ESTIMATION OF HABITAT-SPECIFIC DEMOGRAPHY AND POPULATION GROWTH FOR PEREGRINE FALCONS IN CALIFORNIA

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Abstract. American Peregrine Falcons in California (*Falco peregrinus anatum*) have been managed in one of the largest reintroduction programs in the history of endangered species management. However, as for most other widespread natural populations, the spatial and temporal dynamics of California Peregrines have remained poorly understood. Long-term monitoring data on this highly managed species present a unique opportunity for retrospective analysis of the factors contributing to the successful recovery of Peregrine Falcons in California, as well as demographic differences between habitat types. We used a newly developed mark–recapture model (the Barker model), which allows the simultaneous use of recaptures, dead recoveries, and live resightings, to provide estimates of first-year, second-year, and adult survival of Peregrine Falcons in the mid- and south-coast regions of California. Annual survival rates for second-year and adult Peregrines were estimated at 86%. Through model fitting, we show positive effects of urban habitats on first-year survival. In our best-fit models, first-year birds fledged in urban areas had a survival rate of 65%, whereas rural (non-urban) first-year survival was only 28%. The introduction method also influenced first-year survival after dispersal; in rural areas, estimated survival of hacked young (after independence) was lower than estimated survival of wild-reared young. We also show that birds in urban habitats have significantly higher fecundity rates than birds in rural habitats, even though the fecundity of rural breeders has increased significantly over the last two decades. We argue that the strong habitat differences in first-year survival combined with lower fecundity rates in rural habitats (due to slower improvement in eggshell thinning rates) facilitates spatial structuring of the California Peregrine population. Matrix population models constructed for both rural and urban habitats support this assessment. The temporally averaged population growth rate in urban habitats was estimated as $\lambda = 1.28$, compared to $\lambda = 0.99$ in rural habitats. Yearly analytical λ values in rural habitat predict declining population growth ($\lambda < 1$) throughout the 1980s and increasing population growth ($\lambda > 1$) in the 1990s due to improved reproductive performance. These results indicate that the introduction effort was pivotal in recovering the rural population in this portion of its former habitat, because intrinsic growth rates alone would have been insufficient to yield the observed population recovery.

Key words: American Peregrine Falcon; DDT; eggshell thinning; endangered species; Falco peregrinus anatum; *habitat heterogeneity; hacking; mark–recapture; population modeling; recovery; source–sink; structured population.*

INTRODUCTION

The dynamics and management of endangered species is one of the central concerns of conservation biology and has spawned a more general renewed interest in spatial and temporal population dynamics. However, in most cases, wildlife managers must plan for species survival and recovery using extremely limited data. Typically, we know very little about the factors influencing the viability of endangered species, because most species are not studied extensively until they become imperiled. The uncertainty created by this lack of information has plagued recovery plans (Griffith et al. 1989), leading to disagreement about the type and extent of management actions needed for rare species and the appropriate conceptual frameworks to analyze management decisions.

Additionally, there is a rich body of theoretical work that highlights the importance of spatial and temporal variation in population demography for understanding long-term population dynamics and persistence of species (Gilpin and Soulé 1986, Pulliam 1988, Kareiva 1990, Lande 1993, Kendall et al. 2000). Some endangered populations have been highly managed and monitored for several decades, enough years to allow an assessment of the empirical evidence for the prevalence of these factors that have received so much attention

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in the theoretical literature. Because of these available data, we now have an opportunity to analyze past management activities to better understand the population biology of endangered species, the importance of factors controlling recovery, as well as more fundamental questions regarding spatial and temporal dynamics of wild populations. Indeed, these data sets may now provide the best information with which to understand the structure and dynamics of any wide-ranging species (Sarrazin and Barbault 1996).

