

A METAPOPOPULATION MODEL OF THE PEREGRINE FALCON IN CALIFORNIA: VIABILITY AND MANAGEMENT STRATEGIES¹

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Abstract. We modeled the Peregrine Falcon (*Falco peregrinus anatum*) population in California to determine its viability under different management strategies by modifying Lefkovich stage class matrix models to include the introduction of captive-reared birds and the dynamics of two subpopulations linked by migration. The model projections using published parameter values indicated that the population would not sustain itself without supplemental introductions. Sensitivity analysis suggested that enhancing adult survivorship is more effective than enhancing fledging success to achieve a viable population. The model with connected subpopulations predicted fewer pairs than did nonspatial models and indicated that concentrating management efforts on the healthier, high-density population in northern California, rather than on the poorly performing population in central and southern California, would yield the largest overall population sizes.

Fits of the model to yearly population data from 1980–1989 accurately predicted the size of the southern subpopulation, but slightly underestimated the size of the northern subpopulation, by six pairs. The model fit well when we excluded birds on newly discovered sites that possibly were active in previous years. Increasing northern adult survivorship to predict northern population sizes adequately led to a viable population exhibiting a source–sink relationship between subpopulations. Our results provide insight into the critical data to collect and the most successful strategies to execute in a management program, and give further indication of the importance of spatial structure to the dynamics of populations.

Key words: demography; endangered species; *Falco peregrinus*; management; metapopulations; population models; source–sink populations.

Mathematical models can be useful tools in conserving endangered or exploited species. Models often clarify the critical data required to monitor the health of a population of interest adequately, aid in projecting the outcome of current management strategies, and point to the most effective management strategies given several alternatives (Mertz 1971, Crouse et al. 1987, Lande 1988, Doak 1989, Getz and Haight 1989, Menges 1990). In addition, it has become increasingly apparent that the spatial structure of populations often has important effects on population dynamics (Andewartha and Birch 1954, Huffaker 1958, Levins 1969, 1970, Gadgil 1971, Lidicker 1975, Levin 1976, Gill 1978, McMurtrie 1978, Van Horne 1983, Roughgarden et al. 1984, Vance 1984, Holt 1985, Kareiva 1986, 1987, Pulliam 1988). Therefore, incorporating population substructure into models and population monitoring schemes may be critical to predict future population dynamics accurately, which in turn may lead to new

or different management options (Lande 1988, Pulliam 1988, Doak 1989). Here we present a model that incorporates spatial population structure and analyze it in the context of different management options for a population of an endangered species, the Peregrine Falcon (*Falco peregrinus anatum*) in California. Within the limits of available data, we demonstrate how this approach might usefully apply to the assessment of peregrines and other endangered species.

THE CALIFORNIA PEREGRINE FALCON POPULATION

Population history

The Peregrine Falcon, a bird of cosmopolitan distribution (Cade 1982), experienced drastic population declines in the northern hemisphere associated with the advent and use of persistent organochlorine insecticides at the close of World War II (Peakall 1967, 1970, 1974, Ratcliffe 1967). The case of the Peregrine Falcon is unique in conservation biology because both its decline and subsequent local recovery after the use of pesticides was restricted have been well documented (see Hickey 1969, Cade et al. 1988). In some areas, such as Great Britain, the peregrine recovered “on its

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FIG. 1. Map of California indicating the general areas occupied at present by the two core subpopulations of Peregrine Falcons. Dark shading: northern subpopulation; light shading: mid to south coast (southern) subpopulation. The few territories present in the San Francisco Bay area, the Channel Islands, and the Sierra Nevada Mountains were also included in the southern subpopulation in our analysis.

own" (Ratcliffe 1980). In the United States, aggressive management and captive propagation were required to reintroduce the bird on the East Coast (Barclay and Cade 1983).

In California, peregrine eyries were previously distributed along the coast, on offshore islands, throughout the inner coast ranges spanning the length of the state, in several east-west transverse ranges, and in portions of the Cascade and Sierra Nevada mountains (Thelander 1977). Peregrines reached their greatest breeding densities at coastal locations (Thelander 1977) and in the Channel Islands (Kiff 1980). Thelander (1977) collated 200 known nesting locations for the state, excluding the Channel Islands, and for the latter, Kiff (1980) reported 20 historical eyries. Thus, a total of 220 eyries have been documented in California. This number may still underestimate the former population size, because some regions of the state, such as the north interior, now support nearly double the number of eyries that had been historically reported. It seems very likely that California at one time supported at least 250–300 peregrine eyries.

The decline of the Peregrine Falcon in California largely mirrored that in the eastern United States, except that it was more protracted and did not lead to complete extirpation. Nevertheless, by the early 1960s most breeding peregrines had disappeared from coastal locations, and the majority of nests in the southern portions of the state were abandoned (Herman et al. 1970). The population may have reached its lowest level by the late 1960s and early 1970s. A check of 98 nesting locations in the state in 1970 yielded peregrines at only four sites, two of which fledged young (Herman 1971). Thelander (1977) estimated that by the mid 1970s, only a core population of 20–30 pairs existed in the northern inner coast ranges (north interior), with another 5–10 pairs distributed throughout the rest of

the state. Management efforts begun at this time concentrated on increasing the core population in the north interior and saving the few remaining pairs on the central coast of California (Walton et al. 1988).

Management, current status and spatial patterns

Between 1977 and 1988, captive-hatched young were regularly introduced throughout California by adding them to wild eyries, using hacking techniques (releases from artificial nest sites), and cross-fostering young peregrines in the nests of Prairie Falcons (*Falco mexicanus*). In these years, captive-hatched young comprised anywhere from 5 to 49% of the proportion of young fledged, and the observed number of active peregrine eyries rose from 7 to 82 (Linthicum 1989). The extent to which this increase in eyries represents an actual population increase is difficult to determine, because some eyries were located simply by increased survey effort (Kirven et al. 1988). After 1988, manipulation of peregrine eyries was curtailed in the northern interior portion of the state to allow researchers to assess the natural productivity of the birds in this region, while the mid- and southern-coastal eyries were still actively manipulated (Fig. 1, Kirven et al. 1988, Linthicum 1989).

As of 1989, there were 90 active peregrine nests in California, with 68% of the nests located in the north interior coast ranges, 17% along the mid-south coast, and the remaining 16% located in various southern California coastal cities, the Sierra Nevada mountains, and San Francisco Bay area. Thus, two areas of the state, the north interior and the mid-south coast, support two core populations of peregrines (Fig. 1). From 1980 to 1989, the number of young fledged per year from active, nonmanipulated nests averaged 1.40 in the north interior, but only 1.06 young in the remaining population to the south (Kirven et al. 1988, Linthicum 1989). The mid- and south-coast birds exhibit extremely low natural production, and continue to accumulate high levels of DDE (1,1-dichloro-2,2-bis(*p*-chlorophenyl)ethylene) and other anthropogenic compounds, whereas fewer north-interior birds show high levels of contamination (Fyfe et al. 1988, Linthicum 1988, Peakall and Kiff 1988, Walton and Thelander 1988, Monk et al. 1989).

