

POPULATION PERSISTENCE TIME: ESTIMATES, MODELS, AND MECHANISMS

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Abstract. The conservation and management of populations require some insight into mechanisms of population regulation, yet unambiguous identification of density dependence in vital rates is notoriously difficult. Through the reanalysis of data published by Stacey and Taper for a semi-isolated sub-population of the Acorn Woodpecker we demonstrate the utility of an approach in which a single data set is “attacked” using a suite of models with different assumptions. Tests for density dependence of the reproductive rate and of juvenile survival are inconclusive, but there is evidence for density-dependent adult survival. Since “survival” rates estimated from banded birds confound the effects of mortality and immigration/emigration, we construct and analyze three models: (1) a closed population with density-independent vital rates and an upper limit to population size, (2) a regulated closed population, (3) a regulated sub-population with immigration and emigration. Very small interchanges with other sub-populations can have a very large effect on population persistence; thus our results highlight the importance of distinguishing the effects of interchange from density dependencies in vital rates.

Key words: acorn woodpecker; extinction; fragmentation; *Melanerpes formicivorus*; population persistence time; population regulation.

INTRODUCTION

The probability that a population persists to a given time is now frequently used as a measure of population viability in applied ecological studies (e.g., Shaffer 1983, Dennis et al. 1991, Middleton et al. 1993). In many practical applications persistence time is estimated by multiple realizations of a simulation model, which generally incorporates observed levels of variability in the population’s vital rates. Simulation models are favored in population viability analysis for several reasons, not least of which is the ease with which they can be constructed to incorporate a wide range of biological phenomena. Further, until recently, analytical treatments of persistence time have only been available for a restricted class of population models: those where the population growth rate is independent of population density, and where total population size is unrestricted. These models are typically variants on the form

$$N_{t+1} = \lambda_t N_t \quad (1)$$

where N_t is the population size at time t , and the $\{\lambda_t\}$ are independent, identically distributed positive random variables (e.g., Tuljapurkar 1990 and references therein).

In models based on Eq. 1 the probability distribution

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of population size is asymptotically lognormal (Leontin and Cohen 1969, see also Capocelli and Ricciardi 1974 and Tuljapurkar and Orzack 1980 for similar results in continuous-time unstructured, and discrete-time structured, populations, respectively). An important consequence of this is that the growth in expected population size is a poor descriptor of the behavior of the majority of realizations and a more useful statistic is the *long-run growth rate*, defined by

$$c = E\{\ln(\lambda_t)\}. \quad (2)$$

If $c \leq 0$, this model predicts that extinction is certain and mean persistence time is inversely proportional to $|c|$ (Lande and Orzack 1988). As a result, much applied research relating to conservation of endangered species and to the impact of variable environments on population dynamics has focused on estimating and modelling this long-term growth rate (Heyde and Cohen 1985, Caswell 1989, Dennis et al. 1991). If $c > 0$, the model predicts that the probability of extinction is < 1 . The expected persistence time *conditional* on the extinction threshold being reached is again inversely proportional to c (so the conditional mean decreases as c increases), but the probability of ever reaching this threshold decreases exponentially with increasing c .

The somewhat surprising predictions of the model with density-independent vital rates are because there is no upper limit to population size. This is clearly established by contrasting the dynamics with those of a particularly instructive model that assumes density independent population dynamics supplemented by an

TABLE 1. Stacey and Taper's (1992: Table 1) data for the population of Acorn Woodpeckers in Water Canyon, New Mexico, with additional data on the number of fledglings actually produced (M. L. Taper, *personal communication*).

Year	Adult survivorship ^{†,§}	Juvenile survivorship ^{‡,§}	Reproductive rate (young/pair)	Population size [¶] (no. adults)	Number of emigrants [#]	Number of young fledged
1975	0.53	0.56	3.38	46	3	44
1976	0.68	0.64	1.27	46	4	19
1977	0.71	0.30	2.77	40	1	36
1978	0.38	0.40	2.17	51	2	26
1979	0.54	0.00	0.05	52	0	1
1980	0.69	0.38	4.00	32	0	4
1981	0.66	0.18	2.37	46	1	38
1982	0.49	0.25	0.50	49	1	10
1983	0.61	0.44	1.60	35	1	24
1984	2.00	36
Mean	0.588	0.350	2.011	43.3	1.44	22.4
Sample variance	0.012	0.038	1.490	50.0	1.77	234.0

[†] The probability that an individual alive at the start of the year's breeding season is still alive at the start of the next year.

[‡] The probability that a bird survives from fledging to the start of the following breeding season.

[§] Survivorships were calculated from the histories of banded individuals.

^{||} The mean number of young produced per breeding pair, from observations of all nesting attempts.

[¶] The total number of birds residing in the study area in May at the start of the breeding season.

[#] Birds known to have survived the winter but which left the area before the breeding season.

upper limit to population size (Goodman 1987a, Lande 1993, Foley 1994, Middleton et al. 1995). The effect of introducing the upper limit is that the probability of ultimate extinction becomes 1, and the criterion for population persistence—defined as a specified probability of lasting some given time—becomes more stringent than the simple requirement of the unregulated model that the long-run growth rate be positive (Middleton et al. 1995, see also Eq. 5 below). Similar results are found with a number of simple stochastic models of closed, regulated populations (Nisbet and Gurney 1982: Chapters 6 and 7 and references therein).

An important property of many models of regulated populations is that the distribution of persistence times has an exponential "tail" (Goodman 1987b, Mangel and Tier 1993, Middleton 1993). Knowing this, it is possible to make reasonable inferences concerning extinction probabilities once we know the mean persistence time, a quantity for which analytic approximations are commonly available (e.g., Lande 1993 for the model described in the previous paragraph).

