STATE OF CALIFORNIA
THE RESOURCES AGENCY
DEPARTMENT OF FISH AND GAME
WILDLIFE MANAGEMENT DIVISION
NONGAME BIRD AND MAMMAL SECTION

PRELIMINARY POPULATION VIABILITY ANALYSIS FOR BANK SWALLOWS (*Riparia riparia*) ON THE SACRAMENTO RIVER, CALIFORNIA

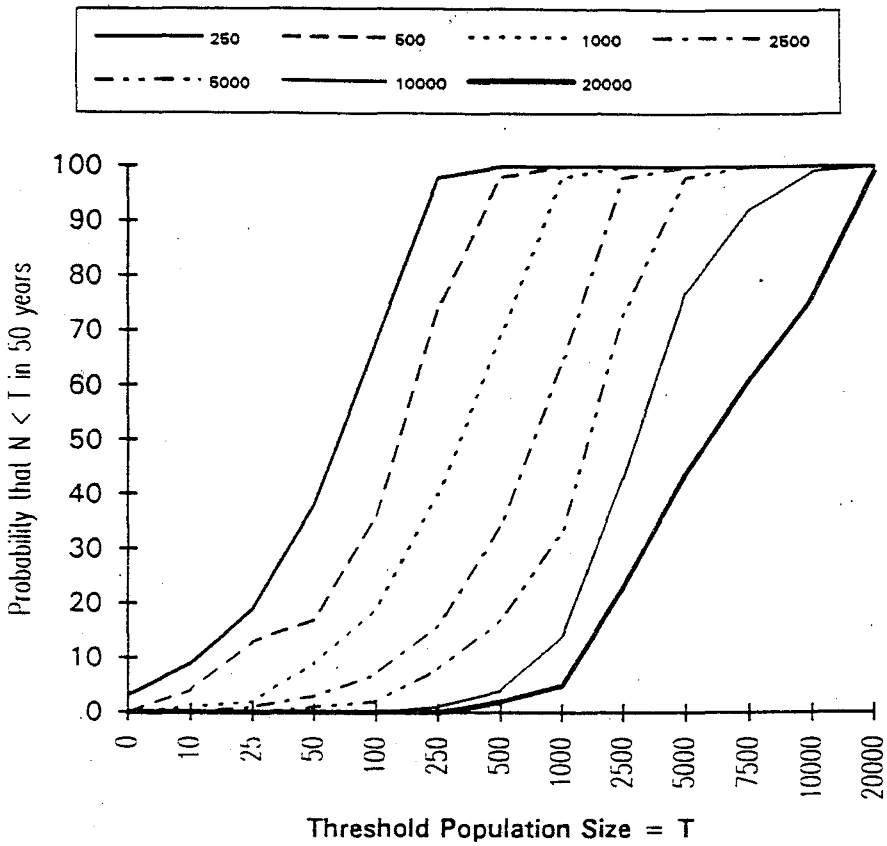
A Computer Simulation Analysis Incorporating Environmental Stochastcity

by

Marybeth Buechner

1992

Probability of Severe Population Decline
Effect of Initial Population Size



NONGAME BIRD AND MAMMAL SECTION REPORT 92-01

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PRELIMINARY POPULATION VIABILITY ANALYSIS FOR SACRAMENTO RIVER, CALIFORNIA BANK SWALLOWS (*Riparia riparia*) ON THE SACRAMENTO RIVER, CALIFORNIA

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ABSTRACT

This paper reports on a preliminary population viability analysis (PVA) for the Bank Swallow population on the Sacramento River. Bank swallows historically nested throughout the lowland areas of California at both inland and coastal sites. The remaining populations of Bank Swallows in California occur in a fraction of the species former range. Seventy-five percent of remaining colonies exist along the upper Sacramento River and other Central Valley streams. Since 1979, losses of Bank Swallow colony sites to bank protection projects along the Sacramento River have been documented and proposed projects conflict with the needs of the species along several reaches of the river. On March 3, 1989 the California Fish and Game Commission designated the Bank Swallow as a Threatened species.

An important part of a PVA is risk assessment, the estimation of the likelihood that a population will decline severely or become locally extinct. In order to estimate the risk of population decline or extinction for the Bank Swallow along the Sacramento River in California, I used RAMAS/age, a Monte Carlo simulation of the dynamics of age-structured populations. The program runs models which track the course of the simulated population over a 50-year period. It utilizes mean age-specific survival, fecundity, and migration rates and the year-to-year variance in those rates to estimate the probability that the population will fall below specified threshold levels within the next 50 years.

While some parameters could reliably be estimated from available literature, more information is needed on juvenile survival rates, the proportion of breeding pairs which produce two broods within a given breeding season, the net loss or gain to the population as a result of migration in given years, and the variation in fecundity, survival and migration parameters in the Sacramento River population over time.

Models utilizing the best available information indicated that:

1. The risk of low numbers in some years is substantial for the Sacramento River Bank Swallow population and, under most modelled conditions, is considerably higher than the risk of near extinction.

2. Under all but the most optimistic conditions, a single isolated colony has a substantial (37% or greater) chance of falling to less than 50 breeding pairs and a somewhat smaller (9% or greater) chance of disappearing entirely. Under the "most likely" conditions, a single colony had a very large (62%) chance of falling to less than 50 breeding pairs and a substantial chance (30%) of disappearing entirely.

3. Under most conditions modelled, an isolated group of colonies has a substantial chance (15% or greater) of falling to less than 100 breeding pairs and a somewhat smaller chance (7%) of becoming extinct. Under the "most likely" conditions, an isolated group of colonies faces substantial chances of dropping to 100 breeding pairs (probability = 47%) or disappearing entirely (probability = 33%).

4. For most conditions modelled, a population of Bank Swallows about the size of the current population occurring along the Sacramento River (10,000 breeding pairs) has a substantial (20% or greater) probability of falling to low numbers (1000 breeding pairs). Under the conditions of the "most likely" model, the risk of the population disappearing entirely is also substantial (33%).

5. Even under very optimistic conditions, the number of breeding pairs required to ensure a large continuing population of Bank Swallows is much larger than the current population size. Utilizing the "most likely" model, it appears that a population of Bank Swallows of 100,000 breeding pairs (more than 10 times larger than the current population) would be necessary to ensure a less than 50% chance of falling below 5,000 breeding pairs within 50 years.

These results suggest that the current Bank Swallow population faces a risky future. It may be necessary to protect very large numbers of Bank Swallows and very large areas of natural river bank habitat in order to assure that the population does not fall to low numbers in the near future. While the current PVA is only preliminary in nature and any conclusions in the absence of more complete information must remain tentative, this model represents our best estimates of existing conditions and probable future scenarios for the Sacramento River population of Bank Swallows. Until additional data are available, the information contained in this report represents the best estimate of risk for this population of Bank Swallows and will be used to establish target populations for the recovery of the species in California. As more information becomes available, refinement of the population analysis and risk estimates will be possible.

tlc

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RECOMMENDATIONS

1. Conduct annual surveys of the Bank Swallow population along the Sacramento River to determine abundance and distribution of colonies and breeding pairs.

2. Select colonies for in depth study to gather information on juvenile survival rates, the proportion of breeding pairs which produce two broods, and the net loss or gain to the population as a result of migration.

3. Conduct population and reproductive research for several consecutive years in order to estimate the variation in fecundity, survival and migration parameters.

4. Apply management strategies to ensure the protection of existing Bank Swallow populations and their habitat.

5. Preserve and protect all natural river bank habitats currently or potentially utilized by Bank Swallows through legislation, acquisition, and cooperative agreements.

6. Where feasible, protect or enhance other areas which could be settled by Bank Swallows, allowing the population to expand its local range and increase above its current numbers.

7. Implement management and habitat protection strategies to prevent single colonies or small groups of colonies from becoming isolated from the rest of the Bank Swallow population along the Sacramento River.

8. As more data become available revise population viability analyses, risk assessments, and target population figures necessary for recovery of the Bank Swallow in California.

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Population viability analyses and risk assessment

Population viability analyses (PVA's) are used to determine the population size and distribution necessary to ensure the long-term survival of populations of focal species . A complete PVA, in theory, would be based on complete genetic, demographic and environmental information about the focal species, would address all significant impacts, and would specify detailed management strategies resulting in long-term population viability (Shaffer 1981, 1987, Gilpin and Soule 1986). In practice, however, PVA's are often based on limited information, focus on a limited subset of threats and suggest possible management options which seem likely to reduce the risk of local extinction.

A large number of factors can affect the ability of a given population to persist in the face of habitat loss or disturbance. These factors can be divided into two general types of effects: deterministic and stochastic. Deterministic effects are those which operate in a systematic way, whose occurrence is predictable, and which produce foreseeable outcomes. For example, the replacement of a large segment of habitat by human development fairly straightforwardly reduces the number of animals which can be supported in an area. an impacts effect can be determined

Stochastic factors are those which come about as a result of chance events and whose outputs can only be predicted as probabilities, not as certainties. The stochastic factors affecting population persistence are generally divided into four categories: Rivers walk = stochastic

1. **genetic stochasticity**, fluctuations in the genetic structure of a population, including such factors as inbreeding depression or the loss of heterozygosity in small populations.

2. **demographic stochasticity**, fluctuations in such factors as the number of offspring produced by individual organisms, the age at which individuals first breed, the sex ratio produced in a group of offspring, etc.

3. **environmental stochasticity**, fluctuations in climate and resources (food, den or nest sites, water, etc.), and the associated changes in the growth rate of the population.

4. **catastrophes**, such as fire, flood, drought, epidemics, etc. which dramatically reduce population size or growth rate (Shaffer 1981, 1987, Soule, 1986).