For the most intensively managed populations, this type of analysis must be able to assess population viability in the face of management actions, such as sustained introductions or translocations, which may have substantially altered population trends (e.g., Sarrazin et al. 1994). To our knowledge, this is an emerging complication with population viability assessment that has received little attention. Much of the monitoring data that exists for many managed populations is in the form of population censuses or count data. Because releases and translocations may bolster numbers and alter age structure, they will often obscure the connection between population censuses and underlying vital rates. Thus, the true status of a population may not be accurately discernable from count data alone (van Horne 1983). In the most extreme case, extensive population augmentation could make it impossible to distinguish management-induced population increase (i.e., from large-scale introductions) from real amelioration of demographic rates. To resolve these complications, a framework is needed to assess population health in the face of augmentation by distinguishing between the demography of the natural population and the demography of introduced animals. These demographic rates can then be incorporated into population models to assess both intrinsic population growth of the wild population and the overall observed population growth expected due to the introduction of animals.

The American Peregrine Falcon (*Falco peregrinus anatum*) in California is an exceptional candidate for an analysis of population structure and recovery from near extirpation. The recovery of the Peregrine Falcon across the United States was hailed as an important success story of the Endangered Species Act when the Peregrine was delisted from the endangered species list in 1999 (Cade et al. 1997, Millsap et al. 1998, Federal Register 1999). Besides its apparent success, many other characteristics of the recovery of the Peregrine Falcon population in California make it suitable for analysis. Most notable among these are: (1) a long-standing recovery effort from 1977 to 2001, (2) an extensive banding and monitoring program over the same 24-year period, and (3) considerable knowledge of the biology of the species. Much of the monitoring data that exists for the American Peregrine Falcon is in the form of population censuses, and previous efforts to model the California Peregrines have been hampered

by the lack of reliable estimates of adult survival for the species in California (Wootton and Bell 1992).

In this study, we make use of recently developed mark–recapture methods to provide the first estimates of management- and habitat-specific survival rates for Peregrines in California. The Barker model (Barker 1997, 1999) allows for the use of data collected opportunistically, such as dead recoveries or occasional resightings by wildlife observers. Using this model, we have been able to make use of a remarkably disparate set of banding data, which includes planned releases, nest bandings of wild young, routine recaptures, unplanned recaptures, volunteer and researcher sightings, and chance recoveries of dead individuals. Our objective was to estimate age-specific survival rates and to make statistical inferences about the demographic factors that contributed most to the recovery of this population. We also examined how the treatment of reencounter parameters, such as recapture and recovery rates, may influence the ability to correctly estimate survival rates of interest.

Using habitat-specific fecundity trends and the estimated survival rates in a time-varying matrix model, we estimated population growth rates for Peregrines in rural and urban habitats of mid- and south-coast California. The population models indicate strong differences in population growth rates between rural and urban habitats. In addition, our population modeling indicates that the rural subpopulation was intrinsically failing ($\lambda < 1$) throughout the 1980s, when census counts recorded a steady increase in the breeding population. Thus, for Peregrine Falcons in our study area, the effect of population augmentation explains the discrepancy between population monitoring data (census counts) and demographic models of population growth. As our study shows, analytical population growth rates may be more indicative of true population health than census counts for recovering species subject to intensive introduction programs.

Peregrine Falcon management in California

The Peregrine Falcon suffered drastic global population declines with the advent of organochlorine pesticides, specifically DDT, in the post-World War II era. These declines were first noticed in the Northern Hemisphere by North American and British ornithologists and falconers, who undertook substantial efforts to keep the Peregrine from going extinct. DDT use was restricted in the United States in 1972 and the American Peregrine Falcon was immediately listed following the passage of the Endangered Species Act.

American Peregrine Falcons in California declined throughout the 1950s and 1960s, paralleling the decline of Peregrine Falcon populations around the world. Bond (1946) estimated that there were 100 nesting pairs in California in the era preceding DDT use, although this number is now considered to be an underestimate (B. J. Walton, *personal communication*). In 1970, a

TABLE 1. Sample sizes of Peregrine Falcons banded as hacked fledglings or in the nest of wild falcons in the south coast of California, and recaptures, recoveries, and resightings by age class for birds included in the mark–recapture analysis.