The recent expansion of the repertoire of stochastic models of bounded and/or regulated populations suggests that in modelling any particular population, it will be valuable to use a number of different models embodying different assumptions concerning population regulation. This enables us to test the sensitivity of predictions to specific assumptions, and can help direct future field work. Our aim in this paper is to demonstrate the applicability to conservation and management studies of this approach in which a single data set is "attacked" using several models. We accomplish

this by the reanalysis of data published by Stacey and Taper (1992) for a semi-isolated sub-population of the Acorn Woodpecker. This study was chosen because of the authors' use of a simulation model with density-independent vital rates, but an upper bound to population size, very similar to that used in the studies cited above. We investigate persistence time under different biological scenarios, discussing the sensitivity of the estimated persistence probability on choice of model. Our results highlight the importance of distinguishing the effects of density dependence in birth or death rates from those introduced as a consequence of immigration and emigration.

STACEY AND TAPER'S DATA

Stacey and Taper (1992) present data for the Acorn Woodpecker, *Melanerpes formicivorus*, a species that occurs in small, rather isolated populations in the southwest of the United States. Their data relate to the population of woodpeckers in a single canyon (Water Canyon) in the Magdalena Mountains of New Mexico from 1975 to 1984 (though the population is known to have been present in the canyon for at least 70 yr). A large proportion of the birds are color-banded, allowing the calculation of year-by-year survivorship and reproductive rates for the population from individual histories. Stacey and Taper note that each year a number of unbanded individuals were present in the canyon, indicating some (not directly quantified) interchange with other sub-populations. For ease we reproduce Stacey and Taper's data as Table 1.

A data set such as this where the vital rates have

been measured directly from banding studies (rather than inferred solely from the population size data), and using the majority of individuals in the population, is a valuable resource. An obvious first question to ask of such a data set is whether there is evidence of density dependence in the vital rates. Adult and juvenile survival and reproductive rate are all negatively correlated with population size (Spearman's rank correlation, $\rho = -0.68$, -0.33 , and -0.52 , respectively) and the number of emigrants is positively correlated with population size ($\rho = 0.19$). All these correlations are in the right direction for density-dependent regulation of the population. Unfortunately, assigning a useful significance level to these correlations is not a simple task, though the methods in the Appendix suggest that only the correlation of adult survival with population size is statistically significant. In fact, especially for time series of only 10 yr length, the problems of reliably detecting the action of density-dependent population regulation are considerable (see, for example, Murdoch 1994 and references therein). Nevertheless there is some evidence that the observed vital rates are not entirely random and could act to regulate population size (see Appendix).

In the following section we introduce several measures of population growth rate that may be constructed from these observed vital rates. In all cases a decrease in population growth rate with increasing population size is apparent ($\rho = -0.72$ where emigration is excluded, Eq. 4 below; $\rho = -0.75$ where emigration is included, Eq. 6 below; see the Appendix for a discussion on the significance of these correlations). In addition the log of the *realized* growth rate based only on the observed population sizes (Eq. 10), is negatively correlated with population size ($\rho = -0.77$).

We consider three models, with the aim of disentangling the various mechanisms contributing to population persistence:

- 1) a closed population with density-independent demographic rates and an upper limit to the number of individuals,
- 2) a closed population with a density-dependent growth rate,
- 3) a model with density-dependent vital rates plus immigration and emigration.

THE THREE MODELS

A closed population with density-independent vital rates and an upper limit

Like Stacey and Taper we begin by considering the fate of the population were it to be completely closed (i.e., no immigration or emigration), with rates of survival and reproduction as measured by the studies of banded individuals but independent of population size. The simulation model described verbally by Stacey and Taper can be written more formally as

$$N_{t+1} = \begin{cases} \lambda_t N_t & \text{if } \lambda_t N_t \leq N_{\max} \\ N_{\max} & \text{otherwise} \end{cases} \quad (3)$$

with

$$\lambda_t = \frac{r_t j_t}{2} + a_t \quad (4)$$

where N_t is the population size in year t , r_t is the reproductive rate per pair, j_t is the probability that a fledgling survives to breed in year $t + 1$, and a_t is the probability that an adult survives to breed in the subsequent year. N_{\max} is the maximum number of breeding individuals that the area can support, twice the maximum number of breeding pairs. The number of territories for the Acorn Woodpecker appears to be determined by the availability of acorns and other nuts that are collected by the birds in autumn and stored in holes in "granary trees" as a winter food supply (Stacey 1979). In this model, any excess of birds over the maximum number determined by the limited number of territories available are lost to the system. This imposes an upper limit to population size at N_{\max} , which is set at 52 in this paper: twice the maximum number of territories observed by Stacey and Taper in the period 1975–1984.