The two core populations of peregrines now breeding in California (north interior and mid-south coast) are for the most part isolated from peregrines breeding elsewhere in North America. Historically, peregrines have been sparse breeders in the western Great Basin country of eastern Washington, Oregon, Nevada, and eastern California (Bond 1946). Nevada had no breeding pairs as of the mid-1980s (Ryser 1985), Oregon has 13 sites, but these are failing worse than the California birds (J. E. Pagel, *personal communication*), and Baja California, while supporting a population in the

Gulf of California, has lost most of its peregrine eyries located along the Pacific coast (Porter et al. 1988). Healthy populations appear to exist in the southern Rocky Mountains and portions of Arizona (Ellis 1988), but to date there is no evidence of emigration from those areas into California (B. Walton, *personal communication*). In addition, the distances between populations makes such emigration unlikely (Cade et al. 1988:94).

THE MODELS

A model of Peregrine Falcon populations was previously presented by Grier (1980, Barclay and Cade 1983, Grier and Barclay 1988) who used Monte Carlo simulations to account for possible demographic stochasticity. With different combinations of demographic parameters thought to encompass likely values from natural populations, this model predicted a range of dynamics encompassing increasing and decreasing population trajectories. Results of this model with demographic parameters adjusted to produce a static population (i.e., neither growing nor declining on average) in a deterministic model demonstrated that the probability of extinction caused by demographic parameters after 35 yr was extremely low for population sizes of >100 birds (Grier and Barclay 1988).

Our models differ from those of Grier (1980, Grier and Barclay 1988) in that they are deterministic, incorporate introduced fledglings and simple spatial substructure, and use data from natural populations to test the validity of the model and to make predictions about likely population trajectories. We present deterministic models both because population sizes are currently large enough that effects of demographic stochasticity will be small, and because they clearly indicate the most likely trajectory of the population, providing easier comparisons between different management strategies. However, we considered the effects of environmental and demographic stochasticity in different parameters, within the limits of available data, by calculating confidence intervals for population growth rates as outlined in Caswell (1989).

We used modified Lefkovich stage class matrix models (see Caswell 1989, Getz and Haight 1989), which operate on a discrete time scale and predict population sizes at time $t + 1$ by multiplying population sizes at time t by a projection matrix containing the transition probabilities of surviving, reproducing, and growing from one class to another. These models include the Leslie (1945) matrix familiar to most ecologists, but also come in other forms that are not necessarily divided into populations of single-year age classes. Initially, our model included two stages: non-breeding (i.e., 1-yr-old) birds and breeding (i.e., paired, territorial) adults (Fig. 2). In their basic form, Lefkovich models assume a single, well-mixed population with no spatial structure and no density dependence in the variables, assumptions that we relax below. Thus

they assume homogeneous probabilities of survivorship and breeding success within each stage, independent of other factors such as age. We adopted a convention used in most demographic models by only modeling the dynamics of females. Our model structure also assumed a uniform **age of first reproduction at 2 yr** (see Ratcliffe 1980). In addition, we modified the model to include **birds introduced** as fledglings, the current management technique. Our model without spatial structure thus took the form:

$$\begin{bmatrix} F_{t+1} \\ N_{t+1} \end{bmatrix} = \begin{bmatrix} 0 & yb \\ r & s \end{bmatrix} \times \begin{bmatrix} F_t \\ N_t \end{bmatrix} + \begin{bmatrix} yI/2 \\ 0 \end{bmatrix}, \quad (1)$$

where b is annual number of female young fledged per paired, territorial female, y is the probability of fledgling survival to age 1, r is the probability of age 1 birds surviving and recruiting to the breeding population, s is the annual survival probability of birds 2 yr of age or older, I is the total number of captive-reared fledglings released annually (therefore $yI/2$ is the number of females released that survive to the following breeding season), F_t is the number of nonterritorial females (age 1 birds) at time t , and N_t is the number of paired, territorial females at time t . The break between time intervals implied by the structure of a discrete model is important to identify and to resolve with population census points; **our model structure implies censuses of peregrine populations are taken at the start of the breeding season.**

This basic model can be solved analytically for conditions where the territorial population is unchanging ($N_t = N_{t+1}$), leading to the following equation:

$$1 = ryb + s + ryI/(2N). \quad (2)$$

Here N is the number of paired territorial females when the population is unchanging. In the absence of population supplements, if the right side of Eq. 2 (i.e., $ryb + s$) is greater than or less than 1, the population of paired, territorial females will increase or decline, respectively.

As discussed above, the location of active nest sites and the observed variation in local demography within the California population suggested the presence of at least two subpopulations, a violation of the assumption of homogeneity in demographic parameters inherent in Eq. 1. Specifically, fledging success depends on whether falcons nested in the southern or northern portions of their range (Monk et al. 1989). **Other spatial subdivision** might be present in this population (e.g., **Sierra Nevada Mountain vs. coastal birds** within the southern subpopulation), but we only considered the case of two subpopulations because the current data did not permit a finer resolution.

We developed an expanded model based on Eq. 1 to account for differences in reproductive success by linking two populations with a migration rate (Fig. 2). Here, a larger matrix was required, yielding the following Eq. 3:

$$\begin{bmatrix} F_{n,t+1} \\ N_{n,t+1} \\ F_{s,t+1} \\ N_{s,t+1} \end{bmatrix} = \begin{bmatrix} 0 & y_n b_n & 0 & 0 \\ r_n h & s_n & r_n m c & 0 \\ 0 & 0 & 0 & y_s b_s \\ r_s m c & 0 & r_s h & s_s \end{bmatrix} \times \begin{bmatrix} F_{n,t} \\ N_{n,t} \\ F_{s,t} \\ N_{s,t} \end{bmatrix} + \begin{bmatrix} f y_n I/2 \\ 0 \\ (1-f) y_s I/2 \\ 0 \end{bmatrix}, \quad (3)$$

where m is the probability of a nonbreeding female leaving a subpopulation, c is the probability of surviving migration, h is the probability of remaining in a subpopulation ($= 1 - m$), and f is the proportion of captive-reared fledglings introduced into the northern population; all other variables are the same as in Eq. 1, but have the subscripts n or s to refer to the northern or southern population, respectively. The transition matrix has been structured to aid in its interpretation. The 2×2 submatrices in the upper left and lower right corners represent the dynamics of the northern and southern subpopulations, respectively, and their structure is similar to that of Eq. 1, but includes migration out of the population. The 2×2 submatrices in the upper right and lower left corners represent migration from south to north and north to south, respectively. The column matrix added at the end represents the captive-reared birds introduced to the subpopulations.

Aside from the assumptions of the basic model, this model assumes equal probability of migration between any two populations, and that migration occurs only when birds are nonbreeders in their 1st yr of life (Fig. 2). Again, this set of equations can be solved for conditions where the whole territorial population does not change in size (i.e., $N_{n,t} = N_{n,t+1}$ and $N_{s,t} = N_{s,t+1}$). Without the introduction of captive-reared birds or fledgling removal, the population will be stationary when

$$1 = \frac{(1 - y_n r_n b_n (1 - m) - s_n)(1 - y_s r_s b_s (1 - m) - s_s)}{m^2 c^2 y_n y_s r_n r_s b_n b_s}. \quad (4)$$

When this ratio is less than (or greater) than 1, the territorial population will increase (or decrease).

