	.43	0	5155	2675	100	1	5171	2579	99	1	5796	2465	99	--
125				10	.33	.12	.35	0	5976	2236	100	0	6625	1752	100	0	6730	1641	99	--
126				5	.33	.13	.24	0	7340	1171	100	0	7416	1014	100	0	7460	945	100	--

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Table 4b. Three Nesting Attempts per Year, 15% Droughts, No Inbreeding Effects

Scenario	Input Values				Results															
	%Brd	0-1 mort	Ad. mort	EV mort	Population Growth			20 years				50 years				100 years				TE
					Deter r	Stochastic r	SD	PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
127	90	88	35	15	-.08	-.29	.53	48	122	400	90	98	135	274	79	100	--	--	--	21
128				10	-.08	-.24	.40	19	75	148	91	100	--	--	--	100	--	--	--	27
129				5	-.08	-.21	.28	2	52	52	94	100	--	--	--	100	--	--	--	30
130			25	15	.02	-.17	.48	15	477	1162	95	79	170	568	85	99	21	30	62	33
131				10	.02	-.11	.35	2	624	949	98	47	243	885	89	95	47	55	86	52
132				5	.02	-.09	.23	0	482	450	99	10	106	232	91	87	37	116	70	72
133		79	35	15	.13	-.13	.52	5	532	905	96	61	280	580	87	94	657	2048	80	44
134				10	.13	-.08	.36	0	864	1299	98	20	463	1107	90	74	285	570	79	71
135				5	.13	-.06	.25	0	739	578	99	4	309	511	94	53	151	361	80	96
136			25	15	.21	.01	.46	0	2594	2671	99	4	2491	2732	95	19	2798	2726	93	--
137				10	.21	.05	.31	0	3730	2544	100	0	4667	2577	99	1	4877	2470	99	--
138				5	.21	.06	.21	0	4771	2423	100	0	6700	1524	100	0	6727	1534	99	--
139		69	35	15	.31	.02	.46	0	2678	2563	99	4	2746	2662	97	14	3048	2754	94	--
140				10	.31	.05	.34	0	3869	2527	100	0	4725	2605	99	0	4540	2735	97	--
141				5	.31	.06	.26	0	5054	2376	100	0	6463	1879	100	0	6619	1719	99	--
142			25	15	.38	.13	.42	0	5712	2476	100	0	5994	2230	99	0	6021	2325	99	--
143				10	.38	.16	.32	0	7007	1477	100	0	7199	1279	100	0	7021	1448	100	--
144				5	.38	.17	.24	0	7564	917	100	0	7538	876	100	0	7595	838	100	--

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Palila PHVA

APPENDIX I
HAWAI'IAN FOREST BIRDS CAMP TAXON REPORT

SPECIES: *Loxoides bailleui* - Palila

STATUS:

Mace-Lande: Endangered
USFWS: Endangered
CITES: Not listed
State of Hawai'i: Endangered
IUCN: Rare

Taxonomic status: Species

Distribution: Hawai'i, Mamane forest on Mauna Kea; range 139 km²;
elev: 6478'-9360'

Wild Population: 1317-6400 (over last 12 years), 1 pop., large
fluctuations

Field Studies: Well studied: Ph.D. study by van Riper (1978); 5 year intensive study by
USFWS; annual censuses; see Palila PHVA Report

Threats: Large population fluctuations, climate (drought), catastrophes (fire, hurricanes),
disease, loss of habitat (grazing, development), predation (pueo, rats, cats).

Recommendations:

Research Management: Monitoring; Limiting factors research; Limiting factors
management; Life history; Translocation
PHVA: Yes, December 1992
Other: Need to acquire and rehabilitate additional habitat; determine how to reduce
fire threat

Captive Population: 0

Captive Programs: Program at Nucleus level of management should be implemented
immediately (0-3 years); surrogate research. Nucleus program should include an active research
component (see above).

Palila PHVA

APPENDIX II

**PALILA PHVA
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SECTION 4.

**VORTEX: A COMPUTER SIMULATION MODEL FOR
POPULATION VIABILITY ANALYSIS**

Robert C. Lacy

VORTEX: A Computer Simulation Model for Population Viability Analysis

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Abstract

Population Viability Analysis (PVA) is the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival into models of the extinction process. Extrinsic forces, such as habitat loss, over-harvesting, and competition or predation by introduced species, often lead to population decline. Although the traditional methods of wildlife ecology can reveal such deterministic trends, random fluctuations that increase as populations become smaller can lead to extinction even of populations that have, on average, positive population growth when below carrying capacity. Computer simulation modelling provides a tool for exploring the viability of populations subjected to many complex, interacting deterministic and random processes. One such simulation model, VORTEX, has been used extensively by the Captive Breeding Specialist Group (Species Survival Commission, IUCN), by wildlife agencies, and by university classes. The algorithms, structure, assumptions and applications of VORTEX are described in this paper.

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, to determine the number of progeny produced by each female each year, and to determine which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Fecundity is assumed to be independent of age after an animal reaches reproductive age. Mortality rates are specified for each pre-reproductive age-sex class and for reproductive-age animals. Inbreeding depression is modelled as a decrease in viability in inbred animals.

The user has the option of modelling density dependence in reproductive rates. As a simple model of density dependence in survival, a carrying capacity is imposed by a probabilistic truncation of each age class if the population size exceeds the specified carrying capacity. VORTEX can model linear trends in the carrying capacity. VORTEX models environmental variation by sampling birth rates, death rates, and the carrying capacity from binomial or normal distributions. Catastrophes are modelled as sporadic random events that reduce survival and reproduction for one year. VORTEX also allows the user to supplement or harvest the population, and multiple subpopulations can be tracked, with user-specified migration among the units.

VORTEX outputs summary statistics on population growth rates, the probability of population extinction, the time to extinction, and the mean size and genetic variation in extant populations.