Analytical approximations to mean persistence time in such models have recently been presented (Lande 1993, Foley 1994, Middleton et al. 1995). Middleton et al. in addition derived a robust approximation to the *distribution* of persistence times. This approximation requires the estimation of the long-run population growth rate (see *Introduction*) and its variance. These can be estimated as the mean and variance of $\ln(\lambda_t)$ where λ_t is given by Eq. 4 above (see Table 2). This yields a negative value for the long-run growth rate (-0.07), which (as discussed in the *Introduction*) ensures long-term population decline. (Though, as the data allow calculation of λ_t for only 9 yr, the 90% confidence intervals on this rate are fairly large: -0.26 to 0.11 .) The presence of an upper limit to population size makes the criteria for population persistence more stringent than the simple requirement that the long-run growth rate be positive. Middleton et al. suggest a population can be considered persistent if the long-run growth rate exceeds some critical value c_0 given by

$$c_0 = 2Dm_0/\ln(N_{\max}/N_{\min}) \quad (5)$$

where $2D$ is the variance in the long-run growth rate, and N_{\min} is the level at which the population is considered to be extinct (two individuals in this case). Note that we estimate $2D$ as the sample variance in $\ln(\lambda_t)$ (see Dennis et al. 1991: Eqs. 25 and 26). The variable m_0 is the critical value of a dimensionless parameter group that is discussed further by Middleton et al. (1995). For a 50% probability of persistence to 1000 yr, Middleton et al. suggest $m_0 \approx 3.7$, in which case $c_0 \approx 0.15$ with 90% confidence interval (0.09, 0.25), using accelerated bootstrap confidence intervals on Eq. 5 (Efron 1987, Hall 1988). There is therefore only a slight overlap between the top end of the confidence interval

TABLE 2. Various quantities derived from Stacey and Taper's (1992: Table 1) data for the population of Acorn Woodpeckers in Water Canyon, New Mexico.

Year	$\ln(\lambda_t)$ without emigration, Eq. 4†	$\ln(\lambda_t)$ with emigration, Eq. 6‡	Realized $\ln(\lambda_t)$, Eq. 10‡
1975	...	0.34	0.00
1976	0.08	-0.00	-0.14
1977	0.39	0.10	0.24
1978	-0.21	-0.26	0.02
1979	-0.62	-0.62	-0.49
1980	0.37	0.37	0.36
1981	-0.14	-0.16	0.06
1982	-0.59	-0.63	-0.34
1983	-0.04	-0.07	0.03
1984
Mean	-0.07	-0.10	-0.03
(90% BC _a CI)‡	(-0.26, 0.11)	(-0.30, 0.08)	(-0.18, 0.09)
Sample variance	0.13	0.13	0.07
(90% BC _a CI)‡	(0.08, 0.22)	(0.07, 0.22)	(0.05, 0.14)

† For the models with a density-independent growth rate, the mean of $\ln(\lambda_t)$ estimates the long-run growth rate c , and $\text{var}\{\ln(\lambda_t)\}$ its variance ($2D$).

‡ The 90% confidence interval calculated by accelerated bootstrap (Efron 1987, Hall 1988).

for c (Eq. 2) and the bottom end of the confidence interval for c_0 .

Stacey and Taper assess persistence time using simulation where the yearly demographic parameters are drawn, independently, from the sets of observed values; the population is considered to be extinct if it falls below two breeding individuals in size. Fig. 1 compares the distribution of population persistence times estimated by Stacey and Taper (their Fig. 2) with that of the Wiener process approximation of Middleton et al. (1995). A large discrepancy is immediately apparent. Our original supposition was that Stacey and Taper had decided to include the observed emigration but had done so in a manner that produced inverse density dependence in their simulated population growth rates.

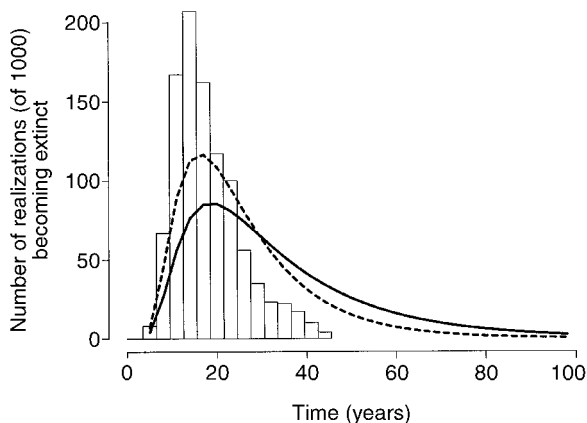


FIG. 1. Histogram: Stacey and Taper's (1992) Fig. 2 showing their estimate of the persistence time distribution for the Water Canyon Acorn Woodpecker vital rates randomly selected from the observed values. Solid line: Wiener process approximation to the persistence time distribution for the model, Eq. 3, with growth rate given by Eq. 4. Dashed line: approximate persistence time distribution when growth rate includes observed emigration, Eq. 6. The latter distributions have been scaled to match Stacey and Taper's Fig. 2.

In fact, the errors in Stacey and Taper's distribution result from truncation in their model code (M. L. Taper, *personal communication*). It is these errors that produce the inversely density-dependent vital rates. The short persistence times estimated by Stacey and Taper (they estimate a median time to extinction of 16 yr) for a closed population are thus likely to be overly pessimistic, a feature of the fact that the inverse density dependence lowers the realized growth rates in the model at lower populations when there is no evidence that this is actually happening in the real population.

It is, however, of interest to take account of known emigration, while retaining density-independent growth rates in the model. To do this we can treat the emigrants as additional deaths (which reduce the realized adult survival) and write the multiplicative growth rate as

$$\lambda_t^e = \frac{r_t j_t}{2} + \frac{a_t N_t - E_t}{N_t} \quad (6)$$

where the e superscript indicates the inclusion of observed emigration. If we again assume that the observed values for this quantity arise independently, then we can again (see Table 2) estimate long-run growth rate as the mean of $\ln(\lambda_t^e)$ and continue to use the Wiener process approximation to estimate the distribution of persistence times (see Fig. 1). Persistence times will obviously be shorter in this case than when the growth rate was estimated without taking account of the observed immigration, but are still longer than those estimated by Stacey and Taper. In this case the 90% confidence interval for c_0 (0.09, 0.26) does not overlap the confidence interval for the long-run growth rate (Table 2).