Our analysis emphasizes the dynamics of paired, territorial females in each subpopulation (i.e., $N_{n,t}$ and $N_{s,t}$) at relatively low density. Therefore, the above models do not include negative density-dependent terms because the densities of depleted populations, such as many endangered species, are probably below those that significantly impact the abundance of limiting resources. Furthermore, floaters (unpaired or nonterritorial females > 1 yr old) are not explicitly accounted for because they are likely to be a tiny fraction of any low-density recovering population, and because it is difficult to monitor their population size accurately. Nonetheless, in order to gain a clearer picture of likely

population trajectories, when density-independent models indicated that subpopulations were growing, we altered the model during simulations to include density dependence and floaters. Our analysis of data presented by Nelson (1988) for a healthy peregrine population in British Columbia indicated that density dependence acted through recruitment rates to limited territory openings, rather than by changing fecundity or adult survivorship (see also Newton 1988). Therefore we placed a cap on the breeding density that could be attained in each subpopulation (T_x), based on historical estimates of the breeding population size in California (100 pairs in the north, 120 pairs in the south, see Thelander 1977). When one subpopulation saturated all of its territories in a simulation in the absence of supplemental introductions, we changed the model to incorporate density-dependent recruitment to the territorial populations and permitted those birds that did not recruit to remain in the nonterritorial population as floaters. Thus, if the northern subpopulation reached its maximum ($T_n = 100$), we changed the model to:

$$\begin{bmatrix} F_{n,t+1} \\ N_{n,t+1} \\ F_{s,t+1} \\ N_{s,t+1} \end{bmatrix} = \begin{bmatrix} d_n h & y_n b_n & d_n m c & 0 \\ 0 & s_n & 0 & 0 \\ 0 & 0 & 0 & y_s b_s \\ r_s m & 0 & r_s h & s_s \end{bmatrix} \times \begin{bmatrix} F_{n,t} \\ N_{n,t} \\ F_{s,t} \\ N_{s,t} \end{bmatrix} + \begin{bmatrix} -(1 - s_n) T_n \\ (1 - s_n) T_n \\ 0 \\ 0 \end{bmatrix}.$$

In this model nonterritorial birds ($F_{n,t}$ and $F_{s,t}$) now include both 1-yr-old birds and floaters (unpaired or nonterritorial females 2 yr of age or older) in each subpopulation. Here, the column vector representing introduced birds in Eq. 3 is absent, and a new vector is included that accounts for a constant rate of recruitment of nonterritorial birds to the northern territorial population as a result of adult mortality. In our simulations, we assumed that the annual survivorship of floaters in subpopulation x (d_x) was the same as that for territorial adults (s_x).

PARAMETER ESTIMATES

Estimates of the parameters (Table 1) came from several sources. We attempted to derive as many of the parameters as possible from the California population (Linthicum 1989, Monk et al. 1989), but this was not always possible. Estimates of the paired, territorial population were derived from direct counts, classified by subpopulation. Because Peregrine Falcons are an endangered bird species, total territorial population counts are feasible, their presence in an area is noticed, and a great deal of effort is expended to determine the location of all nesting pairs. As a result, compared to other natural populations, the current es-

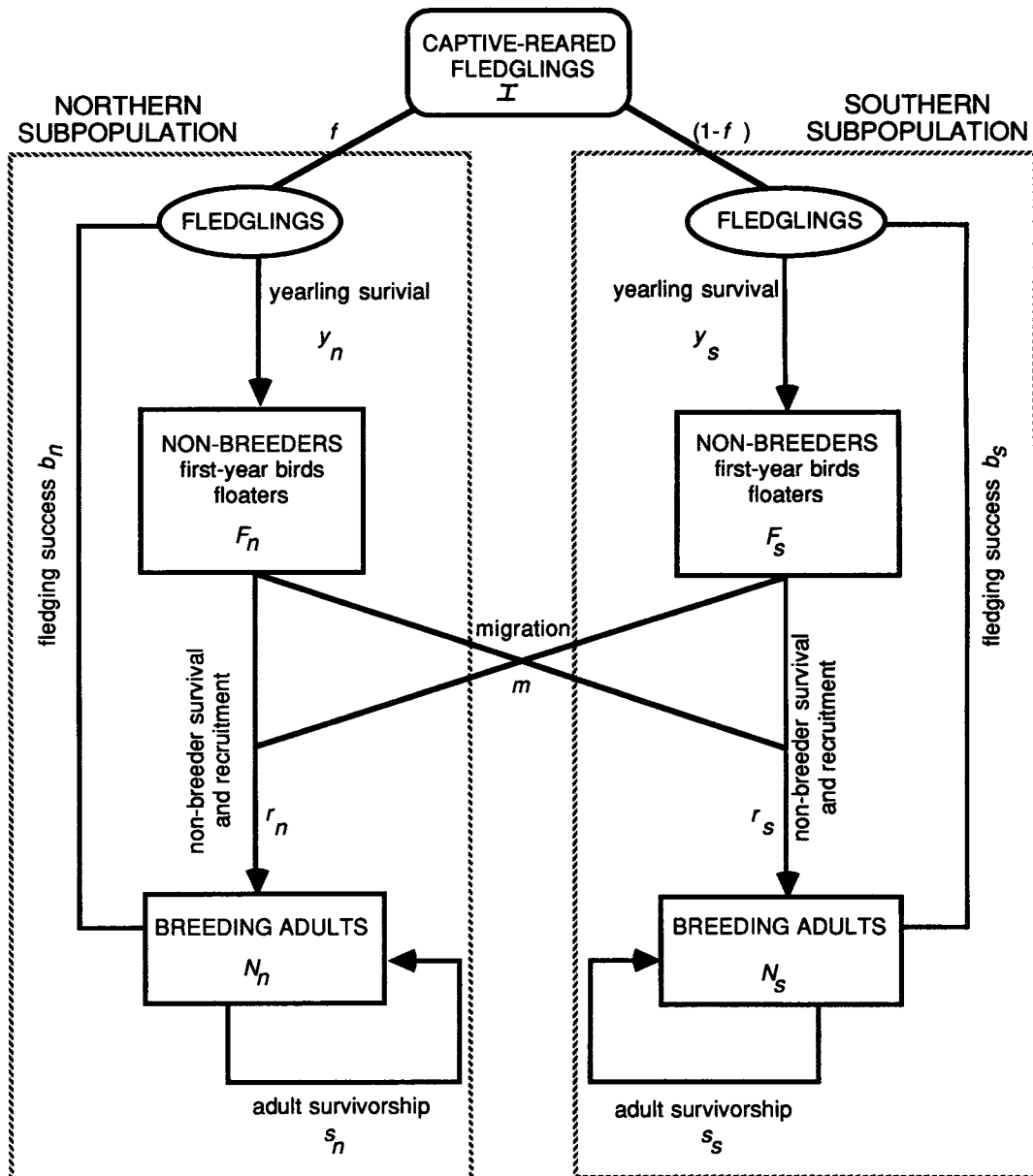


FIG. 2. Life cycle flow diagram of the Peregrine Falcon used to guide the structure of the density-independent metapopulation model developed in this paper. The flow diagram assumes a uniform age at first reproduction of 2, contains two subpopulations (boxes) linked by migrating nonbreeders, and includes the introduction of young produced in captivity. Arrows represent the transitions from one stage (delineated by boxes) to another over the course of a year. Intermediate stages that birds pass through during the year (e.g., fledglings), represented by ovals, are not explicitly part of the model. Parameter abbreviations used in the model are presented in italics.

timates within California probably represent a fairly complete accounting of the size of an approximately closed breeding population ranging across a large geographic area. The annual number of captive-reared fledglings introduced and the known number of naturally produced fledgling birds are also reported for California, classified by the subpopulation to which they belong (northern or southern). Finally, no separate information on the survivorship of fledglings to age 1

(y) or the probability of 1-yr-old birds surviving and recruiting to the territorial population was available. However, we could estimate the recruitment rate of fledglings to the territorial population ($y \times r$), based on the rate that introduced, marked fledglings entered the territorial population in California. We then partitioned the recruitment rate of fledglings to the territorial population into its component parts by assigning y as the mean of 1st-yr survivorship data summarized

TABLE 1. Parameter and response variable definitions, initial estimates, standard deviation estimates, and sources for simulations of both unstructured and spatially structured models.