VORTEX necessarily makes many assumptions. The model it incorporates is most applicable to species with low fecundity and long lifespans, such as mammals, birds and reptiles. It integrates the interacting effects of many of the deterministic and stochastic processes that have an impact on the viability of small populations, providing opportunity for more complete analysis than is possible by other techniques. PVA by simulation modelling is an important tool for identifying populations at risk of extinction, determining the urgency of action, and evaluating options for management.

Introduction

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat, have been reduced to one or more small, isolated populations. The causes of the original decline are often obvious, deterministic forces, such as over-harvesting,

habitat destruction, and competition or predation from invasive introduced species. Even if the original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Shaffer 1981; Soulé 1987; Clark and Seebeck 1990). Of particular impact on small populations are stochastic processes. With the exception of aging, virtually all events in the life of an organism are stochastic. Mating, reproduction, gene transmission between generations, migration, disease and predation can be described by probability distributions, with individual occurrences being sampled from these distributions. Small samples display high variance around the mean, so the fates of small wildlife populations are often determined more by random chance than by the mean birth and death rates that reflect adaptations to their environment.

Although many processes affecting small populations are intrinsically indeterminate, the average long-term fate of a population and the variance around the expectation can be studied with computer simulation models. The use of simulation modelling, often in conjunction with other techniques, to explore the dynamics of small populations has been termed Population Viability Analysis (PVA). PVA has been increasingly used to help guide management of threatened species. The Resource Assessment Commission of Australia (1991) recently recommended that 'estimates of the size of viable populations and the risks of extinction under multiple-use forestry practices be an essential part of conservation planning'. Lindenmayer *et al.* (1993) describe the use of computer modelling for PVA, and discuss the strengths and weaknesses of the approach as a tool for wildlife management.

In this paper, I present the PVA program VORTEX and describe its structure, assumptions and capabilities. VORTEX is perhaps the most widely used PVA simulation program, and there are numerous examples of its application in Australia, the United States of America and elsewhere.

The Dynamics of Small Populations

The stochastic processes that have an impact on populations have been usefully categorised into demographic stochasticity, environmental variation, catastrophic events and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate and sex ratio of a population even if the probabilities of birth and death remain constant. On the assumption that births and deaths and sex determination are stochastic sampling processes, the annual variations in numbers that are born, die, and are of each sex can be specified from statistical theory and would follow binomial distributions. Such demographic stochasticity will be important to population viability only in populations that are smaller than a few tens of animals (Goodman 1987), in which cases the annual frequencies of birth and death events and the sex ratios can deviate far from the means. The distribution of annual adult survival rates observed in the remnant population of whooping cranes (*Grus americana*) (Mirande *et al.* 1993) is shown in Fig. 1. The innermost curve approximates the binomial distribution that describes the demographic stochasticity expected when the probability of survival is 92.7% (mean of 45 non-outlier years).

Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. The second narrowest curve on Fig. 1 shows a normal distribution that statistically fits the observed frequency histogram of crane survival in non-outlier years. The difference between this curve and the narrower distribution describing demographic variation must be accounted for by environmental variation in the probability of adult survival.

Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analysed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease,

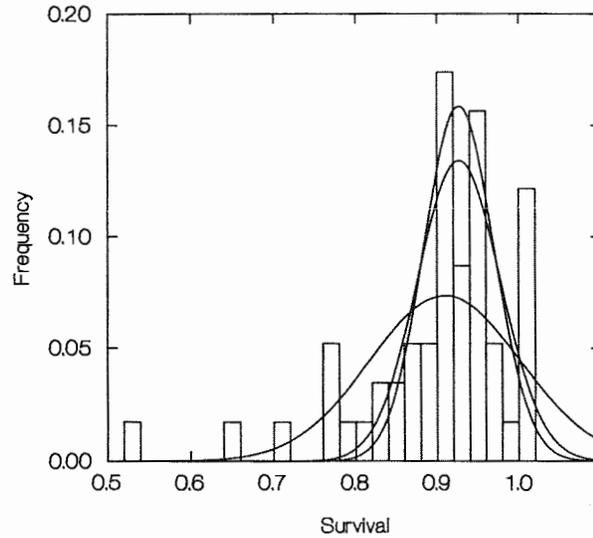


Fig. 1. Frequency histogram of the proportion of whooping cranes surviving each year, 1938-90. The broadest curve is the normal distribution that most closely fits the overall histogram. Statistically, this curve fits the data poorly. The second highest and second broadest curve is the normal distribution that most closely fits the histogram, excluding the five leftmost bars (7 outlier 'catastrophe' years). The narrowest and tallest curve is the normal approximation to the binomial distribution expected from demographic stochasticity. The difference between the tallest and second tallest curves is the variation in annual survival due to environmental variation.

hurricanes, large-scale fires, and floods are outliers in the distribution of environmental variation (e.g. five leftmost bars on Fig. 1). As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls *et al.* 1988; Lacy *et al.* 1993). Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations have a negative impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerate genetic drift (Crow and Kimura 1970). These synergistic destabilising effects of stochastic process on small populations of wildlife have been described as an 'extinction vortex' (Gilpin and Soulé 1986). The size below which a population is likely to be drawn into an extinction vortex can be considered a 'minimum

viable population' (MVP) (Seal and Lacy 1989), although Shaffer (1981) first defined a MVP more stringently as a population that has a 99% probability of persistence for 1000 years. The estimation of MVPs or, more generally, the investigation of the probability of extinction constitutes PVA (Gilpin and Soulé 1986; Gilpin 1989; Shaffer 1990).

Methods for Analysing Population Viability

An understanding of the multiple, interacting forces that contribute to extinction vortices is a prerequisite for the study of extinction-recolonisation dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991). Because demographic and genetic processes in small populations are inherently unpredictable, the expected fates of wildlife populations can be described in terms of probability distributions of population size, time to extinction, and genetic variation. These distributions can be obtained in any of three ways: from analytical models, from empirical observation of the fates of populations of varying size, or from simulation models.