The impact of these, and similar, factors on population viability depends on the effective size of the population (Crow and Kimura 1970, Wright 1977, Franklin 1980, Ehrlich and Ehrlich 1981). Habitat fragmentation exacerbates the effects of these factors because it reduces population size, increases the impact of surrounding areas, and increases isolation between subpopulations (Terbourgh and Winter 1980, Wilcox 1980, Frankel and Soule 1981, Harris 1984, Wilcox and Murphey 1985, Buechner 1987, Schonewald-Cox and Buechner in press).

Demographic and environmental stochasticity are often combined in analyses because in the field it is very difficult to untangle the effects of the two.

Fluctuations in climate or resource levels certainly influence the demography of a population. Alternatively, the demography of a population may affect its ability to respond to fluctuations in the environment.

The greater the variation in key demographic parameters, especially in age-specific birth and death rates, the greater the probability that a population will become extinct. Variation in these parameters can be caused by various factors such as fluctuations in the resource base, disturbance from human activities, etc. These factors can reinforce one another, so that the occurrence of one can lead to a cascade of other effects. For example, if human disturbance results in a number of females losing litters, the overall variation in the number of offspring produced per female is likely to increase, in turn making the population more sensitive to other destabilizing factors, such as variation in prey levels. If demographic stochasticity reduces population numbers the population may become too small to resist the effects of genetic stochasticity and be "doubly doomed."

A number of theoretical studies are available which analyze the long term persistence of a population based upon demographic or environmental stochasticity (e.g. Wright and Hubbell 1983, Strebel 1985, Belovsky 1987, Ewens, et al. 1987). These studies indicate that increased variation in reproduction or mortality decreases the expected persistence time of modelled populations. Estimated times to extinction based only on demographic variance are long for all but fairly small populations (MacArthur and Wilson 1967, Richter-Dyn and Goel 1972). However, populations large enough to be considered "safe" from the problems associated with genetic stochasticity may still be at risk from demographic stochasticity.

Empirical observations suggest the importance of environmental stochasticity by noting that the size of real populations varies much more widely than expected on the basis of intrinsic demographic variation alone (e.g. Diamond 1984). This observation has lead to a consideration of environmental stochasticity as a potential threat to population persistence. Predictive models have been developed which suggest that in a varying environment, population persistence is more sensitive to environmentally produced fluctuations in population size and growth rate (including variation in birth and death rates) than it is to the original size of the population (Leigh 1981, Wright and Hubbell 1983, Goodman 1987). Even large populations, with census population sizes in the thousands, may be threatened by environmental stochasticity.

Various characteristics, such as low density or large fluctuations in population size, have been identified as reasonably good predictors of susceptibility to extinction resulting from habitat loss (Terborgh 1974, Faaborg 1979, Terborgh and Winter 1980, Wilcox 1980, Goodman 1987). However, the details of the extinction process have not been well defined. Further, the effects of habitat loss and disturbance may be subject to sharp thresholds. It is becoming apparent in numerous cases that up to a given level of habitat loss or disturbance, extinction risks remain relatively low; however, beyond that level, risk can increase precipitously.

PVA's can be conducted for a single group of organisms (e.g. a single colony of Bank Swallows), for the population contained within a geographical unit (e.g. all Bank Swallows in the Sacramento River drainage, in California, or in North America), or for an entire species. Each level of analysis has its own advantages and drawbacks. In general it is more practical to limit the PVA to a relatively small area unless a great deal of information is available on the species. In most cases, data limitations will constrain the level of analysis.

An important part of a PVA is risk assessment, the estimation of the likelihood that a population will decline severely or become locally extinct. This type of analysis is often based on information about: (1) The general trend in population size over fairly long time periods (e.g. on average has the population been increasing or decreasing in the recent past). Given this information we assume that the trend will continue into the future unless impacts change. (2) The year-to-year fluctuations of the population around the general trend. For example, if the overall trend has been a roughly steady population, we might ask how likely is it that in any given year the population will either increase or decrease due to random factors. When information is available population trends and fluctuations can be analyzed in more detail by using age-specific fecundity and survival rates rather than overall population numbers. The goal of risk assessment is to estimate the probability that a population will fall below a given threshold size within a given time period.

Increased data from the field and from lab work will help to reduce the problems resulting from a lack of information about areas and species. However, even if enormous amounts of data became available, we could still not predict exactly how many species would be lost following a given level of habitat disturbance. This is because it is impossible to predict the future of the individual animals and plants in the communities of concern. Unpredictable environmental events, such as storms, droughts, changes in temperature, etc. can dramatically impact the species we are interested in. Even if the environment is relatively stable, the extinction of a given plant or animal species is not completely predictable. The demography and genetics of a population, and hence its likelihood of extinction are influenced by numerous stochastic events.

PVA's are not purely biological exercises. They are based, in part, on knowledge of local and regional planning and policy. They make assumptions about the likelihood of future actions on the part of interested parties (resource agencies, developers, planners, conservation groups, etc.). Moreover, the definition of "acceptable risk" is not a biological decision. Biological models may produce estimates of the form "there is a 50% probability that the population will drop to less than 100 individuals within the next 50 years". Whether the biologically defined risk is acceptable is a policy question. Agencies, planners and policy analysts must specify the threshold population size and the level of risk to be considered acceptable.

Bank Swallow population biology summary

The following is a brief summary of some aspects of the population biology of the Bank Swallow (*Riparia riparia*); more information may be found in numerous publications and reports including: MacBriar and Stevenson (1976), Freer (1977, 1979), Mead (1979a,b,c), Svensson (1986), Humphrey and Garrison (1987), Persson (1987a,b,c), Laymon et al. (1988) and California Fish and Game (1990).

The Bank Swallow is a small swallow with a white breast crossed by a distinctive brown breast band. As suggested by the species common and latin names, it is generally found along steep river banks or bluffs such as those found along the Sacramento River. The species is distributed across North America and Europe. In Europe the species (*Riparia riparia*) is called the Sand Martin.

The birds nest in burrows dug into sandy soil where erosion has cut nearly vertical earthen banks (Bent 1942, Hickling 1959, Laymon et al. 1988, Cal. Fish and Game 1990). The species is colonial, forming nesting colonies consisting of 10-3000 burrows. The birds forage over water and grassland habitats adjacent to the colony, feeding on flying terrestrial and aquatic insects.

Bank Swallows are a migratory species breeding in the Northern Hemisphere and wintering in the Southern Hemisphere. North American populations spend September through March on wintering grounds in Central and South America in riparian and grassland areas. California populations arrive on the breeding sites from late March to mid-April. Courtship and pairing are followed by the completion of a nest burrow and the production of a clutch of 3-6 eggs. Although the colony is generally sited in an area of fresh erosion, in some cases, burrows remaining from a previous season may be reused. Hatching occurs 21 days after egg laying, which can occur as early as mid-April along the Sacramento River (Cal. Fish and Game 1990). Nestlings fledge approximately 21 days after hatching. Pairs generally produce 2-4 fledglings per brood (Freer 1977, Mead 1979b, Hjertaas et al. 1988). Second broods are common in some populations (Freer 1977, Mead 1979b, Persson 1987b). Nesting activities are usually completed by mid-July and the colony sites are abandoned.

Bank Swallows have a short life span of two to three years on average, with five or more years being exceptional (Freer 1977, Cal. Fish and Game 1990). Annual survival rates are generally 0.25-0.45 for adults (reviews in Freer 1977, Mead 1979c, Hjertaas et al. 1988); survival rates for juveniles are substantially lower than for adults but are difficult to estimate accurately (Freer 1977, Mead 1979b, Hjertaas et al. 1988).

Although little is known about the long-term migratory patterns of individual birds from North American populations, evidence from Europe indicates that at some colonies most of the individuals returning from the wintering grounds nest within 10 kilometers of their last breeding colony site (MacBriar and Stevenson 1976, Freer 1977, 1979, Mead 1979a,b, Mead and Harrison, 1979). The scant data available from North American populations do not contradict this pattern (Stoner 1941, Freer 1977). The major difficulty with these types of data is that overall capture return rates for banded birds are generally very small (Freer 1977).

The degree of environmental stochasticity faced by Bank Swallows is almost certainly very large. Bank Swallow populations exploit the rapidly changing habitat of a meandering river system. Breeding sites occur with some consistency within long reaches of the river, but particular sites are ephemeral, appearing and disappearing as the river cuts new banks. Many of the variables affecting the Bank Swallow population parameters, e.g. winter river flow levels and spring rainfall amounts, are highly variable in northern California. Bank Swallow populations which have been studied over long periods of time show substantial fluctuations in population numbers (Cowley 1979, Svensson 1986, Persson 1987a,b,c)

Historically, Bank Swallows nested throughout the lowland areas of California at both inland and coastal sites (Grinnell and Miller 1944, Laymon et al. 1988, Cal. Fish and Game 1990). The majority of the remaining California populations of the Bank Swallow occurs over a small portion of the species historic range along the upper Sacramento River. Seventy-five percent of the California population is found along Central Valley streams (Humphrey and Garrison 1987). A few scattered colonies exist throughout the rest of northern California (Laymon et al. 1988). Bank Swallows no longer occur in central or southern California (Cal. Fish and Game 1990). Past bank protection projects on the Sacramento River may have seriously affected the species, although data documenting these impacts are available only from the past decade or so (Cal. Fish and Game 1990). Since 1979, losses of several Bank Swallow colony sites to riprapping projects along the Sacramento River have been documented (Cal. Fish and Game 1990). Current and proposed projects conflict with the needs of the species along several reaches of the river (Cal. Fish and Game, 1990). For example, about 25 miles of bank protection has yet to be constructed along a reach of the Sacramento River where approximately 35 colony sites have been active recently (Jones and Stokes Associates, 1987). On March 3, 1989 the California Fish and Game Commission designated the Bank Swallow as a Threatened species in the State.