Basic (unstructured) model	
Variables	
N = number of paired, territorial females*	90
F = number of age 1 (nonterritorial) females*	55
Parameters	
b = annual number of female fledglings per paired, territorial female*	$0.69 \pm 0.11\dagger$
y = probability of fledglings surviving to age 1‡	$0.36 \pm 0.05§$
r = probability of age 1 birds surviving and recruiting to territorial population*·‡	$0.72 \pm 0.05§$ $r \times y = 0.26^*$
s = probability of survival by a territorial adult to the following year‡	$0.77 \pm 0.08¶$
I = number of captive-reared fledglings introduced*	0 or 50
Metapopulation (spatially structured) model	
Variables	
N_n = number of territorial females, north*	60
N_s = number of territorial females, south*	29
F_n = number of nonterritorial females, north*	19
F_s = number of nonterritorial females, south*	20
I = number of introduced fledglings*	0 or 50
Parameters	
b_n = annual number of female fledglings per territorial female, north*	$0.71 \pm 0.11\dagger$
b_s = annual number of female fledglings per territorial female, south*	$0.53 \pm 0.24\dagger$
y_n = probability of fledglings surviving to age 1, north‡	$0.36 \pm 0.05§$
y_s = probability of fledglings surviving to age 1, south‡	$0.36 \pm 0.05§$
r_n = probability of nonterritorial females recruiting to the breeding population, north*·‡	$0.72 \pm 0.05§$
r_s = probability of nonterritorial females recruiting to the breeding population, south*·‡	$0.72 \pm 0.05§$ $r_n \times y_n = 0.26^*$
s_n = annual probability of survival by a territorial female, north‡	$0.77 \pm 0.08¶$
s_s = annual probability of survival by a territorial female, south‡	$0.77 \pm 0.08¶$
m = probability of a nonterritorial female migrating into the other subpopulation#	$0.27 \pm 0.05§$
f = fraction of captive-reared fledglings introduced into the northern subpopulation	0 or 0.5 or 1.0

* Source: Linthicum (1989).

† Standard deviation of annual fledging success derived from the variance in the mean average annual fecundities of the California population for 1980–1989.

‡ Source: Ratcliffe (1980).

§ Standard deviation derived from that expected in a binomial distribution of the parameter.

|| Sources: Mearns and Newton (1984), Nelson (1988).

¶ Standard deviation of adult survivorship derived from the data in Ratcliffe (1980), Mearns and Newton (1984), and Nelson (1988).

Source: Tordoff and Redig (1988).

in Ratcliffe (1980) for peregrine populations throughout the world, and then indirectly calculating r from the ratio of the recruitment rate of marked fledglings to estimated 1st yr survivorship $[(r \times y)/y]$. This procedure seemed reasonable because of the close match between the ry estimate from California (0.26), and the average survivorship to age 2 reported for other falcon populations (0.26 ± 0.04 , Ratcliffe 1980).

Three parameter estimates were not available for the California population. We estimated adult survivorship from the data reported in Ratcliffe (1980), Mearns and Newton (1984), and Nelson (1988), based on peregrine populations in Sweden, North America, Germany, Finland, Scotland, and British Columbia. Migration rates and the cost of migration between subpopulations were also unavailable for California,

so they were estimated from the distance between the point of release and the breeding site of introduced female falcons in the midwestern United States (Tordoff and Redig 1988). Based on these movement data, we estimated the probability of a bird successfully migrating between populations as the fraction of birds that moved > 500 km, the geographic distance between the northern and southern peregrine population centers in California. This estimate included both the probability of leaving a subpopulation (m) and the cost of migrating between subpopulations (c), but the relative contribution of each could not be determined. In our analysis, the cost of migration was assumed to be negligible ($c = 1$).

For the purposes of simulations of the metapopulation model, we used starting values for the variables

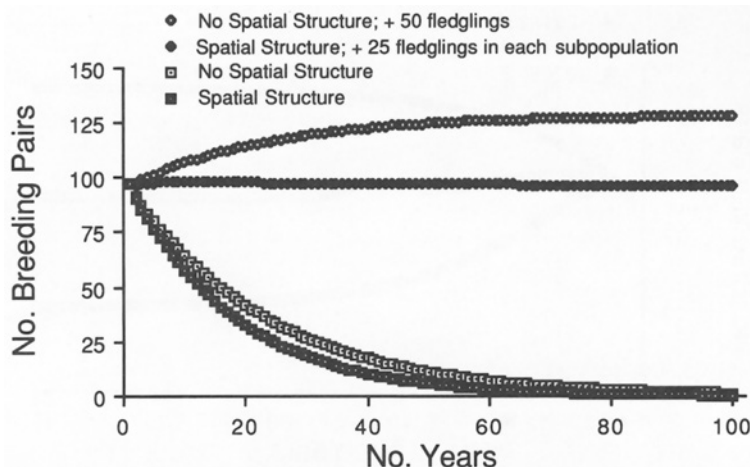


FIG. 3. Projected population dynamics of territorial Peregrine Falcons based on unstructured or spatially structured models with and without the introduction of supplemental fledglings from captive-rearing programs.

derived as follows: (1) the number of breeding females was taken directly from the number present in 1989 in each subpopulation, and (2) the number of non-breeding females was calculated by adding half the number of birds introduced in 1988 to the product of half the average number of young fledged per breeding pair and the number of breeding pairs in 1988, and multiplying this sum by the estimated 1st-yr survival (y). Starting values for the model without spatial structure were the sum of those calculated for each subpopulation in the metapopulation model in order to compare the effect of adding the model structure. Because the models eventually converge to a stable class distribution, the accuracy of these starting values is not critical to the final outcome of the model, but does affect the details of the model dynamics during the first decade of population projections.

We also derived parameter values from a second population, that of Great Britain, to examine the usefulness of our approach to other settings. We obtained estimates of fledging success (0.53 ± 0.10) and population growth rate from Table 18 in Ratcliffe (1980), and adult survivorship (0.91 ± 0.03) from Mearns and Newton (1984). We assumed that the probability of fledglings becoming territorial birds was 0.26, the value reported for California birds (Table 1) and the average survivorship to age 2 reported in Ratcliffe (1980).

MODEL RESULTS

Projecting future dynamics

Simulation of, and analytical solutions to, the basic model without spatial structure suggested that the Peregrine Falcon population in California **could not sustain itself without supplemental fledgling introduction**. Simulations showed the territorial population converging to a constant size with fledgling introductions, but declining to extinction without introductions (Fig. 3), and the calculated growth rate of the territorial popu-

lation (R) was 0.96. When the growth rate was < 1 , the size of the territorial population converged to a constant value determined directly by the rate of fledgling introduction (Eq. 2). This result emphasizes that captive propagation programs alone do not enhance a species' chances of survival on its own, even though its population size may show dramatic increases leading to apparent stability in response to this strategy. The 95% confidence intervals of the net reproductive rate (calculated following the procedures outlined in Caswell 1989) ranged from 0.80 to 1.10, thus encompassing increasing and declining population dynamics. This range of dynamics is much wider than those typically found by Grier and Barclay (1988) for a given set of parameters because our estimates of variance

TABLE 2. Sensitivity of population growth rate (R) to model parameters (defined in Table 1), and the change required in a single parameter to obtain a viable population ($R = 1.0$). Sensitivity is the change in R per unit change in a parameter, elasticity is the proportional change in R per proportional change in a parameter.