As the processes determining the dynamics of populations are multiple and complex, there are few analytical formulae for describing the probability distributions (e.g. Goodman 1987; Lande 1988; Burgmann and Gerard 1990). These models have incorporated only few of the threatening processes. No analytical model exists, for example, to describe the combined effect of demographic stochasticity and loss of genetic variation on the probability of population persistence.

A few studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g. Belovsky 1987; Berger 1990; Thomas 1990), but presently only order-of-magnitude estimates can be provided for MVPs of vertebrates (Shaffer 1987). Threatened species are, by their rarity, unavailable and inappropriate for the experimental manipulation of population sizes and long-term monitoring of undisturbed fates that would be necessary for precise empirical measurement of MVPs. Retrospective analyses will be possible in some cases, but the function relating extinction probability to population size will differ among species, localities and times (Lindenmayer *et al.* 1993).

Modelling the Dynamics of Small Populations

Because of the lack of adequate empirical data or theoretical and analytical models to allow prediction of the dynamics of populations of threatened species, various biologists have turned to Monte Carlo computer simulation techniques for PVA. By randomly sampling from defined probability distributions, computer programs can simulate the multiple, interacting events that occur during the lives of organisms and that cumulatively determine the fates of populations. The focus is on detailed and explicit modelling of the forces impinging on a given population, place, and time of interest, rather than on delineation of rules (which may not exist) that apply generally to most wildlife populations. Computer programs available to PVA include SPGPC (Grier 1980a, 1980b), GAPPs (Harris *et al.* 1986), RAMAS (Ferson and Akçakaya 1989; Akçakaya and Ferson 1990; Ferson 1990), FORPOP (Possingham *et al.* 1991), ALEX (Possingham *et al.* 1992), and SIMPOP (Lacy *et al.* 1989; Lacy and Clark 1990) and its descendant VORTEX.

SIMPOP was developed in 1989 by converting the algorithms of the program SPGPC (written by James W. Grier of North Dakota State University) from BASIC to the C programming language. SIMPOP was used first in a PVA workshop organised by the Species Survival Commission's Captive Breeding Specialist Group (IUCN), the United States Fish and Wildlife Service, and the Puerto Rico Department of Natural Resources to assist in planning and assessing recovery efforts for the Puerto Rican crested toad (*Peltophryne lemur*). SIMPOP was subsequently used in PVA modelling of other species threatened

with extinction, undergoing modification with each application to allow incorporation of additional threatening processes. The simulation program was renamed VORTEX (in reference to the extinction vortex) when the capability of modelling genetic processes was implemented in 1989. In 1990, a version allowing modelling of multiple populations was briefly named VORTICES. The only version still supported, with all capabilities of each previous version, is VORTEX Version 5.1.

VORTEX has been used in PVA to help guide conservation and management of many species, including the Puerto Rican parrot (*Amazona vittata*) (Lacy *et al.* 1989), the Javan rhinoceros (*Rhinoceros sondaicus*) (Seal and Foose 1989), the Florida panther (*Felis concolor coryi*) (Seal and Lacy 1989), the eastern barred bandicoot (*Perameles gunnii*) (Lacy and Clark 1990; Maguire *et al.* 1990), the lion tamarins (*Leontopithecus rosalia ssp.*) (Seal *et al.* 1990), the brush-tailed rock-wallaby (*Petrogale penicillata penicillata*) (Hill 1991), the mountain pygmy-possum (*Burramys parvus*), Leadbeater's possum (*Gymnobelideus leadbeateri*), the long-footed potoroo (*Potorous longipes*), the orange-bellied parrot (*Neophema chrysogaster*) and the helmeted honeyeater (*Lichenostomus melanops cassidix*) (Clark *et al.* 1991), the whooping crane (*Grus americana*) (Mirande *et al.* 1993), the Tana River crested mangabey (*Cercocebus galeritus galeritus*) and the Tana River red colobus (*Colobus badius rufomitratus*) (Seal *et al.* 1991), and the black rhinoceros (*Diceros bicornis*) (Foose *et al.* 1992). In some of these PVAs, modelling with VORTEX has made clear the insufficiency of past management plans to secure the future of the species, and alternative strategies were proposed, assessed and implemented. For example, the multiple threats to the Florida panther in its existing habitat were recognised as probably insurmountable, and a captive breeding effort has been initiated for the purpose of securing the gene pool and providing animals for release in areas of former habitat. PVA modelling with VORTEX has often identified a single threat to which a species is particularly vulnerable. The small but growing population of Puerto Rican parrots was assessed to be secure, except for the risk of population decimation by hurricane. Recommendations were made to make available secure shelter for captive parrots and to move some of the birds to a site distant from the wild flock, in order to minimise the damage that could occur in a catastrophic storm. These recommended actions were only partly implemented when, in late 1989, a hurricane killed many of the wild parrots. The remaining population of about 350 Tana River red colobus were determined by PVA to be so fragmented that demographic and genetic processes within the 10 subpopulations destabilised population dynamics. Creation of habitat corridors may be necessary to prevent extinction of the taxon. In some cases, PVA modelling has been reassuring to managers: analysis of black rhinos in Kenya indicated that many of the populations within sanctuaries were recovering steadily. Some could soon be used to provide animals for re-establishment or supplementation of populations previously eliminated by poaching. For some species, available data were insufficient to allow definitive PVA with VORTEX. In such cases, the attempt at PVA modelling has made apparent the need for more data on population trends and processes, thereby helping to justify and guide research efforts.

Description of VORTEX

Overview

The VORTEX computer simulation model is a Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events, on wildlife populations. VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables, following user-specified distributions. The input parameters used by VORTEX are summarised in the first part of the sample output given in the Appendix.

VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection,

reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. The program was designed to model long-lived species with low fecundity, such as mammals, birds and reptiles. Although it could and has been used in modelling highly fecund vertebrates and invertebrates, it is awkward to use in such cases as it requires complete specification of the percentage of females producing each possible clutch size. Moreover, computer memory limitations often hamper such analyses. Although VORTEX iterates life events on an annual cycle, a user could model 'years' that are other than 12 months' duration. The simulation of the population is itself iterated to reveal the distribution of fates that the population might experience.

Demographic Stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination and death with a pseudo-random number generator. The probabilities of mortality and reproduction are sex-specific and pre-determined for each age class up to the age of breeding. It is assumed that reproduction and survival probabilities remain constant from the age of first breeding until a specified upper limit to age is reached. Sex ratio at birth is modelled with a user-specified constant probability of an offspring being male. For each life event, if the random value sampled from the uniform 0–1 distribution falls below the probability for that year, the event is deemed to have occurred, thereby simulating a binomial process.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), according to the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s , are obtained by first determining the integral number of binomial trials, N , that would produce the value of s closest to the specified value, according to

$$N = p(1 - p)/s^2.$$

N binomial trials are then simulated by sampling from the uniform 0–1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N , s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

The 'carrying capacity', or the upper limit for population size within a habitat, must be specified by the user. VORTEX imposes the carrying capacity via a probabilistic truncation whenever the population exceeds the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation.

Environmental Variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each

demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions. Environmental variation in carrying capacity is modelled as a normal distribution. The variance across years in the frequencies of births and deaths resulting from the simulation model (and in real populations) will have two components: the demographic variation resulting from a binomial sampling around the mean for each year, and additional fluctuations due to environmental variation and catastrophes (see Fig. 1 and section on The Dynamics of Small Populations, above).

Data on annual variations in birth and death rates are important in determining the probability of extinction, as they influence population stability (Goodman 1987). Unfortunately, such field information is rarely available (but see Fig. 1). Sensitivity testing, the examination of a range of values when the precise value of a parameter is unknown, can help to identify whether the unknown parameter is important in the dynamics of a population.

Catastrophes

Catastrophes are modelled in VORTEX as random events that occur with specified probabilities. Any number of types of catastrophes can be modelled. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors by 50% for the year. Such a catastrophe would be modelled as a random event with 0.02 probability of occurrence each year, and severity factors of 0.75 for survival and 0.50 for reproduction.

Genetic Processes

Genetic drift is modelled in VORTEX by simulation of the transmission of alleles at a hypothetical locus. At the beginning of the simulation, each animal is assigned two unique alleles. Each offspring is randomly assigned one of the alleles from each parent. Inbreeding depression is modelled as a loss of viability during the first year of inbred animals. The impacts of inbreeding are determined by using one of two models available within VORTEX: a Recessive Lethals model or a Heterosis model.

In the Recessive Lethals model, each founder starts with one unique recessive lethal allele and a unique, dominant non-lethal allele. This model approximates the effect of inbreeding if each individual in the starting population had one recessive lethal allele in its genome. The fact that the simulation program assumes that all the lethal alleles are at the same locus has a very minor impact on the probability that an individual will die because of homozygosity for one of the lethal alleles. In the model, homozygosity for different lethal alleles are mutually exclusive events, whereas in a multilocus model an individual could be homozygous for several lethal alleles simultaneously. By virtue of the death of individuals that are homozygous for lethal alleles, such alleles would be removed slowly by natural selection during the generations of a simulation. This reduces the genetic variation present in the population relative to the case with no inbreeding depression, but also diminishes the subsequent probability that inbred individuals will be homozygous for a lethal allele. This model gives an optimistic reflection of the impacts of inbreeding on many species, as the median number of lethal equivalents per diploid genome observed for mammalian populations is about three (Ralls *et al.* 1988).

The expression of fully recessive deleterious alleles in inbred organisms is not the only genetic mechanism that has been proposed as a cause of inbreeding depression. Some or

most of the effects of inbreeding may be a consequence of superior fitness of heterozygotes (heterozygote advantage or 'heterosis'). In the Heterosis model, all homozygotes have reduced fitness compared with heterozygotes. Juvenile survival is modelled according to the logarithmic model developed by Morton *et al.* (1956):

$$\ln S = A - BF$$

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is a measure of the rate at which survival decreases with inbreeding. B is termed the number of 'lethal equivalents' per haploid genome. The number of lethal equivalents per diploid genome, $2B$, estimates the number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual (as in the Recessive Lethals model, above), it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles that equate in effect with one lethal allele per individual. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at heterotic loci because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under the Heterosis model, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding.

Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects varies considerably among species (Falconer 1981; Ralls *et al.* 1988; Lacy *et al.* 1993). Moreover, whether a Recessive Lethals model or a Heterosis model better describes the underlying mechanism of inbreeding depression and therefore the response to repeated generations of inbreeding is not well-known (Brewer *et al.* 1990), and could be determined empirically only from breeding studies that span many generations. Even without detailed pedigree data from which to estimate the number of lethal equivalents in a population and the underlying nature of the genetic load (recessive alleles or heterosis), applications of PVA must make assumptions about the effects of inbreeding on the population being studied. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in accord with the median (3.14 lethal equivalents per diploid) reported in the survey by Ralls *et al.* (1988). In other cases, there might be reason to make more optimistic assumptions (perhaps the lower quartile, 0.90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5.62 lethal equivalents).

Deterministic Processes

VORTEX can incorporate several deterministic processes. Reproduction can be specified to be density-dependent. The function relating the proportion of adult females breeding each year to the total population size is modelled as a fourth-order polynomial, which can provide a close fit to most plausible density-dependence curves. Thus, either positive population responses to low-density or negative responses (e.g. Allee effects), or more complex relationships, can be modelled.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodelled) population. The numbers of additions and removals are specified according to the age and sex of animals. Trends in the carrying capacity can also be modelled in VORTEX, specified as an annual percentage change. These changes are modelled as linear, rather than geometric, increases or decreases.