A caveat

By running the program with populations of different sizes and with different variances in life table parameters, we can suggest how changes in population size and demographic stochasticity are likely to affect populations of Bank Swallows. The main drawback of analyses like the current one is that they are only as good as the data which is entered into the program. If the information is based on a sample which is not representative of the population as a whole, or if the trend indicated by the field data is not likely to continue, results may be misleading. As new information is available, it will be necessary to recheck the analysis. In some cases, exploratory computer studies do not produce answers, but rather indicate what questions need to be asked in order to produce more reliable analyses of population viability. This, in itself, is often a valuable step in planning for the management and recovery of the species in question. Nonetheless, the results of any such analyses must be treated as tentative estimates, not "hard" answers.

It should also be noted that these analyses are based strictly on the inherent biological characteristics of the Bank Swallow and no attempt has been made to model human disturbance and habitat destruction. In this respect, the results must be considered conservative because a major threat, bank protection projects and the habitat destruction they produce, has been ignored for the moment in order to model the "natural" constraints on Bank Swallow populations. The base population size, however, which may have been affected by human activities in the past, has a profound influence on the PVA results. Since the current population is fairly small, the impact of "natural" variation in demographic factors is relatively pronounced. If the further complication of continued and systematic habitat loss were to be included in the PVA (as it hopefully will be in future analyses) then the prospects for disastrous consequences for the Bank Swallow population may be increased substantially.

METHODS

The program used (RAMAS/age)

The goal of a modelling program such as RAMAS is to assess the effect of demographic parameters, environmental variability, and population size on the likelihood of population survival over time. The program runs as many individual simulations of the population as requested, up to 500 iterations. Within each iteration, the survival, fecundity and migration values used in each year are chosen randomly from a distribution with the overall mean and coefficient of variation (cv) entered for the class. The results are then summed to generate (1) the expected number of individuals in the population over time for up to 50 years and the variation in those numbers between runs and, (2) the probability that the population will fall below a specified threshold at least once during the time period of interest (up to 50 years).

The results of a program such as RAMAS reflect two basic processes. First, the average growth rate of the population, "Ro", determines whether the population will, on average, decline or increase over time. This value is entirely determined by the mean survival and fecundity rates entered into the program and indicates the expected course of the population in the absence of any year-to- year variance in these rates. In addition, "Ro" is unaffected by the initial size of the population.

The second factor reflected by the way RAMAS works is the relationship between year-to-year variance in survival and fecundity rates and the stability of a population over time. For each year of each run within the simulation, fecundity and survival rates are randomly chosen from a normal distribution (defined by the overall means and cv's entered for the population). Even if "Ro" = 1, indicating a population which would be steady in the absence of variation, some runs will crash to very low numbers while others climb to very high numbers. The probability that a run will drop to very low numbers is determined by the cv's of survival, fecundity and migration, and by the initial size of the population. The impact of initial population size has special importance for endangered populations, most of which are suffering from greatly reduced population size.

The type of data used

This analysis is based on an examination of demographic information on the Bank Swallow. In order to estimate the risk of severe population decline for this species along the Sacramento River in California, I use RAMAS/age, a Monte Carlo simulation of the dynamics of age-structured populations ("Monte Carlo" refers to models which use a certain process for generating random numbers). The program runs models which track the course of the simulated population over a 50- year period. Populations increase as the result of either birth or by immigration; similarly, they decrease as the result of death and emigration. Models such as the one used in this analysis directly include both birth and death rates and the changes in those rates over time. The mean survival and fecundity rates and the year-to-year variance in those rates are input for each age class in the modelled population. Emigration and immigration are not input individually, rather the expected net result of these two migratory processes is entered for each age class. For example, a given age class might be expected to lose an average of 10% of its individuals per year as a result of migratory processes.

Mean fecundity rates are entered for each age class as the average number of female offspring produced per female. Mean mortality rates are entered as the average survival rate through each age class. Migration may also be entered as the average loss or gain of individuals annually. The year-to-year variances in survival, fecundity and migration for the population are assumed to be the result of environmental variation in the habitat of the species. The variance in these rates over the course of many years is entered in the program as the coefficient of variance (cv) of the parameter (cv = the standard deviation divided by the mean). For example, if annual adult survival for each of three years was 0.5, 0.6, and 0.7, the overall mean over this whole time would be 0.6, the standard deviation would be 0.10, and the cv would be 0.1/0.6 = 0.167.

Year-to-year variance in survival can be entered separately for the "young-of-the-year" age class and for adult animals. Year-to-year variance in fecundity and migration, however, are assumed to be the same for the whole population and cannot be entered separately for different classes.

Ideally, all of the above data are estimated from field data covering many years. If this is not possible, the best available professional estimates of the parameters can be used. However, this means that the results of the model are less reliable. In order to reliably estimate mean fecundity and survival rates for each age class, at least 10 years of data are needed. In the present case, short-term data is are available for survival and fecundity from several North American populations (Freer, 1977). Long runs of data on these rates are available only from Scandinavian Bank Swallow populations: 20 years of survival data from Persson (1987b) and 16 years of fecundity data from Svensson (1986). Little data of any sort are available on the details of individual migration patterns.

Other types of information can be used in this type of simulation model. For example, density dependence can be entered by specifying the relationship between survival and fecundity rates and current population size. In addition, correlations between fecundity, survival and migration rates may be entered. I have not used these parameters in this analysis because no information is available for Bank Swallows.

An important input that is not included in this PVA is the impact of further habitat loss on the population. The model assumes not only that additional habitat will not be lost, but that existing habitat is sufficient for growth of the population; the model includes no "population ceiling" above which population growth stops due to a lack of habitat. Population limitation due to a lack of habitat and the impact of continuing habitat loss are likely to profoundly influence the population. Once these parameters can be quantified they should be used to develop further models.

Estimating survival and fecundity rates

Sufficient data have been found in the literature to allow estimates of means and variances for both reproductive and mortality parameters. Estimates of mean reproductive and mortality rates for adult Bank Swallows were based on studies by Freer (1977), Mead 1979a,b,c, Svensson (1986), Persson (1987a,b,c), Hjertaas et. al (1988) and studies of local populations by Humphrey and Garrison (1987) and Leymon, et al. (1988) and on consultation with wildlife biologists currently studying the Sacramento River Bank Swallow population (R.

Schlorff and B. Garrison, pers. comm.) (Table 1; and Appendix 1). Data are relatively weak for estimates of the survival of juvenile birds from fledgling to age one year and for the proportion of pairs which produce two broods within a single season.

Table 1. Summary of the three combinations of juvenile survival and proportion of double broods which were considered. Fecundity rates are shown as the number of female offspring per female. A brood size of 4.0 is assumed for all models; differences in annual fecundity are the result of differences in the proportion of breeding pairs which produce two broods in a single breeding season.

Model 1:
- Annual adult survival rate = .40
- Annual juvenile survival rate = 0.151
- Annual fecundity rate (female offspring/female) = 4.0

Model 2:
- Annual adult survival rate = .40
- Annual juvenile survival rate = 0.22
- Annual fecundity rate (female offspring/female) = 2.8

Model 3:
- Annual adult survival rate = .40
- Annual juvenile survival rate = 0.30
- Annual fecundity rate (female offspring/female) = 2.0

More information on juvenile survival and the proportion of double broods is needed. Because of this gap in the available data, juvenile survival rates and overall fecundity rates were adjusted to result in a population with an R_O of just over 1.0 (i.e. a slowly growing population). Three combinations of juvenile survival and proportion of double broods were considered (see Table 1 and Appendix 1 for details):

1. juvenile survival rate = 0.151, and all breeding pairs produce two broods in an average year giving a fecundity rate of 4.0 (females per female);

2. juvenile survival rate = 0.22, and 40% of breeding pairs produce two broods in an average year giving a fecundity rate of 2.8 (females per female); and

3. juvenile survival rate = 0.30, and no breeding pairs produce two clutches in a average year giving a fecundity rate of 2.0 (females per female).

Model 2 was considered to be the most realistic reflection of actual Bank Swallow population biology on the Sacramento River (B. Garrison and R. Schlorff, pers. comm.).

The overall model also includes the year-to-year fluctuations in survival and fecundity rates caused by environmental variation. This information is entered into the model as estimates of the coefficients of variation (cv) for survival and fecundity rates. The starting point for estimates of these cv's are data from Swedish Bank Swallow populations, the only populations for which many years of data are available. Persson (1987b) reports the mean and variance of survival rates for juvenile and adult Bank Swallows based on 20 years of data from south- west Scandia, Sweden over the years 1964-84. In this population the cv of survival = 0.25 for both adults and juveniles. The estimate of fecundity variation is based on 16 years of data from Svensson (1986). He studied a population in the subalpine birch belt at Ammarnas, Swedish Lapland from 1968-1985. The initial estimate of cv of fecundity = 0.30 is based on that study. The cv's input into the model are based on these Scandinavian estimates. It is possible that the cv's estimated from the Scandanavian populations may be unrealistic for the Sacramento River population; this, in turn, could effect the reliability of the model. Thus, I conducted a sensitivity analysis which examines how changing cv's of survival and fecundity rates might affect risk estimates.

Estimating the impact of migration

One important aspect of the biology of migratory species such as the Bank Swallow is the proportion of individuals which return to the same general area following migration and the proportion which move to distant areas. Migratory species effectively recolonize their breeding range each year. As a result of this recolonization process, some birds which were previously part of a distant population may join the focal population and some birds which were previously members of the focal population may settle in distant areas and be lost to the focal population. Although very little data of any sort is available on these patterns for most birds, some authors have speculated that details of colonization patterns and the "leakage" of individuals away from isolated populations may be important factors in the decline of neotropical migrants from forest patches in the Northeastern United States (e.g. Whitcomb et al. 1981; Lynch and Whigam 1984).

The few data available for Bank Swallows suggest that most individuals return to the same 10-20 kilometer stretch of river following migration, although much longer movements (up to hundreds of kilometers) are possible (MacBriar and Stevenson 1976, Freer, 1977, 1979, Mead 1979a,b,c). Mead and Harrison (1979) and Mead (1979b,c) estimated that in Britain, 93% of adults and 87% of first-year birds return to colonies which are within 10km of the colony where they nested or where hatched the previous year. Only 0.5-2.0% of the birds moved more than 100km from their previous colony (thus effectively leaving the local population). Stoner (1941) reported than in one North American Bank Swallow population 78.5% of the adults and 42.9% of the first-year birds returned to within 0.25 miles (0.40 kilometers) of the colony in which they were first banded.