The mean persistence time in the model (Eq. 3) can be estimated using the formula given by Middleton et al. as

$$E(T) = \frac{\tau}{2} e^{2m} [1 - e^{-\alpha} - \alpha e^{2m}] \quad (7)$$

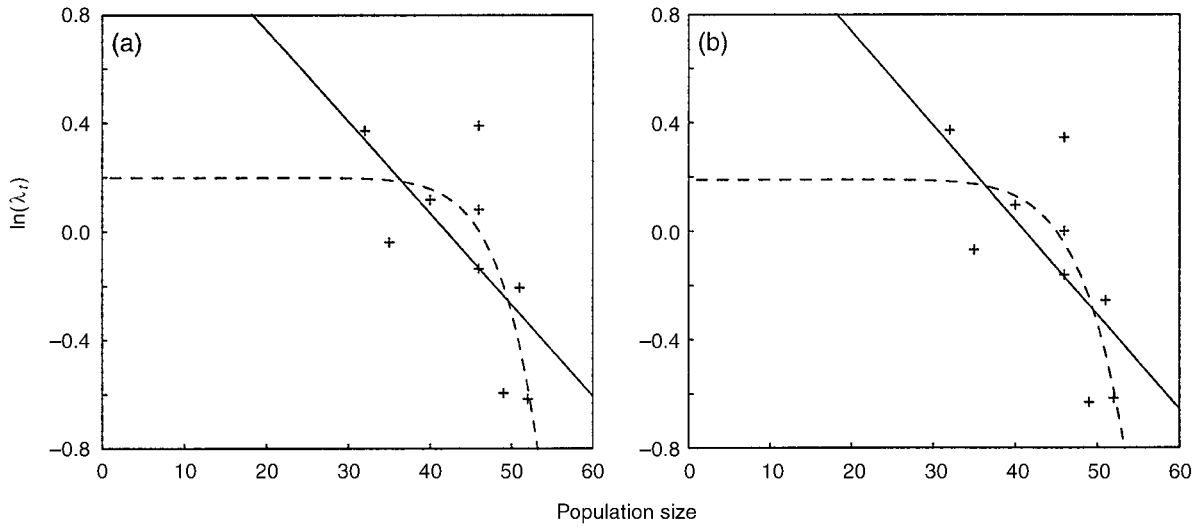


FIG. 2. Points: $\ln(\lambda_t)$ against population size. (a) calculated without observed immigration, Eq. 4; (b) with observed emigration, Eq. 6. Dashed line: θ -logistic; solid line: standard logistic. Parameters for the fitted lines are in Table 3.

where, $\tau = 2D/c^2$, $m = c \ln(N_{\max}/N_{\min})/(2D)$ and $\alpha = c \ln(N_0/N_{\min})/D$. N_0 is the initial population size, which, unless noted otherwise, is here set at 52, the upper limit. When the growth rate is estimated without observed emigration, Eq. 7 estimates mean persistence time as just over 33 yr; when the observed emigration is accounted for, this drops to just over 25 yr.

While the mean alone is an inappropriate statistic for summarizing distributions of persistence times (as such distributions can be highly skewed with much of the probability mass representing times much shorter than the mean; see Fig. 1), it has “added value” if we exploit the result that for large times the distribution decays exponentially with a rate constant inversely proportional to the mean. This implies that persistence for longer than a few times the mean is very unlikely. Thus for the Water Canyon population both the approximate distribution of persistence times (which uses the mean and variance of $\ln(\lambda_t)$ as the best estimate of the long-run growth rate and its variance), and the persistence criterion, c_0 , (which allows us to take account of the confidence intervals on the long-run growth rate) suggest that the prospects for long-term persistence of a closed, bounded population with the vital rates observed arising independently are not very good. As Stacey and Taper note, this contrasts with the known 70-yr persistence of the population and suggests that other mechanisms are at work aiding population persistence.

A regulated, closed population

As we discuss above there is some evidence that the vital rates measured by the banding studies are not independent of population size as portrayed in the previous model, but in fact act to regulate the population. A variety of models are commonly used to describe

density-dependent growth rates. We consider two examples here, both of which have a population growth rate given by

$$\lambda_t = \exp \left\{ r_{\max} \left[1 - \left(\frac{N_t}{K} \right)^\theta \right] + \sigma Z_t \right\}. \quad (8)$$

When $\theta = 1$ we have the standard logistic model; otherwise we have what is known as the θ -logistic.

The models were fitted to the growth rates derived from the banding studies by nonlinear regression via least squares (Statistical Sciences 1993). The fitted parameters are given in Table 3, and the curves illustrated in Fig. 2. Although visually it is difficult to say which is the more appropriate model, especially given the limited range of population sizes spanned by the data, the θ -logistic achieves a lower residual sum of squares in the fitting process (Table 3). A biological reason for favoring the θ -logistic is the fact that the population growth rate does not continue growing rapidly as population size falls, but levels off. Given obvious limitations on the realizable birth rate, this is a desirable feature.

We have estimated the persistence time distributions for these models by simulation, conducting 500 000 realizations of each model and recording the time at which the population size drops below two individuals. We estimate the variation in growth rate as $\sigma^2 = \text{RSS}/(n - 1)$ where RSS is the residual sum of squares in the model fit and n is the number of years for which we have growth rate data (9 yr in all cases here). This differs from the estimate of $\sigma^2 = \text{RSS}/n$ used by Stacey and Taper in their simulations. The use of $n - 1$ as the denominator appears to be more appropriate for short time series in the light of recent work by Dennis and Taper (1994, see also Dennis et al. 1991: Eqs. 25 and 26). Table 3 contains estimates from these simulations

TABLE 3. Parameters for the density-dependent models, Eq. 8.