Migration among Populations

VORTEX can model up to 20 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. This probability is independent of the age and sex. Because of between-population migration and managed supplementation, populations can be recolonised. VORTEX tracks the dynamics of local extinctions and recolonisations through the simulation.

Output

VORTEX outputs (1) probability of extinction at specified intervals (e.g., every 10 years during a 100-year simulation), (2) median time to extinction if the population went extinct in at least 50% of the simulations, (3) mean time to extinction of those simulated populations that became extinct, and (4) mean size of, and genetic variation within, extant populations (see Appendix and Lindenmayer *et al.* 1993).

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction (SE) is reported by VORTEX as

$$SE(p) = \sqrt{[p \times (1 - p) / n]},$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Availability of the VORTEX Simulation Program

VORTEX Version 5.1 is written in the C programming language and compiled with the Lattice 80286C Development System (Lattice Inc.) for use on microcomputers using the MS-DOS (Microsoft Corp.) operating system. Copies of the compiled program and a manual for its use are available for nominal distribution costs from the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, Minnesota 55124, U.S.A. The program has been tested by many workers, but cannot be guaranteed to be error-free. Each user retains responsibility for ensuring that the program does what is intended for each analysis.

Sequence of Program Flow

(1) The seed for the random number generator is initialised with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for input and output devices, population parameters, duration of simulation, and number of iterations.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as

$$N_{max} = (K + 3s) \times (1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change linearly for a number of years in a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size. It is theoretically possible, but very unlikely, that a simulated population will exceed the calculated N_{max} . If this occurs then the program will give an error message and abort.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max} . Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning it has been adjusted downward because of limiting memory often will not hamper the analyses. Except for limitations imposed by the size of the computer memory (VORTEX can use extended memory, if available), the only limit to the size of the analysis is that no more than 20 populations exchanging migrants can be simulated.

(5) The expected mean growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also estimated. Life-table estimations assume no limitation by carrying capacity, no limitation of mates, and no loss of fitness due to inbreeding depression, and the estimated intrinsic growth rate assumes that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life-table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7–26 below. For exploratory modelling, 100 iterations are usually sufficient to reveal gross trends among sets of simulations with different input parameters. For more precise examination of population behaviour under various scenarios, 1000 or more simulations should be used to minimise standard errors around mean results.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age–sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. VORTEX therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy–Weinberg equilibrium, is given by

$$H_e = 1 - \sum(p_i^2),$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1.0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity by means of random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (assuming that the initial value was not zero) (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by VORTEX is the mean inbreeding coefficient of the population.

(9) The user specifies one of three options for modelling the effect of inbreeding: (a) no effect of inbreeding on fitness, that is, all alleles are selectively neutral, (b) each founder individual has one unique lethal and one unique non-lethal allele (Recessive Lethals option), or (c) first-year survival of each individual is exponentially related to its inbreeding coefficient (Heterosis option). The first case is clearly an optimistic one, as almost all diploid

populations studied intensively have shown deleterious effects of inbreeding on a variety of fitness components (Wright 1977; Falconer 1981). Each of the two models of inbreeding depression may also be optimistic, in that inbreeding is assumed to have an impact only on first-year survival. The Heterosis option allows, however, for the user to specify the severity of inbreeding depression on juvenile survival.

(10) Years are iterated via steps 11–25 below.

(11) The probabilities of females producing each possible litter size are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percentage of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates for their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) of the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for linear changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of breeding-age males specified to be breeding.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified sex ratio at birth. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) If the Heterosis option is chosen for modelling inbreeding depression, the genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between a new animal, A , and another existing animal, B is

$$f_{AB} = 0.5 \times (f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals i and j , M is the mother of A , and P is the father of A . The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_{AA} = 0.5 \times (1 + F)$. [See Ballou (1983) for a detailed description of this method for calculating inbreeding coefficients.]

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If the Heterosis model of inbreeding depression is used and an individual is inbred, the survival probability is multiplied by e^{-bF} in which b is the number of lethal equivalents per haploid genome.

If the Recessive Lethals model is used, all offspring that are homozygous for a lethal allele are killed.

(18) The age of each animal is incremented by 1, and any animal exceeding the maximum age is killed.

(19) If more than one population is being modelled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age-sex class, VORTEX continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age class are created. Each immigrant is assigned two unique alleles, one of which will be a recessive lethal in the Recessive Lethals model of inbreeding depression. Each immigrant is assumed to be genetically unrelated to all other individuals in the population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N-K)/N$, so that the expected population size after the additional mortality is K .

(25) Summary statistics on population size and genetic variation are tallied and reported. A simulated population is determined to be extinct if one of the sexes has no representatives.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate, are calculated across iterations and printed out.

Assumptions Underpinning VORTEX

It is impossible to simulate the complete range of complex processes that can have an impact on wild populations. As a result there are necessarily a range of mathematical and biological assumptions that underpin any PVA program. Some of the more important assumptions in VORTEX include the following.

(1) Survival probabilities are density independent when population size is less than carrying capacity. Additional mortality imposed when the population exceeds K affects all age and sex classes equally.

(2) The relationship between changes in population size and genetic variability are examined for only one locus. Thus, potentially complex interactions between genes located on the same chromosome (linkage disequilibrium) are ignored. Such interactions are typically associated with genetic drift in very small populations, but it is unknown if, or how, they would affect population viability.

(3) All animals of reproductive age have an equal probability of breeding. This ignores the likelihood that some animals within a population may have a greater probability of breeding successfully, and breeding more often, than other individuals. If breeding is not at random among those in the breeding pool, then decay of genetic variation and inbreeding will occur more rapidly than in the model.