Rigorous estimates of the mean and variance of the number of individuals which enter or leave the Sacramento River Bank Swallow population as a result of migration movements have not been possible. Since many of the colonies in Southern California are no longer extant and most of the colony sites have been disturbed, any birds stopping in southern areas on their way north to the Sacramento Valley would be unlikely to breed successfully. I have conservatively assumed that in an average year (a) more animals "go astray" each year following migration than join the population, and, thus, migration results in small losses to the population and (b) that these losses are countered by the normal population growth. Thus, on average, over the course of the simulation (50 years), migration results in a small net loss to the population which is balanced by a small positive population growth rate.

In order to access the relative importance of better estimates of migration rates, migration losses were varied from 0-4% of the initial population. In each case the input average value for adult survival was adjusted slightly so that the average growth trend of the population was sufficient to counter losses to migration. This resulted in models which in all cases produced a stable population in the absence of environmental stochasticity.

Because there are no data available allowing even a preliminary estimate of the variance in migration, a relatively large cv of 1.0 is used. Thus, while on average there is a small net loss to migration, in any given year there may be either a net gain or a net loss to the population as a result of the number of animals returning from the wintering grounds in that year. It should be noted that the above assumptions are conservative; migration may be a much larger influence on the population than has been assumed. If this is the case, the results of the current model will be underestimates of the actual risk to the population.

It should be noted that migratory losses were input as a percentage of the initial population size. These losses were not reduced for if population size subsequently fell due to a series of "bad" years. This means that small or declining populations could be hit harder by migratory losses than large or growing populations. This assumption could result in an overestimate of the extinction risk to the population. More information on migration rates is clearly needed but will be very difficult to obtain because of the amount of time and labor involved in the massive banding effort needed to estimate return rates following migration.

"Most likely" model

The "most likely" model, i.e. the model considered to represent the best estimate of the actual population, is: Model 2 juvenile survival and fecundity rates (see Table 1), cv's as observed for the Scandanavian Bank Swallow populations, and a moderate value of migration "losses" (2% of the original population) (Table 2). Risk assessments were based on this model.

Table 2. Summary of parameters of the "most likely" model.

Average values of demographic parameters

- Average annual adult survival rate = 0.40
- Average annual juvenile survival rate = 0.22
- Average annual fecundity rate = 2.80

Coefficients of variation of demographic parameters

- cv of adult survival = 0.25
- cv of juvenile survival = 0.25
- cv of fecundity = 0.30

Impact of migration:
migration losses = 2% of initial population size. Loss to migration was spread evenly across the age classes.

Cases examined

Single colony

The first level of analysis was the case of a single isolated colony of Bank Swallows. Over the 5 years (1986-90) that the Bank Swallow has been studied along the Sacramento River, average colony size has been approximately 390 burrows (R. Schlorff and B. Garrison, pers. comm.). Average burrow occupancy rate ranged from 0.39 to 0.47. Both the average burrow size and average occupancy rates are available for two years (Table 3). Assuming that all occupied burrows represent nesting attempts these data combine to give average population sizes of 156-179 breeding pairs. I have modelled an isolated colony which is slightly larger than average, with 200 breeding pairs. I used RAMAS to calculate the probability that such a colony would drop below threshold population sizes (ranging from 0-150) within the next 50 years.

Several closely spaced colonies

This model addresses an isolated group of colonies, which exchange individuals sufficiently often to be considered as one closely linked population. Some evidence is available which indicates that birds may move frequently between colonies which are less than 10 kilometers apart (Freer 1977, Mead 1979b,c, Persson 1987a). In this case, closely spaced colonies may be demographically linked and act as a single unit with respect to population fluctuations. Thus, I ran a series of models estimating risk of severe decline for groups starting with 1000 pairs of birds, a number which might typically be found in several interacting colonies.

Entire Sacramento River population

Recent data suggest that the population of Bank Swallows along the Sacramento River is currently less than 10,000 breeding pairs, although numbers in the recent past have been higher (Table 4, R. Schlorff and B. Garrison, pers. comm.). Thus, I ran a series of models starting with 10,000 breeding pairs, assessing the risk of severe population decline for the entire Bank Swallow population on the Sacramento River.

Table 3. Sacramento River Bank Swallow field data. Estimates of total number of colonies, average burrows per colony, total number of burrows in all colonies combined, and average burrow occupancy rates for Bank Swallows on the Sacramento River, 1986-1990 are shown (R. Schlorff and B. Garrison, pers.comm.).

Year	1986	1987	1988	1989	1990
No. colonies	70	66			53
Ave. burrows	390	390			390
Tot. burrows	27440	25750			20620
Ave. occupancy	46%	47%	47%		39%

Average no. colonies for those years with data = 63
Average burrows/colony for those years with data = 390
Average occupancy rate for those years with data = 45%
Average total number burrows for those years with data = 24603

Table 4. Calculations of Bank Swallow population sizes along the Sacramento River assuming: (1) one breeding pair per occupied burrow, (2) an occupancy rate of 45% for those years for which this information is not available, and (3) total burrow number of 24,600 for those years for which this information is not available are shown:

Year	1986	1987	1988	1989	1990
Total no. breeding pairs	12622	11587	11070	11070	8042
Ave. no. breeding pairs per colony	179	175	175	175	156

RESULTS

The probability that Sacramento Valley Bank Swallow populations will fall below threshold population sizes within the next 50 years

Comparison of models 1, 2 and 3

The results of models 1, 2 and 3, which differed in juvenile survival rate and the proportion of breeding pairs which produced two clutches, were very similar. I compared the models for the whole population case with moderate cv's and migration losses equal to 0.5% of the initial population (Figure 1). The models also produced very similar results when other combinations of cv's and migration impact were used. The risk assessment values produced by the three models were nearly always within a few percent of one another. Model 2 represents both the intermediate situation and the scenario judged to be most realistic for the Bank Swallow population along the Sacramento River (B. Garrison and R. Schlorff, pers. comm.). However, the results of the three models are very similar. This occurs because all three models assume that the population would be steady in the absence of variation in the input parameters (i.e. all models assume an R_o value of approximately 1.0). Thus, when the reproductive rate was increased, the juvenile survival rate was decreased in order to produce the same average population growth rate in all three models (see Methods). Surveys of the Bank Swallow population along the Sacramento River are needed to determine whether or not the assumption of an average population growth rate of R_o = 1.0 is realistic. About 10 consecutive years of data will be necessary.

Effects of changing the impact of migration

Any models of the sort used here are only as good as the data which is input into the simulations. I believe that the greatest possibility for error in the current model lies in the possibility that the input impact of migration is an unreliable estimate for the Sacramento River population. The model assumes a average annual net "loss" to migration of between 0.5% and 4% of the initial population size. While this seems a small range of values, small changes in this parameter had a large effect on the risk of the population falling to very low numbers. Figure 2 shows the effect of increasing the impact of migration on the risk of the population dropping below threshold values for Model 1; Models 2 and 3 produced very similar results. Increasing the net "loss" to migration (the number of birds surviving migration but not

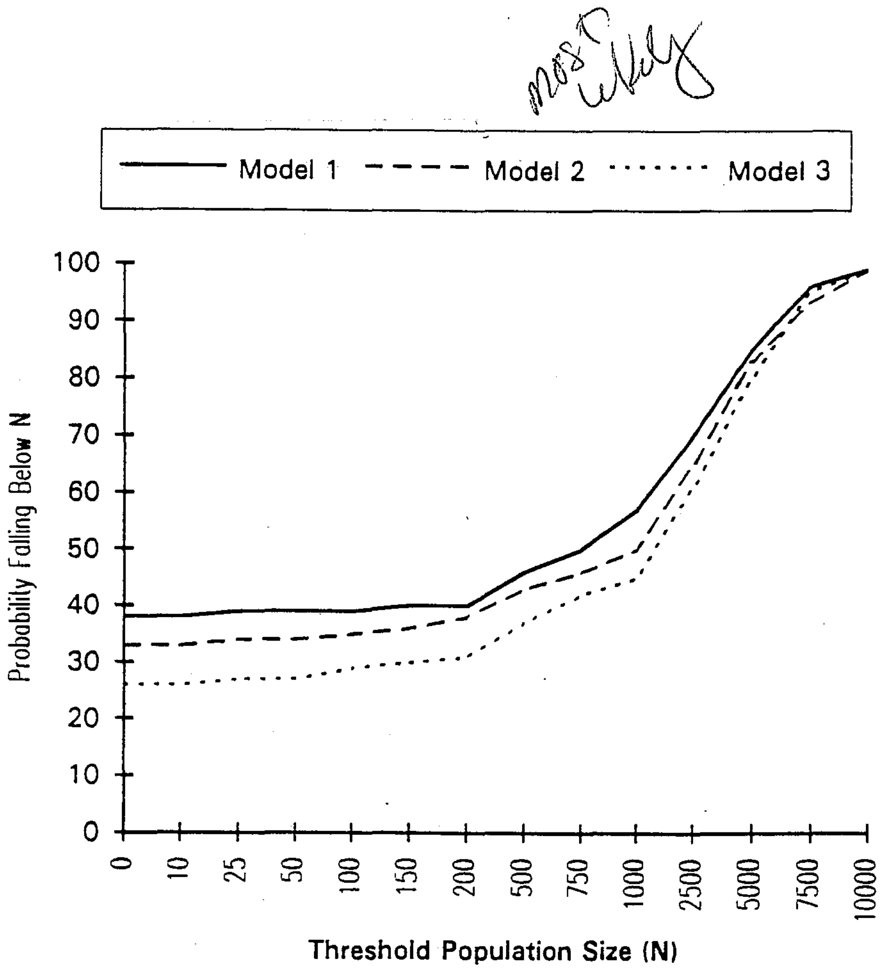

Figure 1. Sensitivity analysis: The three basic models
This figure shows a comparison of the three basic models of Bank Swallow population parameters. Models differ in the rate of juvenile survival and the proportion of double broods. "Model 1": Juvenile survival rate = 0.151; all breeding pairs produce two broods in an average year; "Model 2": Juvenile survival rate = 0.22; 40% of breeding pairs produce two broods in an average year. "Model 3": Juvenile survival rate = 0.30; no breeding pairs produce two clutches in a average year. Each line on the graph indicates the probability of a Bank Swallow population (fitting a given model) falling to below various threshold population sizes within 50 years. Results shown are for the whole population case with migration "losses" of 2% of the initial population size.