Parameter	Change required for $R = 1$	Sensitivity	Elasticity
Basic model ($R = 0.9574$)			
b	0.69 – 0.88	0.22	0.16
y	0.36 – 0.46	0.42	0.16
r	0.72 – 0.93	0.21	0.16
s	0.77 – 0.82	0.84	0.68
Metapopulation model ($R = 0.9438$)			
b_n	0.71 – 1.10	0.14	0.11
b_s	0.53 – 1.02	0.11	0.06
y_n	0.36 – 0.56	0.28	0.11
y_s	0.36 – 0.69	0.17	0.06
r_n	0.72 – 1.11*	0.14	0.11
r_s	0.72 – 1.38*	0.08	0.07
s_n	0.77 – 0.85	0.70	0.57
s_s	0.77 – 0.88	0.51	0.42
m	0.27 – -0.18*	-0.12	-0.04

* Biologically unfeasible (must be between 0 and 1).

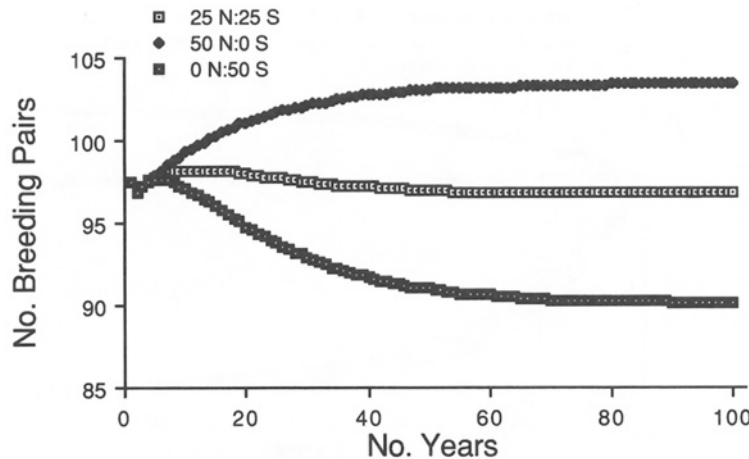


FIG. 4. The effect of differences in the strategy of allocating 50 introduced fledglings to either or both of two subpopulations within a structured territorial population of Peregrine Falcons in California (fledglings introduced into the healthier northern population and/or the poorly performing southern population).

include an element of environmental stochasticity (which changes mean parameter values) as well as demographic stochasticity; therefore the confidence intervals are larger relative to those expected in the binomial and multinomial random distributions used by Grier (1980).

Investigating the sensitivity of R to changes in different parameters provided some insight into the most effective management strategies when several may be possible (Table 2). Sensitivity is defined as the absolute change in population growth rate per unit change in a particular parameter with other parameters held constant ($\partial R / \partial x$), elasticity as the proportional change in growth rate to a proportional change in a parameter $[(x/R)(\partial R / \partial x)]$, Caswell 1989]. Elasticity and sensitivity give a measure of the relative importance of a particular parameter to overall population growth rate (the larger the value, the more important it is), and provide a standard means to compare life history strategies among different populations or species. In our simple model, to increase R from 0.96 to 1.0 required elevating survivorship to age 1 (y), survivorship and recruitment rate of 1-yr-old birds to the territorial population (r), or annual per-capita fledgling production (b), by 28% (Table 2). Notice that the fledgling success required to attain a static population (0.88) is higher than the annual production goal of 0.75 fledglings per breeding adult stated in the Pacific Coast Peregrine Recovery Plan (United States Fish and Wildlife Service 1982). In contrast to fledgling success and probability of recruitment to the territorial population, raising the survivorship of territorial birds (s) by only 6% achieved the same result (Table 2). Therefore strategies aimed at increasing adult survivorship are likely to have the greatest effect on increasing the peregrine population.

The basic model without spatial structure may be usefully applied in other situations. For example, with fledgling success and survivorship parameters derived

from Great Britain (Ratcliffe 1980, Mearns and Newton 1984), the model predicted an annual rate of increase (R) of 1.04 ± 0.04 . The calculated rate of increase in Britain, based on data taken from 1961 to 1979 (Ratcliffe 1980) was 1.03 ± 0.06 .

Models with spatial structure gave the same qualitative results as did our nonspatial models, but quantitative results differed, predicting lower territorial population sizes (Fig. 3). Again, given the a priori parameter estimates, the model predicted a territorial population decline without supplemental introduction, but at a faster rate than in an unstructured population ($R = 0.94$), and a steady size 32% lower when supplemented with captive-reared birds. The higher population sizes predicted by the unstructured model probably resulted from a bias in the estimation of fledgling success for the overall population. A much lower percentage of the total population (31%) nested in the southern subpopulation, so when the fledgling success of all nests was combined to derive a population mean, the relatively low fledgling success of southern nests was overshadowed by the numerous, more productive nests in the northern subpopulation. The 95% confidence intervals of population growth rate ranged from 0.79 to 1.09, again encompassing a range of increasing and rapidly declining population dynamics.

Sensitivity analysis of the spatial model without introduction was qualitatively similar to the simple model, in that a given proportional change in adult survivorship caused a much larger effect on population dynamics than did changes in any other parameters, but the changes required to stabilize population sizes were more pronounced (Table 2). Furthermore, the sensitivities of all northern parameters were higher than southern parameters. Management strategies that improve any demographic parameter are therefore most effective when targeted at the north. To achieve a self-sustaining population, fledgling production could be

raised by 55% in the north or 92% in the south, 1st-yr survivorship could be elevated 55% in the north or 92% in the south, or adult survivorship could be increased by 10% in the north or 14% in the south (Table 2). The changes in rates of survivorship and recruitment by 1st-yr birds (r_x) and of migration (m) required to achieve a viable population are outside the realm of biological possibility (i.e., are not between 0 and 1).

The projections from the metapopulation model also indicated that the strategy of allocating captive-reared birds affected the size of the territorial population (Fig. 4). Introducing all birds to the northern population produced a higher overall population size than did introducing all birds to the southern population, because the northern population was more viable. This result suggests that a counter-intuitive introduction strategy may be most effective at building the population to the largest size possible for a given amount of investment in captive-reared birds. Rather than supplementing the struggling population, which is likely to exhibit the lowest density, introductions will be most effective in the higher density, healthier population, at least until negative density dependence becomes strong. This result also demonstrates that the health of a population cannot be assessed from census data by terminating supplementation programs in a subset of its subpopulations.

Testing the model

Although investigating the above predictions of the models provided a useful exercise to gain general insight into the effect of population substructure and the relative impact of different management strategies (e.g., allocation of introduced birds, determining the best subpopulation to focus resources on, changing specific demographic variables, identifying critical data to collect), it was important to know how well the model predicted population dynamics in order to confidently make more refined management recommendations based on the model (for instance, when the introduction of captive-reared birds should be terminated). Annual data on population size, fledging success, and number of birds introduced were available from 1980 through 1989 to determine how well the model projected population size. We tested how well the model predicted the size of the breeding population in year $t + 1$, given the breeding population size, average fledging success, and number of birds introduced in year $t - 1$, and the breeding population size in year t . If the models fit well quantitatively, the difference between observed and predicted territorial size should not differ from 0 over a range of predicted population sizes.