(4) The life-history attributes of a population (birth, death, migration, harvesting, supplementation) are modelled as a sequence of discrete and therefore seasonal events. However, such events are often continuous through time and the model ignores the possibility that they may be aseasonal or only partly seasonal.

(5) The genetic effects of inbreeding on a population are determined in VORTEX by using one of two possible models: the Recessive Lethals model and the Heterosis model. Both models have attributes likely to be typical of some populations, but these may vary within and between species (Brewer *et al.* 1990). Given this, it is probable that the impacts of inbreeding will fall between the effects of these two models. Inbreeding is assumed to depress only one component of fitness: first-year survival. Effects on reproduction could be incorporated into this component, but longer-term impacts such as increased disease susceptibility or decreased ability to adapt to environmental change are not modelled.

(6) The probabilities of reproduction and mortality are constant from the age of first breeding until an animal reaches the maximum longevity. This assumes that animals continue to breed until they die.

(7) A simulated catastrophe will have an effect on a population only in the year that the event occurs.

(8) Migration rates among populations are independent of age and sex.

(9) Complex, interspecies interactions are not modelled, except in that such community dynamics might contribute to random environmental variation in demographic parameters. For example, cyclical fluctuations caused by predator-prey interactions cannot be modelled by VORTEX.

Discussion

Uses and Abuses of Simulation Modelling for PVA

Computer simulation modelling is a tool that can allow crude estimation of the probability of population extinction, and the mean population size and amount of genetic diversity, from data on diverse interacting processes. These processes are too complex to be integrated intuitively and no analytic solutions presently, or are likely to soon, exist. PVA modelling focuses on the specifics of a population, considering the particular habitat, threats, trends, and time frame of interest, and can only be as good as the data and the assumptions input to the model (Lindenmayer *et al.* 1993). Some aspects of population dynamics are not modelled by VORTEX nor by any other program now available. In particular, models of single-species dynamics, such as VORTEX, are inappropriate for use on species whose fates are strongly determined by interactions with other species that are in turn undergoing complex (and perhaps synergistic) population dynamics. Moreover, VORTEX does not model many conceivable and perhaps important interactions among variables. For example, loss of habitat might cause secondary changes in reproduction, mortality, and migration rates, but ongoing trends in these parameters cannot be simulated with VORTEX. It is important to stress that PVA does not predict in general what will happen to a population; PVA forecasts the likely effects only of those factors incorporated into the model.

Yet, the use of even simplified computer models for PVA can provide more accurate predictions about population dynamics than the even more crude techniques available previously, such as calculation of expected population growth rates from life tables. For the purpose of estimating extinction probabilities, methods that assess only deterministic factors are almost certain to be inappropriate, because populations near extinction will commonly be so small that random processes dominate deterministic ones. The suggestion by Mace and Lande (1991) that population viability be assessed by the application of simple rules (e.g., a taxon be considered Endangered if the total effective population size is below 50 or the

total census size below 250) should be followed only if knowledge is insufficient to allow more accurate quantitative analysis. Moreover, such preliminary judgments, while often important in stimulating appropriate corrective measures, should signal, not obviate, the need for more extensive investigation and analysis of population processes, trends and threats.

Several good population simulation models are available for PVA. They differ in capabilities, assumptions and ease of application. The ease of application is related to the number of simplifying assumptions and inversely related to the flexibility and power of the model. It is unlikely that a single or even a few simulation models will be appropriate for all PVAs. The VORTEX program has some capabilities not found in many other population simulation programs, but is not as flexible as are some others (e.g., GAPPS; Harris *et al.* 1986). VORTEX is user-friendly and can be used by those with relatively little understanding of population biology and extinction processes, which is both an advantage and a disadvantage.

Testing Simulation Models

Because many population processes are stochastic, a PVA can never specify what will happen to a population. Rather, PVA can provide estimates of probability distributions describing possible fates of a population. The fate of a given population may happen to fall at the extreme tail of such a distribution even if the processes and probabilities are assessed precisely. Therefore, it will often be impossible to test empirically the accuracy of PVA results by monitoring of one or a few threatened populations of interest. Presumably, if a population followed a course that was well outside of the range of possibilities predicted by a model, that model could be rejected as inadequate. Often, however, the range of plausible fates generated by PVA is quite broad.

Simulation programs can be checked for internal consistency. For example, in the absence of inbreeding depression and other confounding effects, does the simulation model predict an average long-term growth rate similar to that determined from a life-table calculation? Beyond this, some confidence in the accuracy of a simulation model can be obtained by comparing observed fluctuations in population numbers to those generated by the model, thereby comparing a data set consisting of tens to hundreds of data points to the results of the model. For example, from 1938 to 1991, the wild population of whooping cranes had grown at a mean exponential rate, r , of 0.040, with annual fluctuations in the growth rate, SD (r), of 0.141 (Mirande *et al.* 1993). Life-table analysis predicted an r of 0.052. Simulations using VORTEX predicted an r of 0.046 into the future, with a SD (r) of 0.081. The lower growth rate projected by the stochastic model reflects the effects of inbreeding and perhaps imbalanced sex ratios among breeders in the simulation, factors that are not considered in deterministic life-table calculations. Moreover, life-table analyses use mean birth and death rates to calculate a single estimate of the population growth rate. When birth and death rates are fluctuating, it is more appropriate to average the population growth rates calculated separately from birth and death rates for each year. This mean growth rate would be lower than the growth rate estimated from mean life-table values.