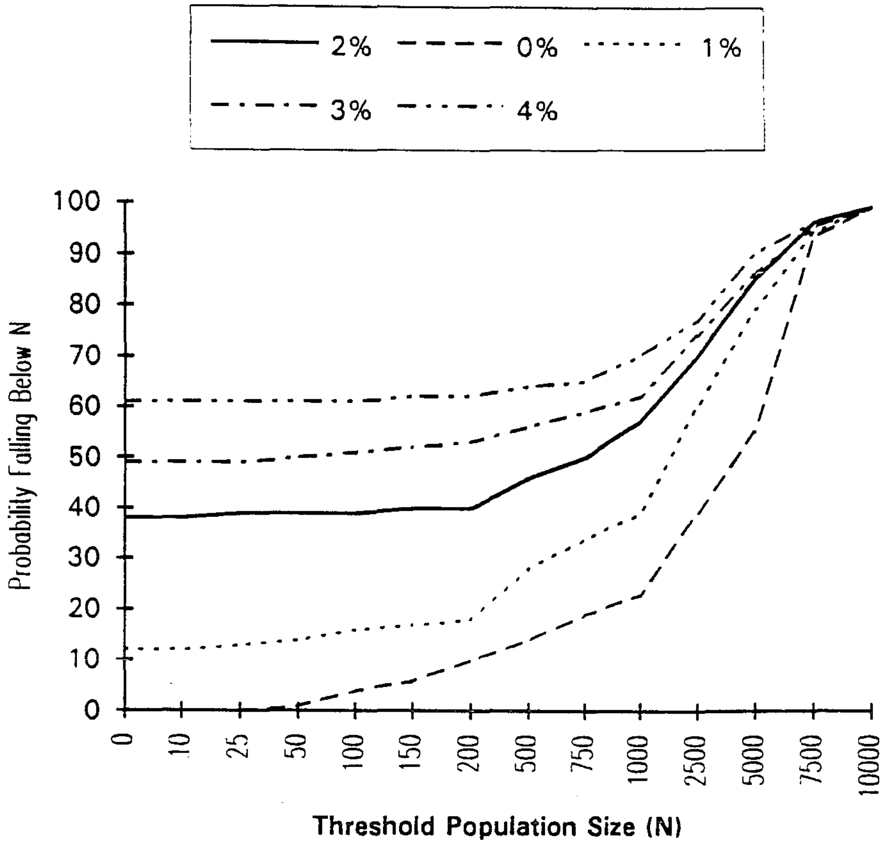

Figure 2. Sensitivity analysis: changing the impact of migration.
This model shows the effects of migration "losses" on the risk that the Bank Swallow population will fall below various threshold values within 50 years. It is assumed that: (1) a certain number of birds "go astray" and do not return to their population of origin, resulting in a net loss to the population as result of migration; and (2) This loss is balanced by a positive population growth rate, so that in an average year losses to migration are made up by reproduction. The average annual loss to migration was varied from 0 to 4% of the original population. The results shown here for are for Model 1 with the cv's as observed in Scandinavian Bank Swallow populations. The results of the other models, including the "most likely" model were very similar to those shown here.

returning to the population) from 1% to 4% of the initial population size resulted in a 6-fold increase in the risk of extinction (Figure 2). The affect of this parameter is greatest on the risk of complete extinction of the population (threshold = 0 breeding pairs). Changing the net "loss" to migration had considerably less effect on the probability to falling below large thresholds than it did on the probability of falling below small thresholds. This occurred because the average number of birds lost due to migration wanderings did not change if population size happened to become smaller over the course of a simulation run. As a result, any population which became small during the 50 years of the simulation was likely to be heavily impacted by migration "losses"; populations falling to near extinction were frequently pushed over the brink. While little information is available, there is no a priori reason to reject this assumption as unrealistic. A moderate net loss to migration, equal on average to 2% of the original population, was judged to be the most realistic scenario (B. Garrison and R. Schlorff, pers. comm.; see Methods). More information concerning the migration patterns of the Bank Swallow population along the Sacramento River is needed. In particular, data are needed on the number of birds annually lost or gained by the population as a result of individuals returning to a different population than the one which they left the previous fall.

Effects of changing coefficients of variation (cv's).

Estimates of cv's for survival and reproductive rates are based on relatively reliable data (see Methods). Nonetheless, it is possible that variation in survival and fecundity are different for California populations than for the Scandinavian populations. It seems unlikely that cv's are substantially lower for the California populations than for the Swedish populations, since a number of the major factors which may influence survival and fecundity (e.g., spring temperatures and annual water flow) are highly variable in California. I explored the effect of changing the cv for each parameter on the overall likelihood that the population would decline below threshold values by running models which started with 10,000 breeding pairs and varying all cv's from 0.10 to 1.00. The cv's were changed both singly and collectively.

Figure 3 shows the results of changing cv's on the probability that the population will fall below 100, 500, 1000, and 5000 breeding pairs, respectively. [**Note the scale of the graph.** This scale is intended to make it easier to read risk estimates for low population thresholds]. In all cases, changing the cv of adult survival rates (cvA) has relatively little affect on estimated risk of falling below threshold population size. Changing the cv of fecundity rates (cvF) and changing the cv of juvenile survival rates (cvJ) have similar, moderate effects on estimated risk. This is not surprising since these parameters (fecundity and 1st year survival) both directly affect the number of new breeders present in the population in the next year. As one might expect, changing the cv's of fecundity, juvenile survival, and adult survival simultaneously produced the most dramatic changes in estimated risk. **This analysis suggests that it is important to obtain more information on the year-to-year variance in demographic parameters, especially fecundity and juvenile survival rates.**

Effects of starting population size.

Obviously, the larger the starting size of the population, the less likely it is that the population size will fall below given threshold numbers. Figure 4 shows this relationship for a Bank Swallow population fitting model 2 with a low impact of migration (migration loss = 1/2%); results for the other two

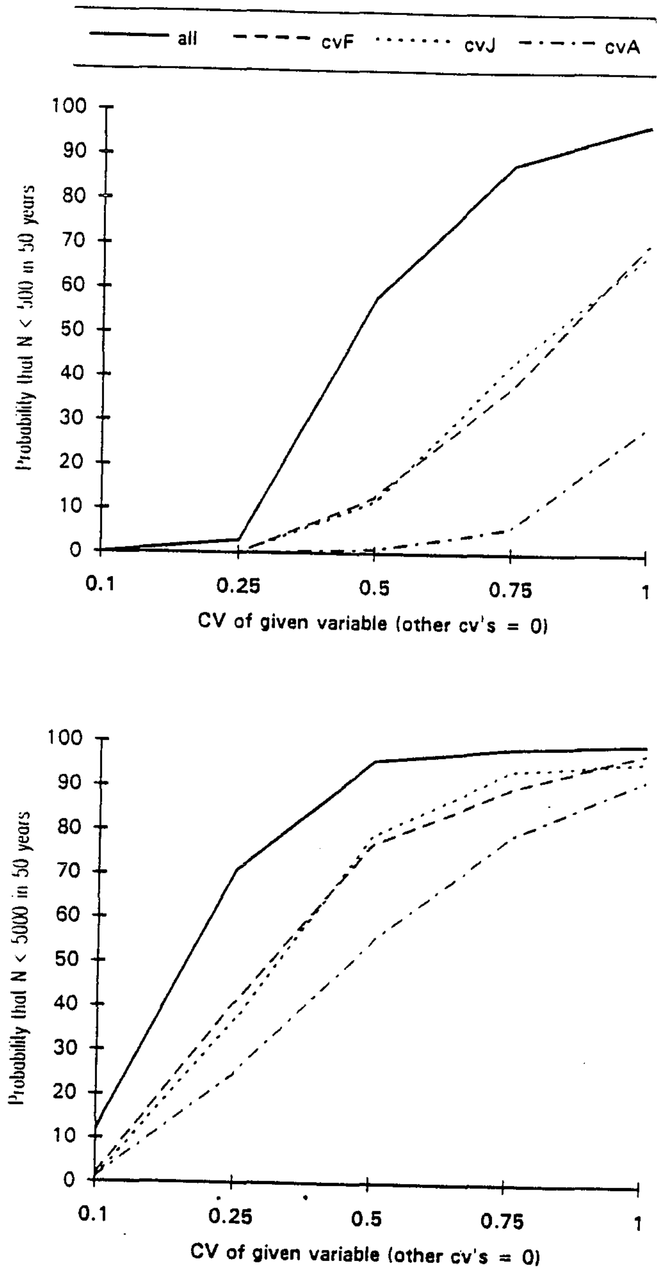

Figure 3. Sensitivity analysis: Coefficients of variation

This figure shows the effects of changing the coefficients of variation of demographic parameters on the probability that the population will fall below 500 or 5000 breeding pairs within 50 years. As the cv's of fecundity (cvF), juvenile survival (cvJ), adult survival (cvA) or all of three parameters are increased, the probability that the population will fall below given threshold sizes increases. Results are shown here for Model 1 with cv's as observed in Scandinavian Bank Swallow populations. The results of the other models, including the "most likely" model, were very similar to those shown here.

