

ENVIRONMENTAL VARIATION AND THE PERSISTENCE OF SMALL POPULATIONS¹

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Abstract. Understanding the factors that determine the continued survival of small populations is a central problem in conservation biology. The Acorn Woodpecker (*Melanerpes formicivorus*) naturally occurs in small, isolated populations throughout much of the American Southwest. In spite of this distributional pattern, the species is neither rare nor endangered. Thus it appears to have successfully "solved" the problems of habitat fragmentation. We used data from a 10-yr field study and simulation models to examine the effects of environmental stochasticity on population survival times. All simulated woodpecker populations went extinct within 49 yr, and the median survival time was only 16 yr. However, when immigration was allowed, persistence times greatly increased; with an immigrant rate of only five individuals per year, most populations lasted >1000 yr. The results of this and other analyses suggest that this population persists only because it is part of a larger "metapopulation," and because it is regularly rescued from extinction by immigration from other, independently varying, populations. This finding has important implications for the development of management strategies designed to preserve small populations that are faced with fragmented distributional patterns and high levels of environmental variation.

Key words: Acorn Woodpecker; conservation; demography; dispersal; environmental stochasticity; habitat fragmentation; metapopulations; New Mexico; population models; simulation models; stochasticity; survival of small populations.

INTRODUCTION

Understanding the factors that influence the persistence of small populations continues to be one of the primary challenges confronting modern conservation biology. Human development often fragments once-continuous habitats into isolated patches, and each new "subpopulation" may be more likely to go extinct as a result of reduced population size (e.g., Richter-Dyn and Goel 1972, Diamond and May 1976, Wilcox 1980, Wilcox and Murphy 1985, Gilpin and Soulé 1986). In addition, many plant and animal species with highly specialized habitat requirements often naturally occur in small populations that are scattered over the landscape. While the prime habitat of such species may be protected, the immigration corridors and sub-optimal habitats that historically connected each population may be lost (Simberloff and Cox 1987). It is therefore of critical importance to understand the dynamics of small populations, and in particular the factors that determine whether such populations are likely either to go extinct or to persist for extended periods.

Although considerable theoretical progress has been made toward understanding extinction probabilities in small populations (see, for example, recent reviews by Belovsky 1987, Soulé 1987, Lande 1988, Simberloff

1988, and Gilpin and Hanski 1991), the extent to which these models can be used to estimate the specific population size that is required to insure a high probability that a particular species will persist over some predetermined time period (the minimum viable population, [MVP] Soulé 1987) is less certain, primarily because estimated MVP values can range over several orders of magnitude depending on the type of model involved (Lande 1988; see Results, below). One alternative is to follow the fate of species that recently have been fragmented or reduced in size by human development and to determine the population-level parameters that are most sensitive to the disturbance (e.g., Lovejoy and Oren 1981, Shaffer 1981, Petersson 1985, Menges 1990, Murphy et al. 1990).

A second approach is to examine species that are not necessarily endangered or rare but that naturally occur in small and highly fragmented populations (e.g., Pimm et al. 1988, Berger 1990). To the extent to which these species have managed to persist through time, they can be considered to have successfully "solved" the problems of habitat fragmentation. Such species can provide model systems that allow us to unravel the demographic characteristics that enable such small populations to remain viable. We have used this approach in our analysis of the population biology of the Acorn Woodpecker (*Melanerpes formicivorus*). This species is highly dependent upon acorn nuts that the birds store in artificial granaries as a winter food supply (Stacey and Koenig 1984). In the American Southwest the oaks that produce sufficient numbers of acorns to

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support the birds through the winter are found only in riparian habitats in the canyon bottoms of isolated mountain ranges. Populations are thus relatively small and discrete, yet many appear to have persisted for extended periods (Bailey 1928, Ligon 1961). In this paper we use field data collected over a 10-yr period in a series of demographic simulation models to examine the dynamics of a population of Acorn Woodpeckers in Water Canyon, located in the mountains of central New Mexico. We were particularly interested in this population because the environment in central New Mexico is spatially and temporally highly variable, particularly in the amount of rainfall and in mean winter temperature. The unpredictable climate leads to considerable variation in such key population-level parameters as annual birth and death rates. The annual survivorship of adults, for example, can vary from 38 to 71%, while reproductive rates have ranged from means of 0.05 to 4.00 young per breeding pair of woodpeckers in the population. This extreme level of variation provides us with the opportunity to examine the effects of environmental stochasticity using data from a real population and to determine if there are any particular characteristics of the population that has allowed it to persist over extended periods.

STUDY POPULATION AND METHODS

Water Canyon is located in the Magdalena Mountains, 30 km west of Socorro, Socorro County, in central New Mexico. Our study area is centered along a seasonal stream at an elevation of ≈ 1900 – 2200 m; details of vegetation and general habitat are given in Stacey (1979). Although the total population size of Acorn Woodpeckers in Water Canyon is probably never greater than 60 adults, they have been observed in this canyon for at least 70 yr (Bailey 1928). Between 1975 and 1984, we studied 14–25 active summer territories in the main canyon and in two adjacent side canyons; this constituted all but ≈ 5 of the total number of territories in this part of the Magdalena Mountains. Smaller populations of Acorn Woodpeckers are located 6–35 km distant in three additional canyons in the Magdalenas, but are separated from Water Canyon by large areas of unsuitable pinyon–juniper and ponderosa pine habitat. The nearest population of similar size to that in Water Canyon is located in the San Mateo Mountains, 45 km southwest of the Magdalenas and separated from it by high desert grasslands (Bailey 1928). Additional populations occur in various other isolated mountain ranges in central and southern New Mexico.