Model	r_{\max}^{\dagger}	K^{\dagger}	θ^{\dagger}	Residual sum of squares	$G(500)^{\ddagger}$	$E(T)$
ln(λ_t) excluding observed emigration, Eq. 4						
Logistic	1.42	42.0	1	0.62	1.86×10^{-4}	...
θ -logistic	0.20	46.1	11.2	0.46	1	22.3
ln(λ_t) including observed emigration, Eq. 6						
Logistic	1.44	41.2	1	0.57	1.18×10^{-4}	...
θ -logistic	0.19	45.0	9.7	0.45	1	32.0
Realized ln(λ_t), Eq. 10						
Logistic	1.23	43.2	1	0.24	0	...
θ -logistic	0.30	45.2	5.3	0.22	0.41	991.6§

\dagger Fitted by nonlinear least squares regression to the various population growth rates.

\ddagger The proportion of 500 000 realizations of the model becoming extinct (i.e., dropping below two individuals) within 500 yr, given an initial population size of 52 individuals.

\S For the θ -logistic with $G(500) < 1$, the expected persistence time is estimated as $-1/a$, where a is the slope of a linear fit to the linear part of $\ln(g(t))$ vs. t using least median of squares regression (which is less sensitive to the difference in variance at different values of t than standard least squares regression).

of the probability of extinction by 500 yr, and, where possible, the mean persistence time.

For the standard logistic ($\theta = 1$) the proportion of realizations reaching the extinction threshold by 500 yr was < 0.0002 whether or not the growth rate was calculated with the inclusion of observed emigration. However, for the θ -logistic, which provides a better fit to the observed growth rates and avoids "impossibly" large growth rates when the population is small, extinction is rather more frequent, with all realizations becoming extinct by 500 yr. For all but very short times, the estimated persistence time distribution takes the form of a negative exponential distribution (Fig. 3). The mean persistence time is just over 22 yr when the growth rate is calculated without including observed emigration, and almost 32 yr when emigration is included. This slightly surprising result is due to the fact that the curvature in the θ -logistic fit at larger population sizes is less when emigration is included: thus the reduction in population size is less severe when N_t exceeds K in this case than in the case where known emigration is excluded.

For the Acorn Woodpecker data, density-dependent regulation of growth rate in a closed population, where the relationship of growth rate to population size is described by the θ -logistic, does little to enhance persistence times beyond those observed in the model where vital rates were density-independent and the sole regulatory factor was the upper bound to population size.

Incorporating the effects of immigration and emigration

The preceding models made the assumption that the Water Canyon Acorn Woodpecker population was closed to immigration. The data used in parameterizing the models were derived from banding studies. Stacey and Taper note, however, that unbanded individuals (i.e., birds originating in other sub-populations) were

observed in Water Canyon. The data on population size through time provide further evidence that interchange with other sub-populations must be a frequent event. Using the information in Table 1, we can estimate the population size that would occur in the absence of immigration as:

$$N_{t+1} = y_t j_t + a_t N_t, \quad t = 1975, \dots, 1983, \quad (9)$$

where y_t is the number of young fledged. Thus, we can infer the actual interchange between the Water Canyon population and other groups by taking the difference between this predicted level and the observed population size, taking account of known emigration (Fig. 4). It is apparent from this figure that interchange is density dependent, although it is difficult to judge the form of this relationship given the scatter in the data. While a simple linear regression would no doubt give a reasonable fit, a more mechanistic explanation is that below a certain level (set by the maximum number of available territories, as discussed previously) there are opportunities for immigrants to join the population, while above this level birds must leave the canyon in order to seek territories elsewhere. Immigration will be affected by several factors apart from the availability of territories, thus producing the rather variable number of immigrants when the predicted population size is below ≈ 40 individuals.

If we leave aside the data from the banding studies and use only the observed population sizes, we estimate the population growth rate as

$$\ln(\lambda_t) = \ln(N_{t+1}/N_t). \quad (10)$$

(See Table 2). We can again fit this growth rate either by the standard logistic or θ -logistic model. For the standard logistic, none of 500 000 realizations of the model reached the extinction threshold by 500 yr. For the θ -logistic, as before, an exponential distribution of persistence times was apparent, but in this case the mean persistence time was almost 1000 yr, with a prob-