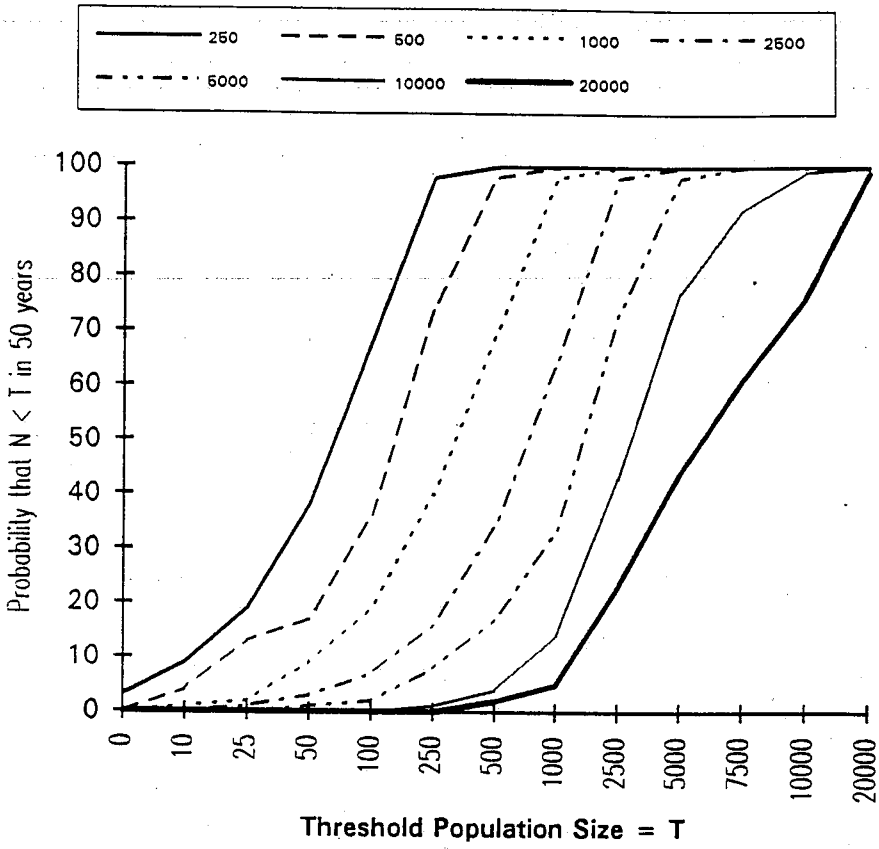

Figure 4. Sensitivity analysis: Initial population size

This figure shows the effects of changing initial population size on the probability of the Bank Swallow population falling below given threshold sizes within 50 years. Each line represents a different initial population size as indicated in the figure legend. Results are shown here for Model 1 with cv's as observed in Scandinavian populations. The results of the other models, including the "most likely" model, were very similar to those shown.

models were very similar. It is, perhaps, not so obvious that relatively large populations are necessary to prevent high risks of falling below substantial thresholds (e.g. 2500 breeding pairs). This does not mean, however, that such populations are necessarily at risk of near extinction (less than 100 breeding pairs). Risk curves for most starting population sizes curve upward rapidly; i.e. in most in most cases the risk of near extinction is much less than the risk of dropping to moderately low numbers in one or more years. For example, a population which began with 10,000 breeding pairs (approximately the current size of the Bank Swallow population on the Sacramento River) had a greater than 40% chance of dropping below 2500 breeding pairs sometime within the next 50 years due to environmental and demographic stochasticity under Model 1 (results of the other models, including the "most likely" model were similar). However, that same population had a less than 1% chance of falling below 100 breeding pairs. Similarly, a population which started with 5,000 breeding pairs had nearly a 70% chance of falling below 1000 breeding pairs in one or more of the 50 years it was followed, but the risk of dropping to below 100 breeding pairs was only about 5% under model 1 (again, the results of the other models, including the "most likely" model were similar).

In order to utilize this information, it will be necessary to specify what threshold population sizes are to be considered as alarming and to indicate what level of risk is acceptable. However, the specification of important thresholds and definition of acceptable risk is a policy decision best dealt with by the appropriate agencies, and, thus, is not addressed here. The risk of low numbers in some years is substantial for the Sacramento River Bank Swallow population and, under most modelled conditions, is considerably higher than the risk of near extinction. It should also be noted that a substantial change in the Bank Swallow population size would necessitate a new PVA using the new base population level as the "initial" population size. A drop in size from the current moderately low population level to a very low population size (e.g. 2500 or fewer breeding pairs) may have the effect of accelerating the extinction process as new factors come into play. For example, demographic and genetic stochasticity assume larger roles as population size decreases. In addition, the rate of habitat losses and the pattern of population distribution across the remaining habitat may change if population size changes dramatically. Substantial decreases in population size combined with exacerbated risk factors (e.g. increased habitat loss, prolonged drought, etc.) can produce what has been called an "extinction vortex" (Gilpin and Soule 1986) sending the population into an ever-accelerating spiral downward toward extinction.

Risk Assessment: Single colony, several colony and whole population models.

<u>Single colony risk assessment</u>

Figure 5 shows the risk that an isolated colony starting with 200 breeding pairs will fall below various threshold sizes within 50 years under the assumptions of the "most likely" model (see Table 2). Note the scale of the graph. This scale is intended to make it easier to read risk estimates for low population thresholds. The risk estimate is shown for populations with (a) the estimated cv's based on available data, (b) populations with cv's one half those of the initial estimates, and (c) populations with cv's twice those initially estimated. Assuming that the input data for this model are realistic, a single isolated colony starting with 200 breeding pairs has an 83% chance of dropping to 100 breeding pairs, a 62% chance of dropping to 50 breeding pairs, a 45% chance of dropping to 25 breeding pairs and a 30% chance of disappearing entirely within 50 years.

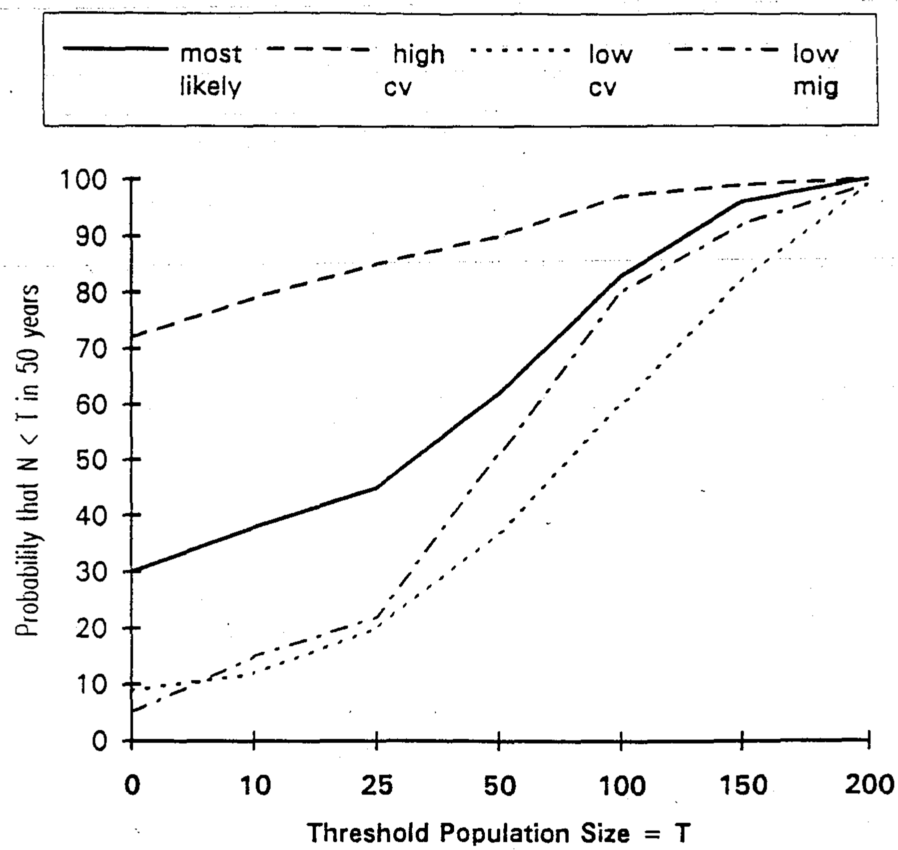

Figure 5. Risk assessment: Single isolated colony
This figure shows the probability that a Bank Swallow colony starting with 200 breeding pairs will fall below given threshold population sizes within 50 years. Results are shown for the "most likely" model; for a "low cv" model with cv's 1/2 of those of the "most likely" model; for a "high cv" model with cv's twice those of the "most likely" model; and for a "low mig" model with migration losses 1/4 those of the "most likely" model.

The sensitivity analysis indicated that the model was sensitive to assumptions about the magnitude of cv's and migration impact. However, even if these parameters are lowered substantially (to perhaps unrealistic values), a single isolated colony is still not "safe". If all cv's are reduced to 1/2 of their original value, a single isolated population still has a 37% chance of falling to 50 breeding pairs and a 9% chance of disappearing entirely. If cv's remain at the observed rate but the average "loss" to migration is reduced to 0.5% of the initial population there is a 50% chance of falling to 50 breeding pairs and a 5% chance of extinction. Only if both cv's and migration impact are made very small does the risk of severe reduction in population size become less than one percent. Under all but the most optimistic conditions, a single isolated colony starting with 200 breeding pairs has a substantial (37% or greater) chance of falling to less than 50 breeding pairs and a somewhat smaller (9% or greater) chance of disappearing entirely. Under the "most likely" conditions, a single colony had a very large (62%) chance of falling to less than 50 breeding pairs and a substantial chance (30%) of disappearing entirely.