	Bandings§		Reencounters		
Natal habitat and age	Hacked	Wild-reared	Recaptures	Recoveries	Resightings
First-year urban	23	43	1	4	9
First-year rural	225	380	6	23	9
Second-year			15	5	8
Year 3–5			26	12	8
Year 6–8			30	2	4
Year 9–11			15	0	3
Year 12+†			9	2	6
Adult‡			5	1	4

† Two recaptures and one resighting occurred in the 16th year.
‡ Age unknown.
§ Banding information here is for first-year birds only; it does not include five birds banded in their second year and 41 birds banded as adults.

comprehensive (although not exhaustive) survey of California Peregrines by Herman (1971) identified only two breeding pairs and four territories. In 1976, the Santa Cruz Predatory Bird Research Group (SCPBRG) initiated one of four release programs across the country, starting with only a few breeders gathered from falconers and a handful of eggs salvaged from the few remaining wild eyries (Peregrine nest sites). Efforts aimed at augmenting the California population included: fostering (placing captive-hatched young in wild nests), cross-fostering (placing captive-hatched young in the nests of wild Prairie Falcons, *Falco mexicanus*), and hacking (releasing fledglings from hack boxes without the presence of adults). Many of the eggs hatched in captivity were wild eggs, salvaged from nest sites in California.

Reintroduction efforts were fairly constant and sustained from 1977 until 1992, when all fostering and cross-fostering efforts and most hacking efforts ended. Management objectives have focused on monitoring and increasing productivity since the large-scale reintroduction efforts ceased in 1992. Since then, translocation of young from specific urban eyrie sites identified as having particularly high fledging mortality risks or from eyries close to colonies of other endangered birds has been the focus of continued management (Bell et al. 1996, Walton 1998).

The number of fledgling Peregrines reintroduced into California since 1977 is substantial: ~800 birds have been released. During the same period, the number of censused pairs occupying territories has increased from seven active sites in 1977 to >140 active eyries by 1997 (Walton 1998). Similar recoveries have been achieved in other regions of the continent through management efforts and natural recovery (Barclay and Cade 1983, Tordoff and Redig 1997, Millsap et al. 1998).

History of bandings and observational data

Peregrine Falcons handled by the SCPBRG were given a USFWS band, including all birds released by hack-ing, fostering, or cross-fostering, as well as wild youngsters banded in the nest and adult birds that were captured. After 1992, alphanumeric bands were also used, enabling visual identification of individuals. The data collected by SCPBRG included any later detection of banded birds, including band recoveries from dead falcons, numerous resightings by biologists, and recaptured Peregrines trapped by the SCPBRG and others (Table 1).

From the late 1970s until 1992, the SCPBRG performed close monitoring of known pairs and their young as part of their reintroduction efforts. During the breeding season, when pair monitoring and reintroductions were taking place, observers recorded band readings for birds that they could identify. Before 1992, statewide and regional surveys were conducted by the SCPBRG with federal and state agencies such as U.S. Forest Service, Bureau of Land Management, California Department of Fish and Game, National Park Service, and others. Since 1992, territories have been monitored opportunistically by a network of agency biologists, falconers, and volunteer naturalists.

Although the monitoring of California Peregrines has been intensive over the last 20 years, the collection of band record information has been fairly opportunistic. Because of habitat and monetary constraints in the montane and northern regions (Interior; Fig. 1), specific band record information relied almost exclusively on chance reportings by bird-watchers or USGS Bird Banding Laboratory reports of deceased falcon band recoveries in these remote areas. The mid- and south-coast regions were the only regions of the state where annual visits and monitoring were routine enough to provide useful band record information. For this reason, we constrained our mark–recapture analysis to this region of the state (Fig. 1).