Much of the data described here were collected as part of a long-term study on the ecological origins of cooperative breeding in Acorn Woodpeckers (e.g., Stacey 1979, Stacey and Ligon 1987, 1991, Stacey and Koenig 1990). Adults and nestlings were color-banded for individual identification. Regular and complete censuses were taken each month during the summer

and at least once during most winters. Population size was considered to be the total number of adult birds residing within the study area in May at the start of the breeding season. The histories of the banded individuals were used to calculate annual survivorship for each study year, defined as the probability that an individual that was alive at the start of one breeding season also would be alive at the start of the next breeding season (adults) or from fledging to the start of the following breeding season (juveniles). We calculated separate juvenile and adult survivorship probabilities since, as in most birds, the mortality rate of juveniles is significantly higher than that among adults, but is constant with age after the first year (Stacey and Ligon 1987: Figs. 2 and 3). This allowed us to use a single annual value for adult survivorship, rather than a series of age-specific rates.

All nesting attempts were recorded, and the number of young fledged was determined for each breeding pair. These data were then used to calculate annual reproductive success, or birth rate, defined as the mean number of young produced per territory or breeding pair. Because the Acorn Woodpecker is a cooperative breeder, there can be > 1 adult bird of each sex present on a territory. However, only a single male–female pair of birds usually breeds (Stacey and Koenig 1984), and the existence of helpers does not affect the demographic calculations.

The Water Canyon population is not completely closed, and immigration by unbanded birds of unknown origin is a regular occurrence. As with most field studies of mobile animals, it was not possible to measure immigration rates directly. There were always a few unbanded birds within the study area, and we could not always determine whether a new bird originated locally or was a true immigrant from somewhere outside the canyon. However, we can indirectly estimate immigration rates using methods described below (see *Results: The effect of immigration*).

Table 1 gives the observed demographic data for the Water Canyon population for the years from 1975 through 1984. We do not include survivorship data for the last year of the study, since this value is defined as the probability of surviving from year x (1984) to the following year. In addition, during the summer of 1979 only a single juvenile was fledged within the population. This bird was not present the following year, which yielded an annual juvenile survivorship value for 1979 of 0. Since this number is based on only one individual, we did not include it in the data set used with the simulation models.

DEMOGRAPHIC SIMULATION MODEL

Simulation models can be useful in understanding the dynamics of small populations because they allow one to examine either the fate of a hypothetical population under different levels of variance in life history parameters, or, for a real population, the expected life-

TABLE 1. Demographic data for the population of Acorn Woodpeckers in Water Canyon, New Mexico from 1975 through 1984.

Year	Adult survivorship	Juvenile survivorship	Reproductive rate (young/pair)	Population size (no. adults)	Number of emigrants*
1975	0.53	0.56	3.38	46	3
1976	0.68	0.64	1.27	46	4
1977	0.71	0.30	2.77	40	1
1978	0.38	0.40	2.17	51	2
1979	0.54	0†	0.05	52	0
1980	0.69	0.38	4.00	32	0
1981	0.66	0.18	2.37	46	1
1982	0.49	0.25	0.50	49	1
1983	0.61	0.44	1.60	35	1
1984	2.00	36	...

* Emigrants are individuals that were known to have survived the winter, but that left the canyon before they established a breeding territory.

† Only one juvenile was produced in 1979. This bird disappeared over the winter, yielding a juvenile survivorship value for that year of 0.

time of that population under new conditions. The parameters in the model that are found to affect the longevity of the population most strongly are then suggested to be those for which management programs should be most sensitive (e.g., Thomas et al. 1990).

The demographic simulation model used in this study was designed to match the Acorn Woodpecker population in Water Canyon as closely as possible; however, the assumptions can be changed to fit different species or goals of the analysis. Briefly, for each cycle or "year," the model first determines the number of active territories by dividing the number of adults present in the population at time t by two; if the result is greater than a specified maximum number (the defined carrying capacity, K) then the value is reduced to K . The maximum number of actual territories we observed from 1975 through 1984 was 26. Like most territorial species, Acorn Woodpeckers require a certain amount of space for foraging and reproduction. Territories are therefore not infinitely compressible, and we believe a total of 26 is very close to the maximum number of breeding territories possible in the canyon. K is therefore a "reflecting" boundary in the model, and any individuals above size K are considered lost from the population (although they may emigrate into other populations; see *Discussion*, below).

Next, a value for the annual reproductive rate is selected randomly from the set of observed values. This value is then multiplied by the number of active territories to produce the number of young fledged. The number of young that survive the winter is determined by multiplying the number of young fledged by a randomly selected juvenile survivorship value, while the number of adults that survive is the number of adults that are present during breeding multiplied by a randomly chosen adult survivorship value. The surviving

adults and young are combined with a preselected number of immigrants (≥ 0) to obtain the population size for the following year, $t + 1$, and the cycle is then repeated. The initial population size at the first year is set at the maximum value possible (K), and the simulation stops (goes extinct) if the population falls below two breeders. We considered the population to persist indefinitely if it lasted for >1000 model years. At least 1000 independent simulations were run for each set of parameter values.