When the simulation model was started with the 18 cranes present in 1938, it projected a population size in 1991 ($N \pm SD = 151 \pm 123$) almost exactly the same as that observed ($N = 146$). The large variation in population size across simulations, however, indicates that very different fates (including extinction) were almost equally likely. The model slightly underestimated the annual fluctuations in population growth [model SD (r) = 0.112 *v.* actual SD (r) = 0.141]. This may reflect a lack of full incorporation of all aspects of stochasticity into the model, or it may simply reflect the sampling error inherent in stochastic phenomena. Because the data input to the model necessarily derive from analysis of past trends, such retrospective analysis should be viewed as a check of consistency, not as proof that the model correctly describes current population dynamics. Providing another confir-

mation of consistency, both deterministic calculations and the simulation model project an over-wintering population of whooping cranes consisting of 12% juveniles (less than 1 year of age), while the observed frequency of juveniles at the wintering grounds in Texas has averaged 13%.

Convincing evidence of the accuracy, precision and usefulness of PVA simulation models would require comparison of model predictions to the distribution of fates of many replicate populations. Such a test probably cannot be conducted on any endangered species, but could and should be examined in experimental non-endangered populations. Once simulation models are determined to be sufficiently descriptive of population processes, they can guide management of threatened and endangered species (see above and Lindenmayer *et al.* 1993). The use of PVA modelling as a tool in an adaptive management framework (Clark *et al.* 1990) can lead to increasingly effective species recovery efforts as better data and better models allow more thorough analyses.

Directions for Future Development of PVA Models

The PVA simulation programs presently available model life histories as a series of discrete (seasonal) events, yet many species breed and die throughout much of the year. Continuous-time models would be more realistic and could be developed by simulating the time between life-history events as a random variable. Whether continuous-time models would significantly improve the precision of population viability estimates is unknown. Even more realistic models might treat some life-history events (e.g., gestation, lactation) as stages of specified duration, rather than as instantaneous events.

Most PVA simulation programs were designed to model long-lived, low fecundity (K-selected) species such as mammals, birds and reptiles. Relatively little work has been devoted to developing models for short-lived, high-fecundity (r-selected) species such as many amphibians and insects. Yet, the viability of populations of r-selected species may be highly affected by stochastic phenomena, and r-selected species may have much greater minimum viable populations than do most K-selected species. Assuring viability of K-selected species in a community may also afford adequate protection for r-selected species, however, because of the often greater habitat-area requirements of large vertebrates. Populations of r-selected species are probably less affected by intrinsic demographic stochasticity because large numbers of progeny will minimise random fluctuations, but they are more affected by environmental variations across space and time. PVA models designed for r-selected species would probably model fecundity as a continuous distribution, rather than as a completely specified discrete distribution of litter or clutch sizes; they might be based on life-history stages rather than time-increment ages; and they would require more detailed and accurate description of environmental fluctuations than might be required for modelling K-selected species.

The range of PVA computer simulation models becoming available is important because the different assumptions of the models provide capabilities for modelling diverse life histories. Because PVA models always simplify the life history of a species, and because the assumptions of no model are likely to match exactly our best understanding of the dynamics of a population of interest, it will often be valuable to conduct PVA modelling with several simulation programs and to compare the results. Moreover, no computer program can be guaranteed to be free of errors. There is a need for researchers to compare results from different PVA models when applied to the same analysis, to determine how the different assumptions affect conclusions and to cross-validate algorithms and computer code.

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Appendix. Sample Output from VORTEX

Explanatory comments are added in italics

VORTEX—simulation of genetic and demographic stochasticity

TEST

Simulation label and output file name

Fri Dec 20 09:21:18 1991

2 population(s) simulated for 100 years, 100 runs

VORTEX first lists the input parameters used in the simulation:

HETEROSIS model of inbreeding depression
with 3.14 lethal equivalents per diploid genome

Migration matrix:

	1	2
1	0.9900	0.0100
2	0.0100	0.9900

*i.e. 1% probability of migration from
Population 1 to 2, and from Population 2 to 1*

First age of reproduction for females: 2 for males: 2

Age of senescence (death): 10

Sex ratio at birth (proportion males): 0.5000

Population 1:

Polygynous mating; 50.00 per cent of adult males in the breeding pool.

Reproduction is assumed to be density independent.

50.00 (EV = 12.50 SD) per cent of adult females produce litters of size 0

25.00 per cent of adult females produce litters of size 1

25.00 per cent of adult females produce litters of size 2

EV is environmental variation

50.00 (EV = 20.41 SD) per cent mortality of females between ages 0 and 1

10.00 (EV = 3.00 SD) per cent mortality of females between ages 1 and 2

10.00 (EV = 3.00 SD) per cent annual mortality of adult females (2 ≤ age ≤ 10)

50.00 (EV = 20.41 SD) per cent mortality of males between ages 0 and 1

10.00 (EV = 3.00 SD) per cent mortality of males between ages 1 and 2

10.00 (EV = 3.00 SD) per cent annual mortality of adult males (2 ≤ age ≤ 10)

EVs have been adjusted to closest values possible for binomial distribution.

EV in reproduction and mortality will be correlated.

Frequency of type 1 catastrophes: 1.000 per cent
 with 0.500 multiplicative effect on reproduction
 and 0.750 multiplicative effect on survival

Frequency of type 2 catastrophes: 1.000 per cent
 with 0.500 multiplicative effect on reproduction
 and 0.750 multiplicative effect on survival

Initial size of Population 1: (set to reflect stable age distribution)

Age	1	2	3	4	5	6	7	8	9	10	Total
	1	0	1	1	0	1	0	0	1	0	5 Males
	1	0	1	1	0	1	0	0	1	0	5 Females

Carrying capacity = 50 (EV = 0.00 SD)
 with a 10.000 per cent decrease for 5 years.

Animals harvested from population 1, year 1 to year 10 at 2 year intervals:

- 1 females 1 years old
- 1 female adults (2 <= age <= 10)
- 1 males 1 years old
- 1 male adults (2 <= age <= 10)

Animals added to population 1, year 10 through year 50 at 4 year intervals:

- 1 females 1 years old
- 1 females 2 years old
- 1 males 1 years old
- 1 males 2 years old

Input values are summarised above, results follow.