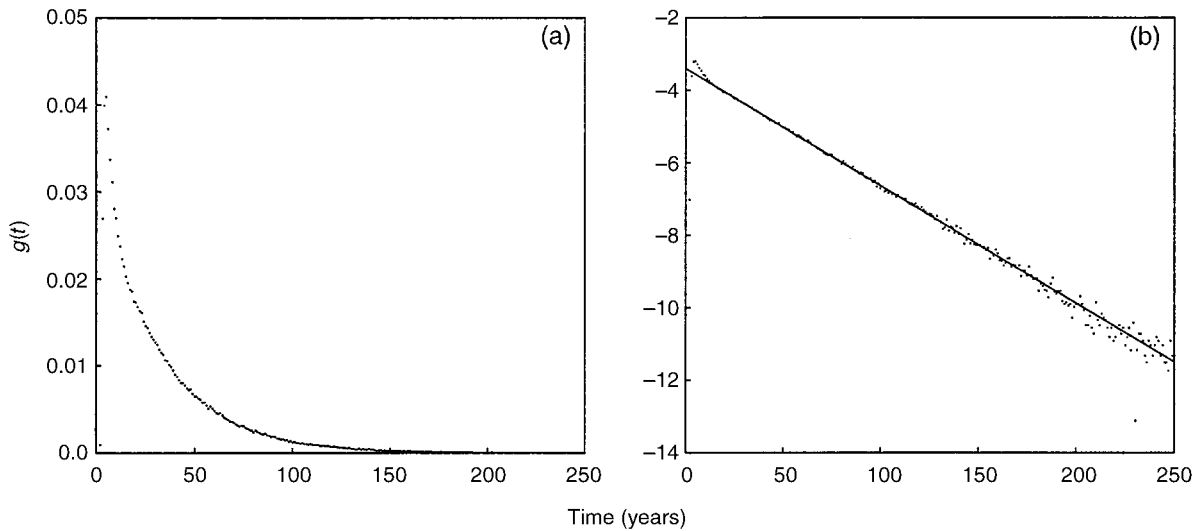


FIG. 3. (a) Distribution of persistence times for the θ -logistic model for a closed population with growth rates estimated including the effect of observed emigration. Estimated by simulation (500 000 realizations). (b) Plot of $\ln[g(t)]$ against time for the same simulation as (a), demonstrating the linear tail as confirmation that (a) is exponential. The line fitted to the linear portion by least median squares regression allows the expected persistence time to be estimated.

ability of only ≈ 0.41 of becoming extinct by 500 yr (Table 3). Density-dependent interchange of individuals with other sub-populations therefore seems to be a critical factor in ensuring population persistence for the Acorn Woodpeckers of Water Canyon.

Note, however, that fitting a simple density-dependent growth curve to the growth rate estimated from population increments actually compounds the mild density dependence in the vital rates (which, as we observed in the previous section, does little to increase population persistence times over the density-independent case) with the strongly density-dependent interchange of individuals with other sub-populations. By representing interchange as "just another" density-dependent factor we obscure some of the important as-

pects of the population dynamics of fragmented populations. Of fundamental importance is the fact that extinction of a sub-population is no longer an absolute event. Immigrants to an area from other sub-populations mean that a suitable habitat is unlikely to remain unoccupied for long. In the case of the Acorn Woodpeckers of the Magdalena Mountains, it appears that not only is interchange sufficient to rescue potentially extinct sub-populations, but the linkage is sufficiently strong to produce a stabilization of sub-population numbers. Thus any excess of birds in one year need not be assumed to be lost from the population forever; rather they may find a place in a group where breeding success has been lower that year.

While our incorporation of the effects of interchange of individuals between sub-populations in the models of this section has been necessarily crude, it has nevertheless illustrated that such interchange appears to be the critical factor in the persistence of the Water Canyon Acorn Woodpecker population.

DISCUSSION

This paper has illustrated the wide relevance of recent theoretical advances in the study of population persistence to population viability studies. The most important message concerns the interpretation of estimates of the long-run growth rate, $E\{\ln(\lambda_t)\}$, from population census data (e.g., Dennis et al. 1991). While a positive long-run growth rate is an appropriate criterion for persistence in an unbounded population with density-independent rates, the existence of an upper bound to population size implies a more stringent criterion (such as the c_0 criterion we employ above). For the data considered in this paper we were able to es-

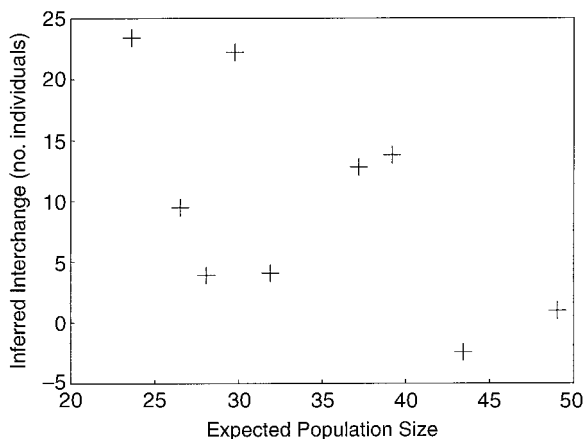


FIG. 4. Inferred interchange of individuals against expected population size (Eq. 9). Negative interchange indicates emigration; positive values of interchange are immigration.

timate the long-run growth rate from birth and survival rates calculated from banding data; in many cases the growth rate has to be estimated solely from changes in population size. However, estimation of long-run growth rate in a bounded population from population census data alone would have to take account of the fact that when the population is near the upper bound its realized growth rate will be reduced due to the regulatory effect of the upper limit, whereas the growth rate of interest is that which would have arisen in the absence of the upper limit.

Of particular interest is the observation that exponential persistence-time distributions are a fairly general feature of models where population size is bounded or regulated through density dependence. The simulations of the θ -logistic illustrated above, and the asymptotic behavior of the bounded model with a density-independent growth rate, add to the growing number of models where exponential persistence time distributions have been demonstrated (Goodman 1987b, Mangel and Tier 1993). The generality of the result, at least as an approximation, is plausible since several density-dependent stochastic population models can be recast in the form of (or at least approximated by) the Ornstein-Uhlenbeck (OU) process (Ricciardi 1977: 170–174, Nisbet and Gurney 1982, Turelli 1986, Middleton 1993). This has an asymptotically exponential first passage time distribution (Nobile et al. 1985; equivalent to the persistence time distribution in the population models considered here). An exponential distribution for persistence time is heuristically satisfactory; if population size is generally distributed around a mean level that is much larger than the extinction threshold, then runs of “bad years” that cause the population to decline to extinction would be expected to arise randomly in time, thus producing an exponential distribution for persistence time. In other words, we are essentially dealing with an embedded Poisson process where the observed “event” is a run of growth rates sufficiently low to bring the population size down to the extinction threshold.