In this analysis we chose the value of each of the three yearly parameters independently because the observed annual values (Table 1) were not significantly correlated with each other (all $P > .10$). Further, we checked with a bootstrap analysis whether even real correlations at the observed level would have an important affect on the dynamics of the Water Canyon population. In this analysis we randomly chose the three demographic parameters for a simulated population lasting 1600 yr. These years were grouped into 200 blocks of 8 yr, and the geometric mean growth rates were calculated for each block. The geometric mean growth rate for the 8 observed years (excluding 1979 because of the 0 value for juvenile survivorship) was then compared to the distribution of the geometric mean growth rates of bootstrapped blocks. The observed mean growth rate was very close to that of the bootstrapped growth rates (in the 49th percentile). This indicates that ignoring within-year correlations among the demographic parameters is a reasonable simplifying assumption for modeling this population (although it might not be in others).

We also assumed that all immigrants were successful in entering the breeding population, and thus the num-

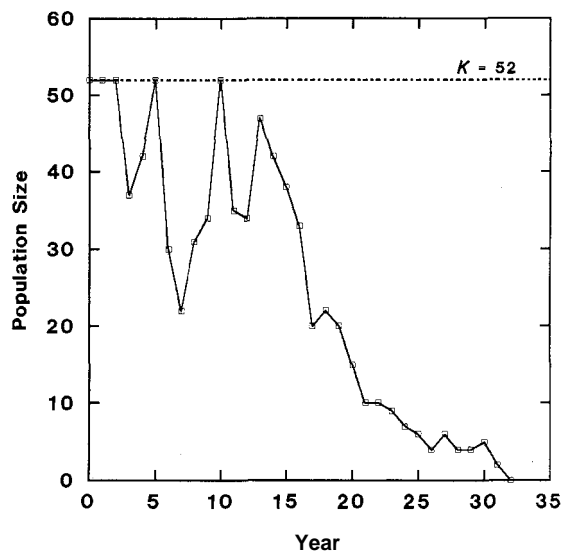


FIG. 1. Annual changes in population size of Acorn Woodpeckers for a typical simulation trial using the observed Water Canyon demographic data set and carrying capacity $K = 52$.

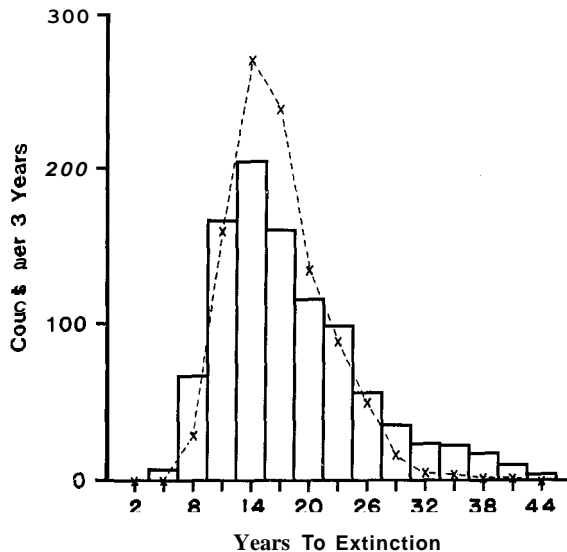


FIG. 2. Frequency histograms of the years to extinction for the Water Canyon population of Acorn Woodpeckers using the observed Water Canyon demographic data (Table 1) and $K = 52$. Superimposed on the histogram is the distribution of extinction times calculated from the equivalent strategic population growth model (see *Results: environmental variation*). The median time to extinction in both models is 16 yr.

ber used in the model represents the *effective* immigration rate rather than an overall immigration frequency where some individuals might die or disperse again before breeding. We also assumed that surplus individuals above K cannot survive in sub-optimal habitats and thus are lost to the system. As we discuss below (see Discussion), this assumption is probably not realistic, and in fact non-breeding surplus individuals often may be critical to the persistence of real populations.

Finally, the simulation model used only the actual year-to-year Water Canyon data and did not include any calculated density-dependent effects; that is, the probability of choosing a particular value for any parameter was not dependent upon the current population size or its deviation from the maximum equilibrium value K . Because density-dependent growth can have a profound effect on persistence in simulation models (e.g., Ginzburg et al. 1990), we examine the rationale and consequences of this assumption in detail below (see Discussion).

RESULTS

Environmental variation

Fig. 1 shows the results of a typical simulation run using the observed data from Water Canyon; this figure also illustrates many of the characteristics of the model, including initial population size, the reflecting boundary at K , and the absorbing boundary at 1, where the population goes extinct. When the population was

closed and there was no immigration, all the simulated populations went extinct within 49 yr; the distribution of extinction times for 1000 runs is shown in Fig. 2. As is true with most models of this type, the distribution of extinction times is right skewed, with shorter time spans occurring more frequently than the longer periods. Thus the mean value of this distribution tends to overestimate the time that most populations survive. We therefore use the median time to extinction as a more appropriate statistic, which for this analysis was 16 yr.

According to these simulations the Water Canyon population is unlikely to persist for very long, even though we are using the actual demographic values observed during the field study. This result illustrates several important characteristics of the Water Canyon population. First, part of the reason for the rapid extinction is the high degree of year-to-year variation in each demographic parameter. Although there will always be good years, there also will eventually be a series of years that are bad for breeding or survival. Because breeding territories are not infinitely compressible (represented in the model by a fixed boundary at K), surplus individuals produced during good years are effectively lost from the population. Unless these individuals can survive somewhere else (probably in marginal habitats), they cannot form a buffer against later population decreases. Environmental stochasticity thus eventually always drives the population to such a low level that it cannot recover (see Fig. 1).

We examined the importance of environmental stochasticity in reducing the survival of this population by running the simulation with exactly the same parameters, using the mean of each demographic variable rather than the individual yearly values. In this case survival times were almost doubled, and each population lasted for 30 yr (with no annual variance in the demographic variables, there is no variability in survival times).