VORTEX now reports life-table calculations of expected population growth rate.

Deterministic population growth rate (based on females, with assumptions of no limitation of mates and no inbreeding depression):

$$r = -0.001 \quad \lambda = 0.999 \quad RO = 0.997$$

Generation time for: females = 5.28 males = 5.28

Note that the deterministic life-table calculations project approximately zero population growth for this population.

Stable age distribution:	Age class	females	males
	0	0.119	0.119
	1	0.059	0.059
	2	0.053	0.053
	3	0.048	0.048
	4	0.043	0.043
	5	0.038	0.038
	6	0.034	0.034
	7	0.031	0.031
	8	0.028	0.028
	9	0.025	0.025
	10	0.022	0.022

Ratio of adult (>=2) males to adult (>=2) females: 1.000

Population 2:

Input parameters for Population 2 were identical to those for Population 1. Output would repeat this information from above.

Simulation results follow.

Population1

Year 10

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 100, P[S] = 1.000
 Population size = 4.36 (0.10 SE, 1.01 SD)
 Expected heterozygosity = 0.880 (0.001 SE, 0.012 SD)
 Observed heterozygosity = 1.000 (0.000 SE, 0.000 SD)
 Number of extant alleles = 8.57 (0.15 SE, 1.50 SD)

Population summaries given, as requested by user, at 10-year intervals.

Year 100

N[Extinct] = 86, P[E] = 0.860
 N[Surviving] = 14, P[S] = 0.140
 Population size = 8.14 (1.27 SE, 4.74 SD)
 Expected heterozygosity = 0.577 (0.035 SE, 0.130 SD)
 Observed heterozygosity = 0.753 (0.071 SE, 0.266 SD)
 Number of extant alleles = 3.14 (0.35 SE, 1.29 SD)

In 100 simulations of 100 years of Population1:

86 went extinct and 14 survived.

This gives a probability of extinction of 0.8600 (0.0347 SE),
or a probability of success of 0.1400 (0.0347 SE).

99 simulations went extinct at least once.

Median time to first extinction was 5 years.

Of those going extinct,

mean time to first extinction was 7.84 years (1.36 SE, 13.52 SD).

123 recolonisations occurred.

Mean time to recolonisation was 4.22 years (0.23 SE, 2.55 SD).

110 re-extinctions occurred.

Mean time to re-extinction was 54.05 years (2.81 SE, 29.52 SD).

Mean final population for successful cases was 8.14 (1.27 SE, 4.74 SD)

Age 1	Adults	Total	
0.14	3.86	4.00	Males
0.36	3.79	4.14	Females

During years of harvest and/or supplementation

mean growth rate (r) was 0.0889 (0.0121 SE, 0.4352 SD)

Without harvest/supplementation, prior to carrying capacity truncation,

mean growth rate (r) was -0.0267 (0.0026 SE, 0.2130 SD)

Population growth in the simulation ($r = -0.0267$) was depressed relative to the projected growth rate calculated from the life table ($r = -0.001$) because of inbreeding depression and occasional lack of available mates.

Note: 497 of 1000 harvests of males and 530 of 1000 harvests of females could not be completed because of insufficient animals.

Final expected heterozygosity was 0.5768 (0.0349 SE, 0.1305 SD)

Final observed heterozygosity was 0.7529 (0.0712 SE, 0.2664 SD)

Final number of alleles was 3.14 (0.35 SE, 1.29 SD)

Population2

Similar results for Population 2, omitted from this Appendix, would follow.

***** Metapopulation Summary *****

Year 10

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 100, P[S] = 1.000
 Population size = 8.65 (0.16 SE, 1.59 SD)
 Expected heterozygosity = 0.939 (0.000 SE, 0.004 SD)
 Observed heterozygosity = 1.000 (0.000 SE, 0.000 SD)
 Number of extant alleles = 16.92 (0.20 SE, 1.96 SD)

Metapopulation summaries are given at 10-year intervals.

Year 100

N[Extinct] = 79, P[E] = 0.790
 N[Surviving] = 21, P[S] = 0.210
 Population size = 10.38 (1.37 SE, 6.28 SD)
 Expected heterozygosity = 0.600 (0.025 SE, 0.115 SD)
 Observed heterozygosity = 0.701 (0.050 SE, 0.229 SD)
 Number of extant alleles = 3.57 (0.30 SE, 1.36 SD)

In 100 simulations of 100 years of Metapopulation:

79 went extinct and 21 survived.

This gives a probability of extinction of 0.7900 (0.0407 SE),
 or a probability of success of 0.2100 (0.0407 SE).

97 simulations went extinct at least once.

Median time to first extinction was 7 years.

Of those going extinct,

mean time to first extinction was 11.40 years (2.05 SE, 20.23 SD).

91 recolonisations occurred.

Mean time to recolonisation was 3.75 years (0.15 SE, 1.45 SD).

73 re-extinctions occurred.

Mean time to re-extinction was 76.15 years (1.06 SE, 9.05 SD).

Mean final population for successful cases was 10.38 (1.37 SE, 6.28 SD)

Age 1	Adults	Total	
0.48	4.71	5.19	Males
0.48	4.71	5.19	Females

During years of harvest and/or supplementation

mean growth rate (r) was 0.0545 (0.0128 SE, 0.4711 SD)

Without harvest/supplementation, prior to carrying capacity truncation,
 mean growth rate (r) was -0.0314 (0.0021 SE, 0.1743 SD)

Final expected heterozygosity was 0.5997 (0.0251 SE, 0.1151 SD)

Final observed heterozygosity was 0.7009 (0.0499 SE, 0.2288 SD)

Final number of alleles was 3.57 (0.30 SE, 1.36 SD)

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