We should point out that none of the various growth rates we use in our simulations match those illustrated by Stacey and Taper in their Fig. 5. The reason for this is that the growth rate they calculated is the one incorporated in our Eq. 9 (i.e., using the number of fledged young, M. L. Taper, *personal communication*). Throughout this paper we have used the assumption that the number of breeding pairs is equal to $N_t/2$. In reality, various factors, such as deviations from a 1:1 sex ratio, may reduce the number of breeding pairs below this level. Stacey and Taper's Fig. 5, and their simulations based on fits to these data, can thus be compared to our Fig. 2 and our results for a closed, regulated population, to investigate the effects of deviations from a 1:1 sex ratio on population persistence. Unsurprisingly, the growth rates calculated using the actual number of fledged young are lower than those

calculated when a 1:1 sex ratio is assumed. However, simulations using a θ -logistic model fitted to these growth rates suggest that the probability of the population dropping to two individuals by 500 yr is only 0.86, with a mean persistence time of >234 yr (parameters are given in Stacey and Taper's Table 2, but we have used $\sigma^2 = \text{RSS}/[n - 1]$ as discussed earlier). Persistence times are thus significantly *longer* than those for the θ -logistic models in our investigation of a closed, regulated population. This appears to be the result of tighter population regulation in this latest model. In reality this result probably tells us more about the problems of fitting a generic density-dependent model to data representing only a limited range of population sizes, than it does about the effect of deviations from a 1:1 sex ratio. Using the fitted model to calculate growth rates for any population size that occurs in a simulation represents considerable extrapolation. This fact, and our previous comments on the problems of our representation of population interchange as parts of a combined growth rate, argue strongly in favor of the use of mechanistic models in place of generic density-dependence functions where possible.

Our reanalysis supports the main insight of Stacey and Taper, namely that interchange between the Acorn Woodpeckers of Water Canyon and other sub-populations is the primary mechanism producing population persistence. *Metapopulation* persistence—the persistence of a linked group of sub-populations—requires us to view questions of persistence from a different perspective, as “extinction” of a single sub-population may be a temporary state with high probability of recolonization of the area by birds from neighboring sub-populations.

Given the fact that environmental factors affecting one sub-population are unlikely to be perfectly correlated with those affecting other sub-populations, and the fact that different sub-populations will generally have different maximum sizes, simultaneous extinction of all sub-populations is rather unlikely. Models where a population persists through the balance of extinction and recolonization of a patchy environment have been known in the literature for some time (see Hanski and Gilpin 1991). For instance, Gurney and Nisbet (1978) explored the fluctuations in patch occupancy in a number of simple models with identical patches and concluded that the average proportion of occupied patches must exceed a value of order of magnitude $3/\sqrt{N}$ (where N is the number of sites) for persistence over appreciable times to be possible by such a mechanism. Hanski et al. (1995) present evidence that a balance between local extinction and recolonization is responsible for the persistence of the butterfly *Melitaea cinxia* in Finland. However, unlike insect populations where local extinctions may be relatively frequent (Schoener and Spiller 1987, Hanski et al. 1995 and references therein), subpopulations of longer lived species may seldom show actual local extinction but may nonethe-

less still rely on the “topping up” of local population numbers by immigration of individuals from neighboring populations, as appears to be the case for the Acorn Woodpeckers of Water Canyon. The persistence time results for models of closed populations, together with the inferred interchange shown in Fig. 4, suggests that Water Canyon may actually be a population sink: unable to exist without the immigration of individuals born elsewhere, and contributing few individuals to other subpopulations in its turn.

An interesting question that arises (of particular importance to those involved in population management and conservation) is to what extent studies of a single sub-population can indicate the likelihood of persistence at the metapopulation level. Does knowledge of the interchange between one sub-population and all others give information on the health of the metapopulation, or is detailed information required on all subpopulations? An answer to this question would give guidance to those who must allocate resources in data gathering, who must decide whether to study a single sub-population intensively, or several subpopulations in less depth. One useful starting point is the work of Verboom et al. (1991, and references therein) who consider the derivation and parameterization of a simple metapopulation model from a much more detailed model of the dynamics of a single subpopulation (clan) of the European badger, *Meles meles*. Verboom et al. suggest that a simple two-state (i.e., a subpopulation is present or absent) metapopulation model can provide an adequate description of the behavior of a fragmented population if three conditions are fulfilled: (1) that the local populations have a quasi-stationary distribution of population size, (2) that this distribution is approached quickly, and (3) that immigration has little effect on established subpopulations. Verboom et al. found that their simple model adequately reflected the behavior of a more complex simulation made up by coupling together replicates based on the more detailed local population model. Thus it appears that a description of the dynamics of the metapopulation can be obtained, in some cases, from detailed knowledge of a single subpopulation. There are, however, some important caveats. Verboom et al. note that the parameterization of the simple metapopulation model is extremely sensitive to the details of migration—the process about which the least is generally known. Further, they did not investigate the consequences of different subpopulations having different dynamics or parameter values; their detailed simulations used the same parameter values for all clans. Finally, as discussed above, the Acorn Woodpecker population of Water Canyon appears to be heavily influenced by the “rescue” effect of immigrants from other subpopulations, a fact that is not compatible with Verboom et al.’s third condition for application of the simple metapopulation model. If such “rescue” effects are found to be commonly important in the dynamics of spatially fragmented pop-

ulations, a further question arises: at what level of interchange between “subpopulations” is the population sufficiently well mixed that treating the metapopulation as a single homogenous population is sufficient for models that are to be used in population management?