Investigating the degree to which the observed breeding population sizes matched the predicted sizes yielded encouraging results (Fig. 5). The substructured model qualitatively predicted the observed population dynamics, as indicated by the lack of a relationship between errors in the model's predictions and the value

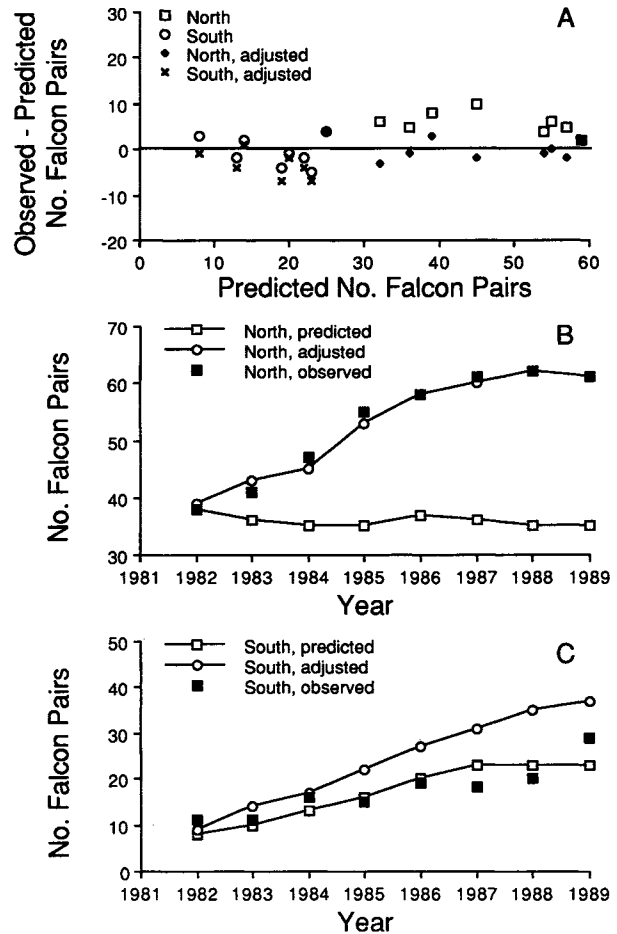


FIG. 5. Comparisons of the number of territorial pairs predicted by the model and actually observed during 1982–1989. Population sizes are shown both with and without adjustment for possible undetected breeders. (A) Plot of differences between observed and expected territorial population sizes projected over a single year against predicted population size. (B) Plot of model projections run for 8 yr compared to observed population trajectories in the northern subpopulation. (C) Plot of model projections run for 8 yr compared to observed population trajectories in the southern subpopulation.

predicted by the model (Fig. 5A). The model also accurately predicted the quantitative size of the southern breeding population (Fig. 5A), demonstrated by the close scatter of differences between observed and predicted points around zero ($\bar{X} \pm 1 \text{ SD} = -0.6 \pm 3.3$, paired t test, $p > .5$). However, the quantitative predictions of the model slightly, but consistently, underestimated the observed size of the northern territorial population by 5.75 ± 5.3 pairs (paired t test, $P < .02$, Fig. 5A). Although the systematic deviations are small, they caused widely diverging model projections in the northern subpopulation over time, whereas projections of the southern population over time were accurate (Fig. 5B, C).

Because precise predictions are a necessity in plotting

conservation strategies, we examined our model assumptions and data sources for the causes and consequences of the small but consistent discrepancy between the predicted and observed size of the northern subpopulation. Underestimating the size of the northern breeding population could have at least three causes: (1) pairs nesting in previously unrecorded locations could be discovered in the northern population at some relatively constant annual rate, (2) the parameter estimates could have been incorrect, or (3) the model was missing important aspects of Peregrine Falcon biology.

The good qualitative agreement between the model and the observed population suggests to us that the model was appropriate to this system. Furthermore, the model structure provided, if anything, optimistic population dynamics. Thus if the model were reformulated to account for delayed breeding by some birds (i.e., a floater population), for stronger negative density dependence when territories were not completely filled, for positive density dependence (Allee effect, see Allee et al. 1949, Lande 1987) at low densities, or for a cost of migration (the four aspects of the model most likely to be called into question), the model would underestimate the actual population size even more.

Newly discovered nests might have played some role in the model bias, because some of these nests could have been undetected and active in previous years, thus contributing to the future population size. Liberal estimates of the effect of undetected nests could be made by subtracting the birds in newly discovered (as opposed to historically known but previously unoccupied) territories from the observed population size and re-examining the relationship between these adjusted data and predicted population sizes. When numbers of breeding pairs from newly discovered sites were subtracted from the observed population, the difference between observed and expected population sizes did not differ significantly from zero in either the northern ($\bar{X} \pm 1 \text{ SD} = -0.5 \pm 2.1$ pairs, paired t test, $P > .5$) or the southern subpopulation -2.5 ± 3.8 pairs, paired t test, $P > .1$, Fig. 5A). Projecting the model 8 yr after adjusting for newly discovered nests suggested that the model's predictions were probably accurate in the north, and slightly optimistic in the south (Fig. 5B, C). However, the effects of undiscovered pairs may have been overestimated by adjusting the data in this manner because some of the newly discovered sites were undoubtedly newly colonized sites. Therefore, the model predictions may still have been underestimates.

Errors in parameter estimation could also have affected the accuracy of the model's predictions. The number introduced into each subpopulation in each year ought to be correct. Errors in estimates of per capita number of young fledged and probability of fledgling recruitment to the territorial population were probably also not important, both because they came from data taken on the California population with rea-

sonable sample sizes ($n > 475$), and because the analysis of sensitivities and elasticities of R to different parameters (Table 2) showed that small errors in these did not greatly affect the behavior of the model. Nonetheless, more accurate information on whether probability of fledgling recruitment differs between captive- and naturally reared birds, or between northern and southern subpopulations, would be desirable. Errors in estimates of the probability of migration between populations might also have contributed to some extent, because estimates of migration between subpopulations were not based on California data. However, the projected population size was extremely insensitive to migration rate, and even eliminating migration would not lead to a viable population (Table 2). In contrast, estimates of adult survivorship were a potentially important factor. These estimates were not derived from the California population, and the model was most sensitive to changes in adult survivorship (Table 2). Thus the values of adult survivorship we used may have underestimated those in the northern subpopulation.

We used the model to estimate actual adult survivorship values in both subpopulations, assuming the other parameters were close to being correct, by determining what level of adult survivorship was required to predict the observed size of the territorial population in year $t + 1$, given observed fledging success per territorial female, territorial population size, and number of young introduced in year $t - 1$, and the territorial population size in year t . Using this procedure, our estimate of adult survivorship in the southern subpopulation (0.80 ± 0.32) did not differ significantly from the original estimate of 0.77 ($P > .75$), but our estimate in the northern subpopulation (0.91 ± 0.07) was significantly greater than 0.77 ($P < .001$). Our re-estimated adult survivorship for the northern subpopulation is comparable to the highest value recorded for peregrines (Mearns and Newton 1984).