METHODS

Formulation of mark–recapture model

In order to make use of the disparate sources of banding data for California Peregrines, we adopted a
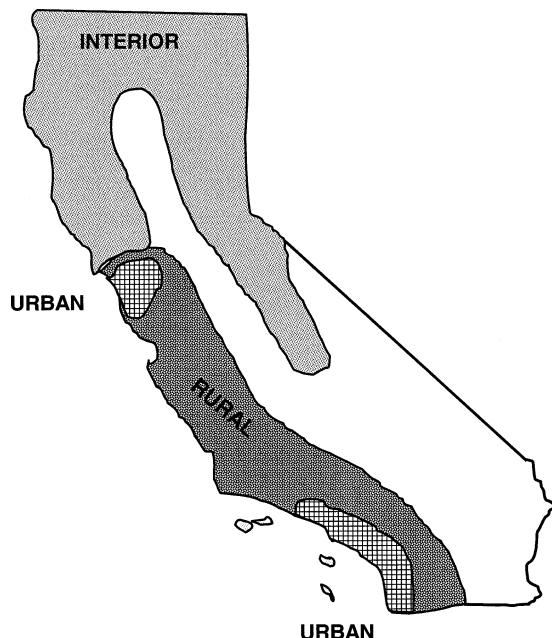
FIG. 1. Peregrine Falcon habitat in California, USA. A large portion of the statewide population exists in the interior region, where banding records were insufficient for inclusion in the mark–recapture analysis. Banding records used in this study were constrained to mid- and south-coast California. Within the study region, rural habitats were distinguished from urban habitats.

recently developed mark–recapture model that allows for the simultaneous use of live recaptures, dead recoveries, and live resightings (Barker 1997). In Barker's model, live resightings can occur throughout the year, between recapture sessions. For Peregrines, this is a very useful extension, because it allows the inclusion of over 20 years of occasional and opportunistic resightings by an eclectic group of wildlife biologists and volunteer observers (Table 1).

Because Barker's model includes live recaptures, live resightings, and dead recoveries, several additional parameters must be estimated aside from traditional survival and recapture rates (Barker 1997). The model's basic parameters as described in Hall et al. (2001) are as follows:

ϕ_i is the probability that an animal alive at time i is alive at time $i + 1$;

p_i is the probability that an animal is captured at time i, given that it is alive and at risk of capture at time i;

r_i is the probability that an animal that dies in the interval between i and $i + 1$ is found and has its band reported;

R_i is the probability that an animal alive in $i + 1$ is resighted alive during the interval between i and $i + 1$;

R_i' is the probability that an animal that dies in the interval between i and $i + 1$ is resighted alive in this interval before it dies;

F_i is the probability that an animal at risk of capture at i is at risk of capture at $i + 1$; and

F_i' is the probability that an animal not at risk of capture at i is at risk of capture at $i + 1$.

Encounter histories

Encounter history files were constructed for almost all birds ($n = 718$) handled by the SCPBRG in the mid- and south-coast regions of the state from 1977 until 1999. Because the most intensive capture and observational effort occurred during the spring breeding season (15 March–15 June), we defined the recapture period to span this important period; birds recaptured or resighted during the spring breeding period were recorded as recaptures. Birds seen or recaptured alive during the remainder of the year (15 June–15 March) were classified as resightings, and those found dead during this same period were coded as dead recoveries.

Stage structure

We modeled survival rates as stage dependent, using the three stage classes commonly recognized in Peregrine Falcons: first-year birds, second-year birds, and adults (Ratcliffe 1980, Wootton and Bell 1992). Generally, Peregrine Falcons do not start breeding until at least their second or third year of life, although one-year-old birds occasionally breed (Newton 1988). We modeled separate survival rates for first-year birds, second-year birds, and adult birds two years and older.

Trap dependence

Many of the "recaptures" recorded each year were actually resightings made during the spring breeding period. Adult breeding birds occupying territories that were visited annually by the SCPBRG during the breeding season were often identified and recaptured over many consecutive years, leading to a recapture rate dramatically higher than for most individuals. Therefore, the recapture rate of these birds was modeled separately, following the convention used for trap-dependent animals (animals that change their behavior after an initial handling, becoming either trap-shy or trap-happy; Sandland and Kirkwood 1981, Pradel 1993). In our case, there was not a behavioral response by the birds to observers, but rather a propensity on the part of the observers to return to known eyrie sites. Trap dependence was modeled by fitting a separate recapture rate for all adult birds (≥ 2 years old) in all years following their first recapture (Pradel 1993).