Several colony risk assessment

Figure 6 shows the risk that an isolated group of colonies starting with 1000 breeding pairs will fall below given threshold values under the assumptions of the "most likely" model (see Table 2). Note the scale of the graph. This scale is intended to make it easier to read risk estimates for low population thresholds. Assuming that the input data for this model are realistic, an isolated group of colonies starting with 1000 breeding pairs has an 83% chance of dropping to 500 breeding pairs, a 47% chance of dropping to 100 breeding pairs, a 36% chance of dropping to 25 breeding pairs and a 33% chance of disappearing entirely within 50 years.

The sensitivity analysis indicated that the model was sensitive to assumptions about the magnitude of cv's and migration impact. However, even if these parameters are lowered substantially (to perhaps unrealistic values), an isolated group of colonies is still not "safe". If all cv's are reduced to 1/2 of their original value, an isolated group of colonies still has a 15% chance of falling to 100 breeding pairs and a 7% change of disappearing entirely. If cv's remain at the observed rate but the average "loss" to migration is reduced to 0.5% of the initial population there is a 19% chance of falling to 100 breeding pairs but a less than 1% chance of extinction. Under most conditions modelled, an isolated group of colonies has a substantial chance (15% or greater) of falling to less than 100 breeding pairs and a somewhat smaller chance (7%) of becoming extinct. Under the "most likely" conditions, an isolated group of colonies faces substantial chances of dropping to 100 breeding pairs (probability = 47%) or disappearing entirely (probability = 33%).

Whole population risk assessment

Figure 7 shows the risk that an isolated group of colonies starting with 10,000 breeding pairs will fall below given threshold values under the assumptions of the "most likely" model (see Table 2). Note the scale of the graph. This scale is intended to make it easier to read risk estimates for low population thresholds. Assuming that the input data for this model are realistic, an isolated group of colonies, constituting the whole population, starting with 10,000 breeding pairs has an 83% chance of dropping to 5,000

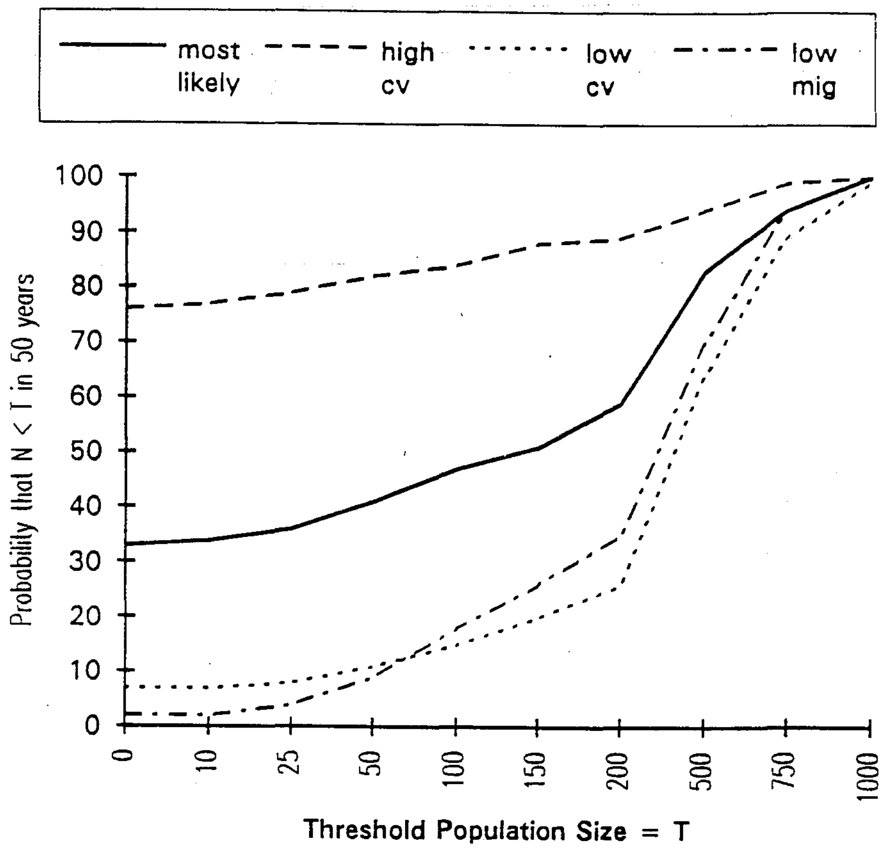

Figure 6. Risk assessment: Isolated group of colonies

This figure shows the probability that a Bank Swallow colony starting with 200 breeding pairs will fall below given threshold population sizes within 50 years. Results are shown for the "most likely" model; for a "low cv" model with cv's 1/2 of those of the "most likely" model; for a "high cv" model with cv's twice those of the "most likely" model; and for a "low mig" model with migration losses 1/4 those of the "most likely" model.

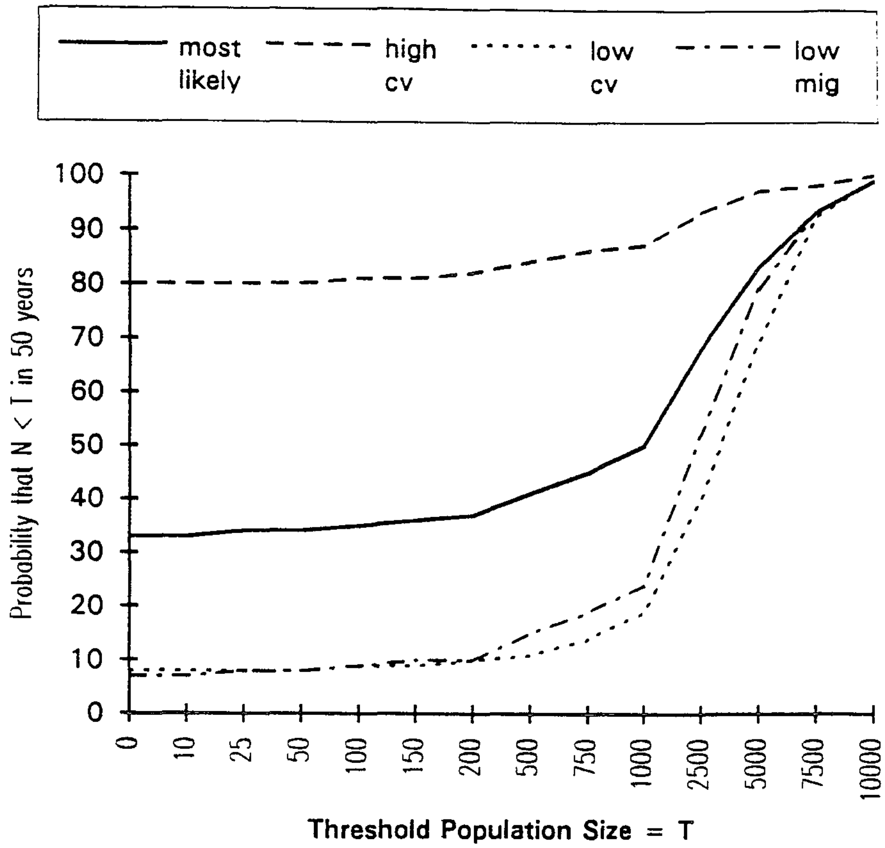

Figure 7. Risk assessment: Whole population

This figure shows the probability that a population of Bank Swallows with an initial size of 10,000 breeding pairs (approximately the size of the current Sacramento River population) will fall below given threshold population sizes within 50 years. Results are shown for the "most likely" model; for a "low cv" model with cv's 1/2 of those of the "most likely" model; for a "high cv" model with cv's twice those of the "most likely" model; and for a "low mig" model with migration losses 1/4 those of the "most likely" model.

breeding pairs, a 68% chance of dropping to 2,500 breeding pairs, a 50% chance of dropping to 1,000 breeding pairs and a 33% chance of disappearing entirely within 50 years.

The sensitivity analysis indicated that the model was sensitive to assumptions about the magnitude of cv's and migration impact. However, even if these parameters are lowered substantially (to perhaps unrealistic values), the entire Bank Swallow population on the Sacramento River is still at risk of falling to low numbers within 50 years. If all cv's are reduced to 1/2 of their original value, the population still has a 20% chance of falling to 1,000 breeding pairs and an 8% change of disappearing entirely. If cv's remain at the observed values but the average "loss" to migration is reduced to 0.5% of the initial population there is a 24% chance of falling to 1000 breeding pairs; however, there is a less than 1% chance of extinction. Although the risk of falling to low numbers is substantial under nearly all conditions modelled, only when migration results in a net "loss" of 1% or more of the initial population size, is there a substantial chance of extinction. For almost all cases modelled, the entire population of Bank Swallow along the Sacramento River has a substantial (20% or greater) probability of falling to low numbers (1000 breeding pairs). Under the conditions of the "most likely" model, the risk of the population disappearing entirely is also substantial (33%).

<u>Population size necessary to reduce risk and ensure a large continuing population</u>

Model 2 was also used to estimate the number of Bank Swallows necessary to ensure a continuing population of substantial size. Utilizing this "most likely" model, it appears that a population of Bank Swallows of 100,000 breeding pairs would be necessary to ensure a less than 50% chance of falling below 5,000 breeding pairs within 50 years. A population of over 200,000 breeding pairs would be necessary to achieve a 50% or less chance of dropping below 7500 breeding pairs. These numbers are 10 to 20 times greater than the current Bank Swallow population along the Sacramento River.

The sensitivity analysis indicated that estimates of average annual "losses" to migration are critical to the results of the model. If migration "loss" is reduced to 0.5% of the initial population size, only 20,000 breeding pairs are necessary to reduce the risk of falling below 5,000 breeding pairs to less than 50%, and only 50,000 breeding pairs are necessary to produce a 50% or smaller risk of falling below 7,500 breeding pairs. **It should be noted that, even under these very optimistic conditions, the number of breeding pairs required to ensure a large continuing population of Bank Swallows is still much larger than the current population size.**

These results suggest that the current Bank Swallow population faces a risky future. It may be necessary to protect very large numbers of Bank Swallows and very large areas of natural river bank habitat in order to ensure that the population does not fall to low numbers in the near future. It should be emphasized, however, that the current PVA is only preliminary in nature and any conclusions in the absence of more complete information must remain tentative.