Metapopulation model with recalculated survivorship

Given the significantly different model-derived estimates of adult survivorship in the northern subpopulation, we again used the model to predict the expected dynamics of the territorial population in the absence of captive-reared birds. With the new northern survivorship estimate, the model indicated that the population would probably be self-sustaining (Fig. 6), and demonstrated an interesting source-sink substructure (Fig. 7).

The model demonstrated that populations with this source-sink substructure have several interesting properties. First, the northern (source) subpopulation sustained the southern (sink) subpopulation; if migration between subpopulations was eliminated, the northern population persisted ($R = 1.08$), but the southern population went extinct ($R = 0.92$, Fig. 7A). In a related

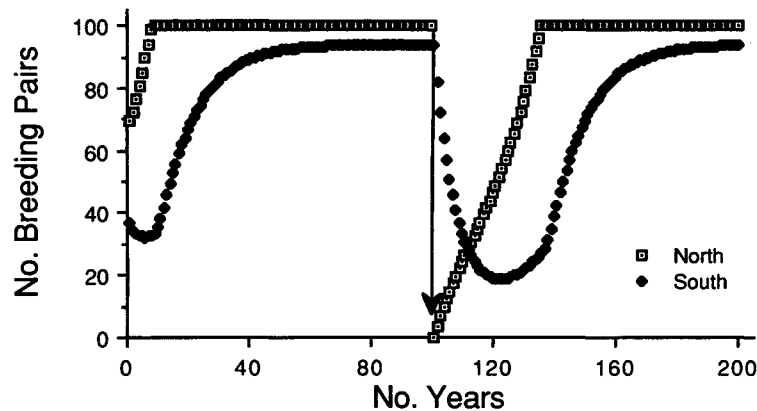


FIG. 6. Projected dynamics of the northern and southern Peregrine Falcon territorial subpopulations in California without supplemental fledgling introduction, using adult survivorship estimates generated by the model. At 100 yr, the northern subpopulation was set to 0 (local extinction) and the simulation continued to determine the ability of the southern (sink) subpopulation to rescue the northern (source) subpopulation.

manner, when the southern population was linked to the northern population, the total population size was larger than when neither was linked together or when the sink population was absent (Fig. 7B), because the sink contributed some reproductive productivity, and

provided more birds with a habitat they could survive in. Second, although the sink population could not maintain itself, it could be important to maintaining the entire population. If a catastrophic event led to the extinction of the northern subpopulation, the southern

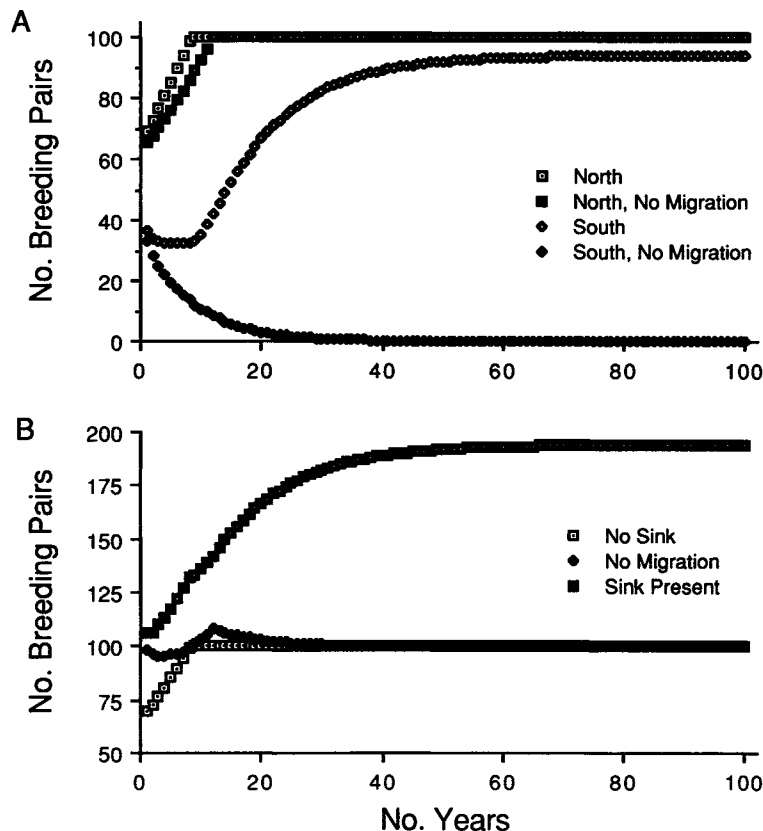


FIG. 7. Source-sink dynamics of the Peregrine Falcon territorial population in California using adult survivorship values estimated by the models. (A) Population trajectories of the northern (source) and southern (sink) subpopulations with and without migration between subpopulations. (B) The total falcon population size projected for a population with source-sink substructure. Open squares: no sink population present; solid diamonds: source and sink subpopulations not linked together by migration; solid squares: source and sink subpopulations linked by migration.

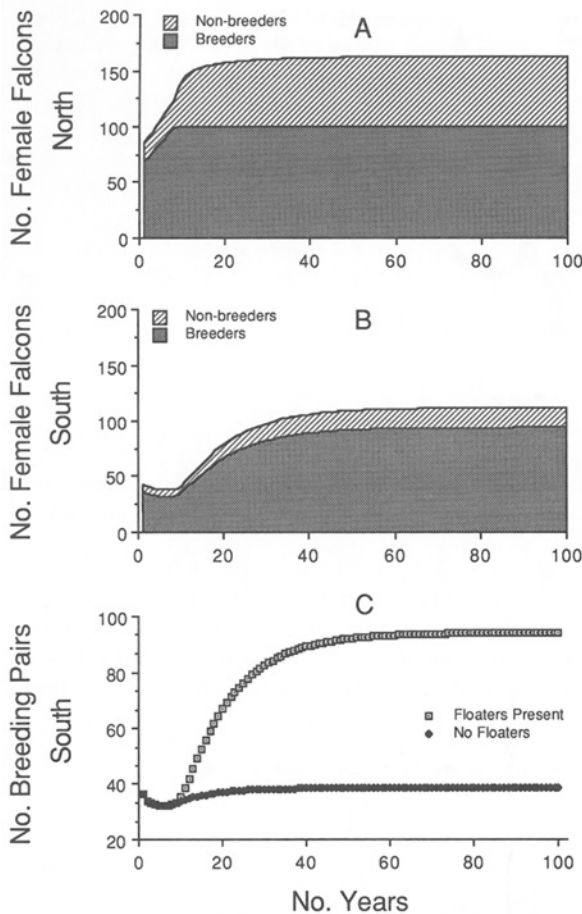


FIG. 8. Patterns and consequences of nonterritorial birds to Peregrine Falcon population dynamics exhibiting source-sink substructure. Stage class composition of (A) the northern subpopulation, and (B) the southern subpopulation. (C) The effect on sink population sizes of nonbreeding birds older than 1 yr of age.

subpopulation could rescue the entire population as a portion of its offspring migrated into the source area (Fig. 6), assuming that the migrants would experience the demographic characteristics of the northern population once they arrived.

Not surprisingly, the class structure of the population also varied depending on the source-sink characteristics of each subpopulation and whether territories were saturated (Fig. 8). Nonterritorial birds (including age 1 birds) comprised 16 and 20% of the total number of birds in the northern and southern subpopulations, respectively, when territories were not saturated, but in the northern source population, they comprised 38% of the total number of birds under territory-limited conditions (Figs. 8A, B). Thus if data on the number of nonterritorial members of subpopulations are available, comparing their contribution to the total population may provide better insight into the relative demographic health of different subpopulations than just knowing overall population size (see Van Horne 1983).