If the variance of each parameter is reduced by one-half from the original values, but the mean is kept the same using the transformation:

$$x' = [(x - \bar{x})/\sqrt{2}] + \bar{x},$$

the median persistence time is 18 yr, only a 2-yr increase over the original 16 yr. This indicates that even a small amount of environmental variation has a large impact on the survival of the population.

The simulated populations in this model always go extinct, even when mean values are used and there is no variance in the demographic parameters. One reason for this is that the overall rate of increase, λ , for the Water Canyon population as calculated from the data in Table 1, is 0.95. Thus, when treating Water Canyon as a closed system, births do not quite equal deaths. If we calculate new values for the data in Table 1, so that the transformed numbers yield a $\lambda = 1$, and then use the mean of the new values (variance = 0), the pop-

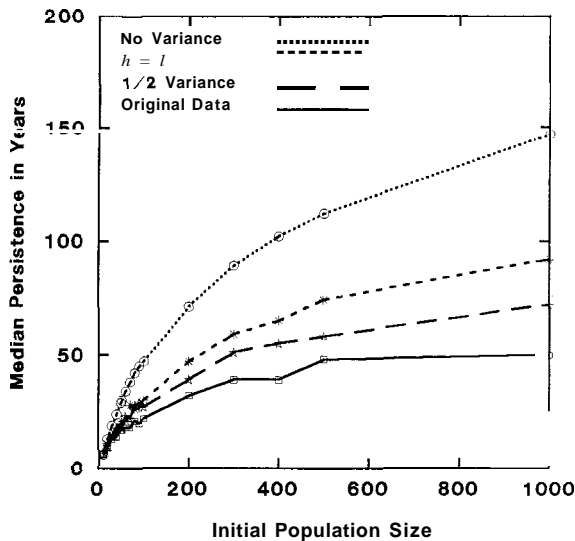


FIG. 3. The median number of years to extinction in the demographic simulation model as a function of initial population size of Acorn Woodpeckers using both the observed Water Canyon data and various transformed data (see *Results: environmental variation*). λ = the overall rate of population increase, and here is given 4 different levels of variance.

ulation will, by definition and confirmed by simulation, persist indefinitely. However, if we incorporate the year-to-year variance in the transformed values, the median survival time for the population is 21 yr, an increase of only 5 yr over the original data. This again indicates that environmental stochasticity is the major factor

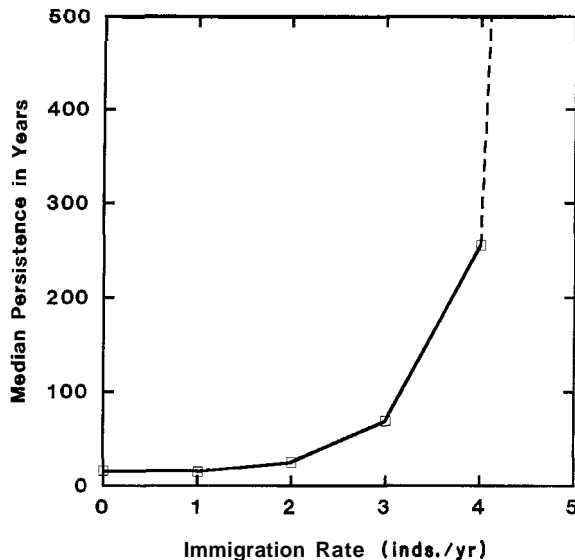


FIG. 4. The median number of years to extinction in the demographic simulation model using the observed Water Canyon data for Acorn Woodpeckers and different values for the effective immigration rate. With five immigrants per year, most simulated populations lasted longer than the arbitrary limit of 1000 yr.

influencing survival times, even when $\lambda = 1$ and the population is not declining rapidly for other reasons.

Population size often has been suggested to be one of the most critical factors affecting population persistence (Soulé 1987). To examine this we ran a number of simulations varying the maximum allowable population size (K) at the four levels of variance in the demographic parameters described in the subsection immediately above (Fig. 3). Median persistence times were more influenced by the degree of environmental variance than by population size. Even at very large population sizes ($n = 1000$), the median survival times in all data sets were < 150 yr, and for the actual Water Canyon data set, the median was only 47 yr.

The effect of immigration

The results of these simulations indicate that environmental stochasticity will rapidly lead to the extinction of the model Water Canyon population, and that this will occur even when the size of the initial population is much larger than could ever actually occur in the canyon. Even if the initial population size were 10 times the maximum observed, the probability of the population surviving 70 yr is < 0.000001 . Why, then, has the real population survived for at least 70 yr, and probably much longer? So far, we have modeled the population as if it were completely closed. Any young produced that forced the population size over K were considered to have died, and immigration was not allowed. However, this is probably unrealistic, both for Acorn Woodpeckers and many other species. Individuals that are unable to find breeding space in one population may disperse and eventually become breeders in another population. Thus, for many species there may be a pool of floaters available that can immigrate into a population when that population declines below K , and thereby greatly affect the probability that the population will persist.

We examined the effect of immigration by adding various numbers of immigrants into the model at the start of each breeding season. The results are shown in Fig. 4. Even a small number of immigrants greatly extended the survival of the population, and when the effective immigration rate was five per year, almost all populations persisted beyond our cutoff point of 1000 yr. Thus, even a small amount of immigration from other populations can counteract the effects of environmental stochasticity, and will effectively "rescue" the population from extinction.