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APPENDIX

Here we consider the problem of assessing whether or not the data of Table 1 provide evidence that the population growth rate is related to population size. As Fig. 2 illustrates, the growth rates calculated from Stacey and Taper's data show a negative correlation with population size, a relationship that can be described quite well by the density-dependent models we consider. However, negative correlations between population growth rate and population size also arise in time series where population growth is density independent (i.e., in random walks; see, for example, Vickery 1991). For short time series, such as that considered in this paper, it is difficult to establish whether an observed negative correlation between the population growth rate and population size is due to density dependence or not.

Testing for density dependence

The density-dependence test of Pollard et al. (1987) avoids the problem of a nonzero correlation being the expectation for a random walk by using bootstrap resampling to assess whether the observed correlation between a_i (equivalent to $\ln[\lambda_i]$ in the main body of this paper) and x_i (the natural log of population size) is extreme relative to that which would have been produced had the a_i arisen in a different order. However, while the Pollard test is successful in avoiding spurious detection of density dependence from random walk simulations, it is only successful in identifying real density dependence in 50–60% of cases (Holyoak 1993).

Here we employ a slightly different approach. For each fitted model we produce a large number of simulated time series of the same length as the observed series and compute the distribution of correlations between (log) population growth rate and (log) population size for comparison with the observed correlation. This differs from the approach of Pollard et al. by drawing the vital rates from some assumed distribution, rather than rearranging the pool of observed rates (in fact we are performing parametric bootstraps). We use Spearman's rank correlation in this process.

The realized growth rate

We consider first the realized growth rate, Eq. 10, which is defined by the change in population size from one year to

the next and so is equivalent to a_i above. We simulated 10 000 random walks of nine normally distributed steps with mean and variance of the step size equal to the mean and variance of the realized growth rate (Table 2). The mean correlation between step size and position was -0.40 . The observed correlation of -0.77 lies between the 5 and 10% quantiles of the simulated correlations. This suggests that the observed correlation is significantly different from the expectation under the null hypothesis of a random walk at the 10% level in a one-tailed test. We investigated this further by simulating 10 000 runs of each of the density-dependent models considered in the main body of the paper (the standard and theta logistics) with parameters given in Table 3. In each case the observed correlation lay between the 45 and 55% quantiles of the correlations from the simulated time series.

Thus our experiments suggest that the observed correlation between realized population growth rate and population size is rather more typical of that expected under a density-dependent model than under a random walk model.

Growth rates inferred from observed vital rates

We can perform a similar exercise to investigate whether the negative correlations observed between population size and growth rate constructed from the observed survival and reproductive rates (Eq. 4, or if the observed emigrants are classed as additional deaths, Eq. 6) are different from the expectation under a random walk model. Table A1 summarizes the results and again illustrates that while the observed negative correlations are only significantly different from the random walk model at the 10% level (one-tailed test) they are rather more typical of a density-dependent model.

The vital rates from the banding study

Finally, it is of interest to investigate whether the various rates of survival and reproduction inferred from Stacey and Taper's banding study (Table 1) show any evidence of density dependence. Although each of these rates is only one component of the overall population growth rate, the problem of cross-correlation between the time series for the vital rates and that of population size (which produces the negative ex-

pected correlation between population growth rate and size, mentioned above) also applies here. We take as our null hypothesis that the population is described by the bounded model, Eq. 3, with each of the components (juvenile and adult survival, and reproductive rate) of the growth rate, Eq. 4, arising independently of each other and of population size. We again use simulation (10 000 replicates, drawing the sur-

vival and reproductive rates from a normal distribution with the moments given in Table 1) to construct the expected distribution of correlations between each of the vital rates and population size. This experiment illustrates that only the observed correlation of $\rho = -0.68$ between adult survival and population size is significantly more negatively correlated with population size than expected under the null hypothesis ($P < 0.05$, one-tailed test).

TABLE A1. Quantiles of the distribution of Spearman rank correlations of $\ln(\lambda_t)$ against $\ln(N_t)$, when different models are fitted to the growth rates constructed from the survival and reproductive rates from Stacey and Taper's (1992) banded Acorn Woodpeckers.

Model [‡]	Quantiles of the distribution of rank correlations, $\rho(\ln(\lambda_t), \ln(N_t))^\dagger$					
	5%	10%	40%	50%	60%	95%
$\ln(\lambda_t)$ excluding observed, emigration, Eq. 4§						
random walk	-0.78	-0.72	-0.50	-0.43	-0.37	-0.13
logistic	-0.95	-0.93	-0.83	-0.80	-0.77	-0.50
θ -logistic	-0.87	-0.82	-0.62	-0.55	-0.50	-0.12
$\ln(\lambda_t)$ including observed emigration, Eq. 6						
random walk	-0.78	-0.72	-0.48	-0.40	-0.33	-0.18
logistic	-0.95	-0.93	-0.83	-0.80	-0.77	-0.52
θ -logistic	-0.87	-0.82	-0.63	-0.58	-0.53	-0.17

[†] Each distribution was constructed from 10 000 simulations of 9 yr.

[‡] Model parameters are given in Tables 2 and 3.

§ Observed correlation $\rho = -0.72$.

|| Observed correlation $\rho = -0.75$.