Simulations of the population without floaters (i.e., assuming that birds that did not recruit to the population at age 2 died) suggested that the migration of nonterritorial birds (> 1 year old) from the source to the sink population strongly affected the abundance of territorial birds in the sink (Fig. 8C). Including floaters in the model elevated the expected number of breeding birds in the south from ≈ 39 to 94 pairs.

DISCUSSION

Examining the models presented here provides potentially useful information for the management of populations of Peregrine Falcons, and probably other endangered or threatened species as well, in at least three ways. First, the model emphasizes the critical data that should be collected as part of a recovery project in order to determine the health of the population. In particular, it is essential to obtain better information on adult survivorship, dispersal rates between subpopulations, and subpopulation-specific recruitment rates. Given the large amount of effort already devoted to enumerating the peregrine nesting populations in California and the ready access to captive-reared fledglings, this information could be obtained without much additional effort by implementing a more detailed scheme of color-banding adults and fledglings.

Second, the model can be used to project population dynamics under current management strategies, given accurate parameter estimates. In this case, the metapopulation model predicts a decrease to 39 breeding pairs in the northern subpopulation, and an increase to 52 pairs in the southern subpopulation, given the present levels of introduction of captive-reared fledglings (≈ 50 birds per year in the south) and our a priori parameter estimates.

Third, the model can be used to compare population dynamics under different alternate management strategies. Our analysis touches on four issues: (1) examining the effects of introducing birds on future population viability, (2) comparing likely population trajectories with and without introduction, (3) comparing different strategies of allocating management effort among subpopulations, and (4) comparing the effectiveness of strategies that focus on different population parameters.

The model clarifies the role of population supplementation as a conservation strategy. Specifically, it serves as a reminder that, although introducing captive-reared birds may be extremely successful in increasing the population size of a species, as is superbly exemplified by the Peregrine Falcon reintroduction program, population supplementation does not contribute to the inherent viability of a population. Instead, it is a tool to avert extinction related to small population size arising from stochastic population processes, Allee effects (positive density dependence, see Allee et al. 1949, Lande 1987), or inbreeding problems.

Viability of a population arises from management strategies that change the reproductive and survival parameters of the wild population that initially caused the demise of the species.

Our conclusions about the likely effect of terminating fledgling introductions are less certain, given the possible errors in the estimates of adult survivorship in the model, and the possible errors in population size estimates used to test the model. The model predictions bracket declining and increasing population growth rates, depending on the adult survivorship estimates used. If the underestimate of the northern subpopulation by the model results from a systematic discovery of previously nesting pairs, then the model predicts that the California population cannot sustain itself. Moreover, in light of our sensitivity analysis (Table 2), even if an average of only 2.5 (43%) of the sites newly discovered in each year were active in previous years, the re-estimated adult survivorship in the northern subpopulation would be insufficient to maintain a healthy breeding population. However, if the high adult northern survivorship estimated by the model is approximately correct, that is $> 57\%$ of newly discovered nests are newly colonized sites, the population will sustain itself, and the subpopulations should cease growing in a decade if estimates of upper population sizes in the north are correct. Clearly a more accurate knowledge of adult survivorship is required to make firmer predictions. Our results thus emphasize that more research regarding this one crucial demographic rate is essential before firm decisions regarding the continuation of peregrine releases can be made.

The model makes interesting predictions about where management strategies (allocation of captive-reared birds, changing demographic parameters) would be most effectively concentrated. Specifically, it shows that management is most effective when targeted toward the relatively healthiest subpopulations, which will often exhibit higher population densities. For example, although supplementing subpopulations that have the poorest demographic performance or population density may appear on the surface to be the best course of action because these subpopulations have the greatest risk of local extinction, this strategy is not the most effective at maintaining the largest population of the species as a whole *when* the subpopulations are linked by migration and the healthier subpopulations are not experiencing strong density-dependent control. Likewise, sensitivity analysis indicates that management strategies that influence any demographic rate in the natural population will be most effective when targeted toward healthier subpopulations. Our density-dependent modifications to the model also suggested one technique to assess the relative health of populations: comparing the ratio of nonbreeders to breeders.

We also used the model as a tool to estimate adult survivorship in the two subpopulations, assuming that the other measured parameters were accurate. Al-

though population parameters estimated in this manner should not be considered correct without independent validation of the model, these estimates are useful both to highlight the importance of collecting solid survivorship data, and to explore thoroughly the realm of likely population trajectories. With the northern adult survivorship estimated from the model, the predicted behavior of the breeding population without the introduction of captive-reared juveniles changed from a declining population to a viable population with source-sink substructure. With this type of substructure, the source population maintains the sink population, whereas the sink population can rescue the source population in the face of local extinction and enhances overall population size, as other investigators have found in empirical and theoretical studies (Gill 1978, Harrison et al. 1988, Pulliam 1988). With source-sink substructure, it is important to identify and execute management strategies that maintain source subpopulations.

The sink dynamics exhibited by the southern subpopulation (and perhaps the northern subpopulation too, depending on survivorship values) remain an area of concern, because they may not be natural. Historically, the breeding population of southern birds numbered at least 120 pairs (Thelander 1977), 28% higher than the projected size of 94 pairs that would be attained under current conditions with our estimate of northern adult survivorship, thus indicating that this subpopulation once exhibited healthier demographic parameters. Therefore the changes in environmental conditions that led to the original falcon decline, specifically heavy DDE and dieldrin residues (Peakall 1967, 1970, 1974, Ratcliffe 1967), have not been reversed sufficiently to permit a viable southern subpopulation, in spite of the fact that the use of DDT for most purposes has been legally banned in the United States since 1972. The poorer performance of the southern birds is consistent with the higher pesticide inputs associated with agricultural run-off and industrial dumping. In addition, although the focus of research has been on nesting failure resulting from the effects of DDE on eggshell thinning, the estimates derived from the model suggest that the southern population may also be experiencing reduced adult survivorship. Because the population dynamics are most sensitive to changes in adult survivorship, it may be worthwhile to investigate possible factors, such as chemical residues, that may be depressing this parameter in the south.

Finally, the results from our models point to the general importance of recognizing the spatial substructure within exploited or endangered populations for several reasons. First, predicted overall population sizes will often be lower, and dynamics may even differ in spatially structured compared to unstructured models because estimates of population parameters will be biased upwards and because the assumptions of the simple models are violated (i.e., probabilities for each stage

in the transition matrix are not the same for all members of the population). Second, management considerations can account for specific needs of each subpopulation and the population as a whole (Pulliam 1988). In the case of Peregrine Falcons, identifying potential source-sink structure suggests which subpopulations should have highest conservation priority, and determining population substructure in general indicates how population supplementation might be most effective. Third, our results and those of others (Gilpin 1987, Quinn and Hastings 1987) also clearly demonstrate that population subdivision may affect the extinction probability of a species, either because populations can be rescued if extinction of local subpopulations is not temporally correlated, or because fragmented subpopulations of small size have a higher probability of going extinct all at once because of demographic stochasticity. With the increasing recognition of the importance of spatial population substructure, data collection efforts should be organized to probe for variations in demographic parameters and to measure dispersal among subpopulations in species of particular conservation interest.

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