We can estimate the number of individuals immigrating into Water Canyon each year as the breeding-season population size minus the expected number of surviving birds from the previous year plus the number of surviving birds known to have emigrated from the population before the breeding season. In general, this estimate will be much better than one might expect based on sample size alone because we are estimating proportions of a finite population. As the sample size

approaches the size of the population, the error decreases to zero (Cochran 1977, Zar 1984). That is, if all individuals had been banded the year before, this calculation is exact. Usually, however, there were one or two unbanded resident birds present each year.

Over the study period, this calculation yields a mean of 10.1 immigrants per year, with a standard deviation of 8.8. The immigration rates are right skewed: in most years the rates were less than the mean, with only a few years of high immigration (i.e., years when environmental variation resulted in low reproduction and/or survivorship). Overall, these results suggest that nearly half of the total recruitment of adults to the population during the study period was from immigration. Although our estimates are inexact, the amount of input of individuals into the Water Canyon population through immigration is extremely important. The field data support this conclusion. For example, the fact that the value of λ calculated from the birth and death rates in Table 1 is < 1.0 , but the number of birds in Water Canyon did not appear to be declining over the 10-yr study period suggests that immigration provides the "missing" input into this system that allows it to persist and actually remain relatively constant over time.

Detecting density dependence

One of the most critical factors that will affect persistence times in demographic models is whether the population is assumed to exhibit some form of density-dependent growth rate (Ginzburg et al. 1990). This is important because if the growth rate increases substantially as population size decreases, the population will be more likely to recover and return toward K after any disturbance. In the computer simulation model we assumed that the growth rate of the population was independent of the population's size, except that no recruits could enter the population when it was already at its maximum size (K). Does this realistically represent the type of density dependence found in Water Canyon? Could a negative density dependence be acting to stabilize this population, and if so, how much difference would it make in our estimates of persistence times?

A population's growth rate can be calculated as

$$r(t) = \ln[n(t+1)/n(t)],$$

where $r(t)$ and $n(t)$ are the growth rate and population size in year t . If growth is "density independent," $r(t)$ will simply fluctuate around its mean value with no relationship between $r(t)$ and $n(t)$.

The detection of density dependence in wild populations has proved difficult (e.g., Ito 1972 and Bulmer 1975 through Reddingius 1990 and Solow 1990). Statistical difficulties arise because of uncertainties in the independent variable (population size, N), autocorrelations in environmentally caused deviations in growth

rates, and the autocorrelations that are intrinsic to population dynamics (see Dennis et al. 1991). Because of these problems, density dependence is usually estimated with quite complex methods (Seber 1982, Biwas and Sehgal 1988), which are often highly model dependent. However, in Water Canyon the population size each year is known essentially exactly, and this allows us to apply a much simpler correlation approach to testing the significance of density dependence. Autocorrelation in environmental errors will influence the size of tests, with negative correlations yielding a liberal test of significance and positive autocorrelations a conservative test. The deviations of the observed annual Water Canyon population size from that predicted by the density-dependent models show strong positive temporal autocorrelation. Thus tests of significance should be conservative. Since our interest is in the possibility that population size may be stabilized by density-dependent growth rates, we use one-tailed tests of significance.

The growth rate, as calculated from the year-to-year changes in the number of birds in the population at the beginning of the breeding season, shows a strong negative correlation with population size (Pearson $r = -0.754$). Thus, the hypothesis that growth rates in this population are independent of density can be rejected. However, this correlation is based on changes in total population size, which will include the effect of immigration as well as local recruitment through reproduction. Do the local processes of reproduction and survival themselves exhibit density dependence? To answer this question, we examined the relationship between population size and the growth rate estimated from the demographic parameters. The correlation between population size and annual growth rate calculated from the reproductive success and survival data are again negative but only marginally significant ($r = -0.494$, $df = 7$, $.10 > P > .05$). The substantial reduction in the strength of density dependence using growth rates based on the within-population demographic data when compared to that based only on year-to-year changes in population size indicates that the processes of immigration and emigration also are probably density dependent in this population.

We can investigate this possibility directly by examining the relationship between the number of individuals that survive the winter and the rates of immigration and emigration at the beginning of the next season. The correlation between survivorship and known number of emigrants is strong and positive ($r = 0.767$, $P < .01$), which indicates that there is probably substantial density dependence in emigration. There is also a negative correlation between the number of birds that survive the winter and the estimated rate of immigration ($r = -0.595$), again suggesting a density dependent effect in this rate as well. Because immigration rates must be estimated indirectly, there are inherent negative correlations of unknown mag-

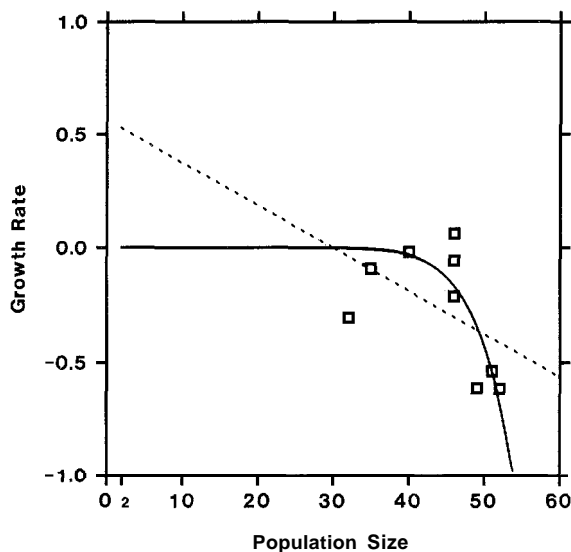


FIG. 5. Water Canyon population growth rates of Acorn Woodpeckers at different population sizes using the logistic (---) and theta-logistic (—) models (see Results: The form of density dependence).

nitude in the errors of the independent and dependent variables in this analysis (expected numbers of survivors and immigrants). Thus we are not able to associate an exact significance level with this coefficient. However, the pattern of greater emigration when population sizes are large and higher estimated immigration when population size is low is exactly what would be expected if the Water Canyon population is not closed, but in fact is exchanging members with other nearby Acorn Woodpecker populations with a rate that is dependent upon local population sizes.