Assuming that the initial estimates of input parameters are reasonably reliable, a population starting with 10,000 breeding pairs has approximately an 80% chance of dropping below 5000 breeding pairs, approximately a 25% chance of dropping below 1000 breeding pairs, and approximately a 15% chance of dropping below 500 breeding pairs at least once within a 50 year period. The population has a less than 1% chance of becoming locally extinct (0 breeding pairs). Again, if cv's have been underestimated, the actual risk may be much higher than calculated. For example, if actual cv's are 2 times those initially estimated, the risk of dropping to less than 500 breeding pairs increases to nearly 70%.

DISCUSSION

This analysis reveals the fluctuating nature of Bank Swallow populations. A colony or group of colonies of average size has a substantial chance of dropping to very low numbers within any 50 year period. Care should be taken in the recovery process to ensure that single colonies or small groups of colonies do not become isolated from the rest of the population. The risk of extinction for such isolated groups is high.

A major implication of the current analysis is that too complete a focus on the risk of extinction or near extinction may result in a false assessment of population "safety". Even when the risk of extinction is very low, the chance that the population will drop to distressingly low numbers may be substantial.

It is vital that critical threshold population sizes be specified and acceptable levels of risk defined. This decision should include a consideration of factors such as the likelihood that if a colony or group of colonies fall to very low numbers in a given year the stretch of river they inhabit will come under increasing pressure for development.

Even a moderate population of 10,000 breeding pairs has a substantial chance of falling to relatively low numbers within a 50 year period. The current population is not large enough to ensure persistence of a large ongoing population. It will be necessary to protect habitat which can accommodate much larger numbers of Bank Swallows than currently exist along the Sacramento River. In order to ensure that the population does not fall below specified thresholds it will be necessary to provide room for population expansion. This means that it will be necessary to protect or enhance habitat potentially utilized by the Bank Swallow which is currently not occupied by this species.

More data are necessary before the results of this analysis can be considered highly reliable. It should be noted that the details of this analysis apply only to populations with the survival and fecundity estimates used in the analysis. Conclusions reaching beyond such a specific population should be made with caution and should be restricted to general results rather than details. Variance in fecundity and juvenile survival rates and data on return rates following migration appear to be critical factors determining the likelihood of population declines. This emphasizes the need to:

1. Measure survival and fecundity rates in the California population over long enough periods of time that accurate estimates of the year-to-year variance in those rates can be obtained. More complete life table data, based on several years of data, from several locations must be developed if more reliable population analyses are to be conducted. Mean age-specific fecundities and survival rates are needed for a ten year period from at least three locations in the State.

2. Obtain data on the average gain or loss to the population from migration. The current assumption that migration results in small gains or losses to the population in any given year needs to be validated. These data can dramatically influence the results of the simulation. Data are also needed on the spatial distribution of returning migrants.

3. Obtain reliable population counts over large areas of the Bank Swallows current range for ten or more consecutive years. These data are vital to (a) establish the current population size, and (b) watch for evidence of population declines or cycles in population numbers.

It would also be useful to obtain data on any density dependence of population growth and any correlations between survival and fecundity rates. The current model assumes no density dependence and no correlations between survival and fecundity. These assumptions are conservative, and may result in underestimates of the risk of population decline (Ferson and Akcakaya 1990). In addition, the present PVA does not model the impact of habitat loss due to bank protection projects or other human activities. Such assessments may be incorporated into the analyses proposed below.

Complete PVA's encompass several levels of analysis. In the case of the Bank Swallow at least three levels need to eventually be examined:

1. **Single population analyses.** The work reported here preliminarily addresses this level. As noted above, more data are necessary to move beyond the current preliminary stage of population viability analysis.

2. **Metapopulation analyses incorporating habitat measurements.** At this level one would analyze the spatial and temporal pattern of appearance and disappearance of whole colonies or interacting groups of colonies. Approaches here could include analyses of the temporal and spatial patterns of habitat availability, the capacity of habitat areas to support populations of the species, and the movement of birds between habitat areas. Currently more field data are needed before this kind of information can be used to determine the optimal number and arrangement of protected areas.

3. **Full population analyses incorporating migratory patterns.** This level includes large-scale analyses of the migratory patterns of the birds and the threats to habitat in both wintering and breeding habitats.

The current population analysis is only preliminary in nature and any conclusions must remain tentative. At present, data are not available from enough years or enough areas to perform a more complete and reliable population viability analysis (PVA). The data suggested above could be gathered as part of the population monitoring program outlined in the Bank Swallow recovery plan. These data could then be used to conduct a more detailed PVA that would aid in predicting long-term Bank Swallow population prospects and determining recovery goals and criteria. More detailed data would allow analyses which focus on threats and management strategies for specific single colonies or interacting groups of colonies as well as the entire California Bank Swallow population.

Such analyses may not be available for some time, as a substantial amount of additional field data must first be gathered. In the meantime, the best available data indicate a need to protect all current Bank Swallow habitat and to encourage the future expansion of the present Bank Swallow population along the Sacramento River which remains the focus of management and recovery of this Threatened species in the State.

ACKNOWLEDGEMENTS

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APPENDIX 1. Input data for the initial models of the Bank Swallow population on the Sacramento River, California.

Starting numbers in each age class calculated based on stable age distribution and are shown for the whole population case (initial population size = 10,000 breeding pairs). As is common in models of this type, only breeding females and their female offspring are counted in this model. Fecundity is, thus, entered as the number of female offspring produced per female. Sufficient males to mate with all breeding females and a 1:1 sex ratio among offspring are assumed.

Studies of reproduction for Bank Swallow populations (Freer 1977, Mead 1979b, Hjertaas et.al 1988) report average clutch sizes of approximately 5 eggs per nest and 4-5 fledged young per successful nest (successful nests = nests producing fledglings). This results in the production of 2-4 fledged young per breeding pair (including those pairs which attempt breeding but are unsuccessful (i.e. produce no fledglings). I used a brood size of 4 young per nest (i.e. 2 female young per breeding female). The extent to which this is an optimistic value will depend on how breeding pairs are counted in field work. If the number of "breeding pairs" is defined as the number of pairs which attempt breeding, or as the number of nest holes found in the bank (nesting attempts) this is an optimistic value, since in this case, it would be assumed that either few breeding pairs were unsuccessful or that the population has a relatively high reproductive rate. If the number of "breeding pairs" is based as the number of successful nests (those producing some fledglings), this value is not as optimistic, since, in this case, it assumes a reproductive rate which is commonly found for this species.

Survival is entered in the model as the proportion of a given age class that survive to enter the next age class. Studies of survival rates for adult Bank Swallows (Freer 1977, Mead 1979b) generally produce estimates of 0.25-0.45 annual survival. I use a mean annual adult survival rate of 0.40 in the models. This is a fairly optimistic assumption, which assumes that, on average, Sacramento River Bank Swallows have relatively high survival rates.

Data are relatively weak for estimates of the survival of juvenile birds from fledgling to age one year and for the proportion of pairs which produce two broods within a single season. Because of this gap in the available data, juvenile survival rates and overall fecundity rates were adjusted to result in a population with an R_o of just over 1.0 (i.e. a slowly growing population). Three combinations of juvenile survival and proportion of double broods were considered. In the tables below fecundity rates are shown as the number of female offspring per female. A brood size of 4.0 is assumed for all models; difference in annual fecundity are the result of differences in the proportion of breeding pairs which produce two broods in a single breeding season.

Model 1:

Age	Starting #	Fecundity	Survival
0 =	39735.00	0.00	0.151
1 =	6000.00	4.00	0.400
2 =	2400.00	4.00	0.400
3 =	960.00	4.00	0.400
4 =	384.00	4.00	0.400
5 =	154.00	4.00	0.400
6 =	60.00	4.00	0.400
7 =	24.00	4.00	0.400
8 =	10.05	4.00	0.400
9 =	4.00	0.00	0.000

These values assume that all females produce two broods per year, with an average brood size of 4.0.

Model 2, "Most Likely Model":

Age	Starting #	Fecundity	Survival
0 =	39735.00	0.00	0.220
1 =	6000.00	2.80	0.400
2 =	2400.00	2.80	0.400
3 =	960.00	2.80	0.400
4 =	384.00	2.80	0.400
5 =	154.00	2.80	0.400
6 =	60.00	2.80	0.400
7 =	24.00	2.80	0.400
8 =	10.00	2.80	0.400
9 =	4.00	2.80	0.000

These values assume that 40% of females produce two broods per year, and 60% of females produce one brood per year, with an average brood size of 4.0.

Model 3:

Age	Starting #	Fecundity	Survival
0 =	39735.00	0.00	0.310
1 =	6000.00	2.00	0.400
2 =	2400.00	2.00	0.400
3 =	960.00	2.00	0.400
4 =	384.00	2.00	0.400
5 =	154.00	2.00	0.400
6 =	60.00	2.00	0.400
7 =	24.00	2.00	0.400
8 =	10.05	2.00	0.400
9 =	4.00	2.00	0.000

These values assume that all females produce one brood per year, with an average brood size of 4.0.

B. The following parameters were used for all models:

Maximum Bank Swallow age = 9 years
Time to run = 50 years
Sex ratio = 1.000 (only females modeled)
Demographic stochasticity was included in the model
Population Number Summation = Adults (age one and older)
The number of replications of the simulation = 250 minimum
Probability distributions:
Survival for age zero = Lognormal
Survival for age 1 and older = Lognormal
Fecundity = Lognormal
Migration = Lognormal
Correlations between survival, fecundity and migration were not used
No density dependence function was used

C. Coefficients of variation observed for the Sçandanavian Bank Swallow populations:

Survival for age 0 = 0.250000
Survival for ages 1+ = 0.250000
Fecundity = 0.30000
Migration = 1.00000