The form of density dependence

The results of the analyses in the previous section indicate that growth rates in the Water Canyon population are not totally independent of population size. Because of the importance of density-dependent effects in estimating population persistence times, we further examined the specific form of the density dependence by fitting a number of simple models of density dependence to the field data to determine which model would explain the most variance in the observed annual growth rates.

We estimated the parameters of the density-dependent models using a recently developed maximum likelihood method (B. Dennis, personal communication and M. Taper, personal observation). These estimates are identical to those calculated using least-squares regressions (either linear or nonlinear, depending on the model), except that the environmental variance is estimated as the error sum of squares divided by sample size.

One of the simplest mathematical expressions of

density dependence is the logistic population growth model, where

$$r(t) = r_i[1 - n(t)/k]$$

Thus growth rate, $r(t)$, decreases linearly with population size from a maximum value, the intrinsic growth rate (r_i). When we fit the logistic model of density dependence to the actual data (Fig. 5), only a relatively small proportion of the variance in the among-year growth rates for the Water Canyon population is explained ($r^2 = 0.24$).

In the logistic density-dependent model, the addition of an individual to the population decreases the growth rate by a set amount regardless of the initial density. This may not be a very reasonable model of density dependence for many species, particularly for those that occupy and defend breeding territories. If all territories were identical and non-compressible, then density dependence would take the form that we used in the computer simulation model where there was no effect of population size on growth rates until the population exceeds some upper boundary (K). However, if territories are not all of the same quality, are compressible, or if there is a cost to territory defense, then we would expect growth rate to have a curved relationship with density, and changes in population size should have a more marked effect on growth rate as population size increases. A density-dependent model of this type is the θ -logistic (Gilpin and Ayala 1973, Ricklefs 1979; see Fig. 5), where

$$r(t) = r_i[1 - (n/k)^\theta].$$

When the θ -logistic model is fitted to the local process data, $r^2 = 0.59$, and 59% of the among-year variance in growth rates can be explained—as compared to only 24% by using the logistic model. This suggests that the actual form of density dependence in Water Canyon is closer in form to the θ -logistic model than to a simple logistic model, as would also be suggested by the territorial nature of the woodpecker's spacing and breeding system. However, because we have only followed the Water Canyon population for 10 yr, we cannot confidently exclude either model. The two models are not very different in the region of our data, because the population in Water Canyon never dropped close to 0 (we discuss why in the following section). However, at low population sizes the effects of the density dependence described by the two models are very different and can have a major effect on the rate of population recovery.

To determine the effect of our uncertainty of the form of density dependence in growth rates on our estimation of persistence times we used a series of simple population growth models. These differ from the demographic computer simulations by being more strategic; instead of using a complex algorithm to mimic the demographic sub-processes of territory occupation, reproduction, adult survival, and juvenile survival, we

TABLE 2. Parameters and median population persistence times of fitted models.*

Model type	r_i	K	0	a^2	Median persistence time (yr)	Sample size
Density independent with reflecting boundary	0.222	52	...	0.061	16	1000
Density independent	-0.266	0.062	14	1000
Logistic	0.563	29.97	...	0.047	$\geq 1 \times 10^7$	1
8-Logistic	0.0007	28.50	11.48	0.026	241	500
Logistic with demographic variation	0.663	29.97	...	1.960	4.10×10^5	500
8-Logistic with demographic variation	0.0007	28.50	11.48	1.219	104	500

*The parameters used in these models are the maximum likelihood estimates for each model. For the models with demographic variation, the variance in growth rate at a given population size $n(t)$ equals $a^2/n(t)$. The models were initialized at the integer value nearest the defined value of K . Parameters of the models include: r_i = the intrinsic growth rate; K = the carrying capacity or equilibrium population size; 0, a parameter in the logistic growth equation describing the non-linearity of density dependence; and a^2 , which scales environmental or demographic variation.

assumed that population growth takes the form of one of the simple models discussed above, where

$$n(t + 1) = n(t) \cdot e^{r_i n(t) + E}$$

and $r_i[n(t)]$ equals the growth rate as given by either the logistic, @-logistic, or density-independent models and E is a normally distributed random error with zero mean and variance equal to the environmental variance in growth rate.

Table 2 gives the parameters and median persistence times for six different models. These models capture much of the nature of more complicated simulation models. For example, if we make growth density independent, but impose a reflecting upper boundary, we have a model that echoes the demographic simulation model described earlier. Setting the growth rate and the environmental variance to the mean and variance of the Water Canyon growth rates used in the demographic simulation (mean = -0.222, environmental variance = 0.061), and an upper boundary of $K = 52$, the median estimated persistence time is 16 yr, the same value as derived from the demographic simulations. In fact the distributions of persistence times from the demographic simulation model and this model are very similar (Fig. 2).

When density-independent effects are included in the model, population persistence times increase substantially: from a median 241 yr in the @-logistic model to at least 10^7 yr in the simple logistic model (we ran out of computer time and terminated the analysis). Even these two models do not span the full range of reasonable models. For example, they do not include Allee effects (Allee 1938), where below a threshold population size the per capita growth rate actually decreases with decreases in population size instead of increasing as in the logistic or @-logistic models (for examples, see Simberloff 1988). Populations with an Allee effect will have even lower probabilities of recovery than populations with @-logistic growth if driven to low population sizes by chance events (Dennis 1989).

One Allee effect that may be common in many pop-

ulations is demographic variability (MacArthur and Wilson 1967, May 1973). In the initial simulations, all variance in growth rate was ascribed to environmental effects. The absence of demographic variation in the models means that each model overestimates persistence time to some degree (Leigh 1981, Goodman 1987). Our data set does not include enough years to directly partition growth rate variance into environmental and demographic portions. Nonetheless, we can get a feel for the magnitude of the discrepancy by considering all variation as demographic variation. Population growth can then be described as

$$n(t + 1) = n(t) \cdot e^{r_i n(t) + E[n(t)]}$$

The difference between this equation and the previous one is that the error, $E[n(t)]$, is now a function of population size. If only demographic variation is involved, this error can be conveniently modeled as a normally distributed random variable with a mean of zero and a variance equal to a constant divided by population size. Thus as population size decreases, the random fluctuations in growth rate increase. Modeling all growth-rate variation as demographic leads to substantial reductions in predicted persistence times (Table 2). As before, these results emphasize that assumptions about the nature of density dependence in growth rates can have a major effect on estimated persistence times of real populations.

DISCUSSION

A central problem faced by conservation scientists is how to determine the minimum number of individuals in a population that are required for that population to persist for some extended, but arbitrarily defined, time period (e.g., Shaffer 1981, Ligon et al. 1986, Dawson et al. 1987). One of the most powerful methods to derive estimates of the minimum viable population (MVP) size is through the use of simulation models that include actual demographic parameters from existing populations (e.g., Shaffer 1983, Thomas et al. 1990, Woolfenden and Fitzpatrick 1991). Yet as

the preceding analysis indicates, it can be exceedingly difficult to provide meaningful estimates of persistence time because the results depend so largely on the assumptions that are used to create the models. Furthermore, even if the model is specified correctly, relatively small errors in the estimation of the parameters can lead to large errors in the predictions (see also Goodman 1984).

The population models discussed in this paper are admittedly simple. Like most models, they can always be expanded to include additional structure or variables, depending on the particular problem or interests of the researcher. Yet as complexity increases, the number of assumptions that must be made about the biology of the system also increases, and with it the range in values of possible outcomes. Even with 10 yr of demographic data we were unable to resolve such key questions as the amount of density dependence in the population growth rate. Yet management decisions must often be made on the basis of very limited information. Clearly, high-quality, long-term demographic studies are critical to derive even crudely accurate estimates of population trends and minimum viable population sizes.

In spite of the inherent uncertainty of demographic models when applied to real populations, we believe the use of such models can yield important insights into the dynamics of small populations. Under all forms of our model, except those that are most unrealistic for vertebrates (e.g., pure logistic growth at low population sizes, with no counteracting Allee or other demographic effects), our data suggest that medium and small closed populations will quickly go extinct if they are subject to even moderate levels of environmental stochasticity. This is due to the fact that when the variation in demographic parameters is random, there eventually will be a series of bad years that drives the population to such a low level that it cannot recover. And if there is catastrophic variation, median time to extinction will be considerably shortened (Ewens et al. 1987). Examples of this phenomenon have been reviewed by Simberloff (1988), and include such well-known cases as the Heath Hen (*Tympanuchus cupido cupido*), Dusky Seaside Sparrow (*Ammospiza maritima nigrescens*), Mauritius Kestrel (*Falco punctatus*; Temple 1986), California Condor (*Gymnogyps californianus*) and black-footed ferret (*Mustela nigripes*).

Even though the population of Acorn Woodpeckers in Water Canyon is small (typically <50 individuals) and subject to considerable environmentally induced variation in both annual reproductive success and survivorship (Table 1), there is no evidence that the population of birds in Water Canyon is going extinct. The simulation models presented here suggest that the only way this population is able to survive is through immigration from other populations. Essentially, the population is regularly "rescued" from extinction (sensu Brown and Kodric-Brown 1977). This conclusion is

supported by several field observations; for example, during the winter of 1978 the number of birds in Water Canyon declined to a total of six individuals on three territories. However, by the next summer the population had recovered to 52 adults. A few of those birds were previously banded individuals that had apparently wintered elsewhere, but at least 70% were unbanded birds from other populations and thus were true immigrants. A similar event occurred during the winter of 1989–1990; because of a local acorn crop failure (a "catastrophic" event) all the birds left the canyon, and the population was locally expatriated. By the summer of 1990, however, most territories were again reoccupied. This event would never have been detected without banded birds and regular winter censuses.

It is likely that the number of birds that successfully immigrate into Water Canyon each year depends to some extent on the number of territories that are vacant at that time, although because of the small sample sizes the density-dependent effect was not statistically significant. Both the strategic analysis and field observations indicate that there is a substantial amount of annual immigration, and this results in a significant dampening of fluctuations in population size, particularly when harsh environmental conditions leads to low reproduction or survival rates.

If immigration is critical to the persistence of the Water Canyon population, can it really be considered a separate population? Certainly in a physical and ecological sense the Water Canyon population is discrete; it is completely surrounded by unsuitable habitat, and the nearest canyon with more than two or three pairs of birds is at least 45 km distant in an entirely different mountain range. It is only in a demographic sense that the Water Canyon population is part of, and intimately connected to, other populations. Thus, our results suggest that the Water Canyon birds actually are part of a larger "metapopulation" (Levins 1970) but in a different manner than metapopulations are usually defined. Most models have conceived the dynamics of a metapopulation in terms of local extinction and recolonization (e.g., Levins 1970, Ehrlich et al. 1975, Ehrlich 1983, Gilpin 1987, Harrison et al. 1988, Burkey 1989, Hastings and Wolin 1989), and this has extended to most analyses of the genetic consequences of metapopulation structure (reviewed by Olivieri et al. 1990). In these models each component of the metapopulation typically goes extinct before it is recolonized, and thus populations "wink on and off" through time (Wilson and Willis 1975, Brown and Kodric-Brown 1977). While this may be characteristic of many invertebrate metapopulations (e.g., Brown and Kodric-Brown 1977, Murphy et al. 1990), our results suggest that metapopulations can also exist at different temporal and spatial scales, and that in some situations constituent populations may be rescued by immigration before they go extinct.

This type of metapopulation structure has profound demographic and genetic consequences. Small but apparently stable populations may be absolutely dependent upon immigration from other units in the metapopulation even in the absence of habitat modification and artificial habitat fragmentation (Pulliam 1988). Cutting the connections between such populations, even when the "best habitats" are preserved, will have disastrous consequences. Immigrants are often either juveniles that have not yet established a breeding territory, or adults that have been forced to move because of poor, but temporary, local environmental conditions. Such individuals often survive in sub-optimal habitats until space becomes available in normal breeding areas. By focusing conservation efforts only on those areas in which resident animals are found, these sub-optimal habitats may be lost. This can sever the connections between the various units of the metapopulation, and while it may take a number of years to detect, the loss of these areas may be as likely to lead to the eventual demise of the species as would the destruction of optimal habitats. Understanding the magnitude and nature of dispersal thus becomes an extremely important problem in the development of successful management strategies for these species.

Frequent immigration also could play an important role in "rescuing" small populations from inbreeding and genetic drift (Harris 1984). Genetic models indicate that even one successful migrant per year is sufficient to make two populations genetically panmictic (Wright 1978). In species where local subdivision leads to low effective population sizes, the potential problems of inbreeding depression are probably avoided through demographic rescue; that is, a small, closed population is likely to go extinct as a result of environmental or demographic stochasticity long before inbreeding or the loss of genetic variation becomes a problem. This may explain why inbreeding depression has proved to be difficult to detect in naturally small populations (e.g., Shields 1982, Simberloff 1988). In addition, because such populations will normally be rescued before extinction, the genetic founder effects that are associated with recolonization in the traditional models may be relatively unimportant. This would result in much less genetic differentiation among the various units of the metapopulation. Analysis of within- and between-population genetic structure can therefore provide a method to determine which type of metapopulation is characteristic of a particular species (P. B. Stacey and M. K. Ramsey, personal communication).

As has been noted for the extinction/recolonization models (e.g., den Boer 1981, Gilpin 1987, Goodman 1987, Gilpin and Hanski 1991) and empirically observed by den Boer (1981), in order for the rescue effect to be effective, it is critical that the various populations within the metapopulation are exposed to relatively independent environmental events, whether it be a new

disease organism or simply a series of bad years. Rescues can only occur if there is a sufficient pool of immigrants available in the overall metapopulation to move into populations that are declining because of poor environmental conditions in that particular locality. It is necessary that some populations are producing surpluses while others are declining. If all populations decline together (or expand together), the entire metapopulation may well go extinct because of environmental stochasticity. Thus, the metapopulation may consist of a series of source and sink populations (Pulliam 1988), but in the concept of the metapopulation presented here, each population shifts between source and sink whenever environmental stochasticity is great. This may explain why individual populations (like the Acorn Woodpeckers in Water Canyon) can have a calculated growth rate of <1 (Table 1), but still remain relatively stable for extended periods.

This phenomenon also may explain another puzzling feature of the simulation models. In both this study and others (see Shaffer 1987), population size has a relatively small effect on persistence times, and even very large populations are likely to go extinct within short time periods. Yet this contradicts conventional wisdom, which suggests that large populations tend to be resistant to extinction. Part of the reason for this paradox may be that in the models a population is usually considered closed no matter what its size, and each negative environmental event affects all members of the population simultaneously. Thus the simulated population—no matter what its initial size—will move inevitably toward extinction. The true value of large populations may not be that it makes the population more resistant to environmental stochasticity per se, but rather because as the size of a population grows larger, the range of environments occupied by individual organisms increases. Eventually the local environments may become uncoupled, creating a de facto metapopulation structure even when the population as a whole appears to be continuously distributed. The minimum viable population size for a species may therefore depend to a large extent on both the scale at which the organism sees its environment and the degree of correlation between local environments. A population that occupies a continuous and uniform habitat may be much more likely to go extinct than a population of the same size that occurs in a region where there is considerable spatial variation in local environmental conditions.

Although the Acorn Woodpecker in New Mexico typically occurs in small and highly fragmented populations, this species is neither endangered nor apparently declining. Like many residents of montane riparian habitats, the Acorn Woodpecker exhibits demographic mechanisms that allow it to cope with this distributional pattern. Likewise, there are probably many other species that could live in this habitat but have not been successful because they do not have the

appropriate characteristics (such as high dispersal rates or the ability to survive in sub-optimal habitats). By studying the successful species, even though they are not declining, we believe that it is possible to gain insight into the characteristics that have allowed these species to persist. This in turn will allow us to develop management plans that will be more likely to preserve species that are forced to deal with this stress as a result of human activities.

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