Habitat effects

In addition to the effects of stage and trapping history, we also modeled the effects of natal habitat on survival. The most relevant distinction between habitat types that may affect survival rates is the difference between urban and non-urban habitats. Other studies (e.g., Cade and Bird 1990) and anecdotal observations have suggested that survival rates may be higher in

urban areas because they offer an abundance of prey, a lack of competition with other raptor species, and an absence of most natural predators. Conversely, non-urban regions that represent natural habitats (and are free of urban mortality factors like wire, window, and vehicle strikes) might be expected to support higher demographic rates. Considerable debate still exists on the importance of these two habitats for Peregrine population health and continued management priorities (Bell et al. 1996, Cade et al. 1996). We also note that some Peregrines will range widely, thus experiencing many different habitats during their daily hunting forays (B. J. Walton, *personal communication*). For model nomenclature, we labeled non-urban habitats as "rural," which includes a variety of wild and natural areas outside of major cityscapes, including the Big Sur coastline, the Channel Islands, and other rural areas in southern and central coastal California.

Habitat effects were incorporated by recording the habitat type (urban or rural) where first-year birds fledged from the nest. We cannot account explicitly for birds that move between these two habitats, so this classification is at best an approximation of the habitat in which birds survived their first year. Although we were interested in exploring the habitat effect on survival for adults as well as first-year birds, it was impossible to establish urban and rural status past the first year of life for most of the birds in the data set.

We also considered the possibility that habitat may affect recapture, resighting, and recovery rates. Generally, urban birds are seen or recovered more often than birds in remote rural settings. In order to accurately estimate survival rates in the face of this observer bias, we modeled habitat effects on the recapture, recovery, and resighting parameters (collectively referred to as reencounter parameters). Again, habitat effects could only be tested for the first year of life and therefore stage structure was always present in models including these effects. We did not model habitat effects in the R' parameter (seen given found dead), because there were too few recoveries of this type to estimate habitat-specific parameters.

Rearing effects

A rearing effect was also tested, which compared first-year survival rates between young birds that were hacked into the wild and fledglings that were reared by wild falcon parents. The objective of this survival comparison was both to better understand the relative success of birds introduced through hacking methods and, more generally, to understand the expected contribution of these introductions to the historical population recovery. Due to the very few instances of birds hacked in urban settings, our comparison of hacked vs. wild-reared young was only performed for birds released or naturally fledged into rural habitats. Wild-reared birds (hereafter referred to as "reared") included wild-

hatched young as well as young that were fostered into wild Peregrine eyries or cross-fostered into Prairie Falcon eyries. For hacked birds, survival was compared after the fledglings reached independence from the hack site, such that known mortality events occurring during the hacking period were not included as dead recoveries. Because of this, the first-year survival rate of hacked young does not include the risky, pre-dispersal stage of a bird surviving its first year, a period that is included in the estimate of survival for wild-reared birds. Thus, we might expect hacked birds to have higher survival rates, because they only enter the study having already survived the dependence period. From a behavioral ecology standpoint, this comparison also addresses whether or not there is a fitness advantage conferred to wild-reared birds that learn to fly and hunt under the protection of wild falcon parents.

Candidate models

Including all these a priori parameter effects, we created a global model to describe the banding data (Burnham and Anderson 1998). Currently, no standard approach exists for arbitrating between parameter combinations when the conceivable number of candidate models is unmanageable (i.e., in some stepwise fashion; Burnham and Anderson 1998). Because the survival parameters are interdependent with the other reencounter parameters, it is likely that the modeling of habitat effects in these parameters will affect the precision and accuracy of survival rate estimation. In order to test the importance of individual parameters and to arrive at a best-fit model, we followed the suggestion of Burnham and Anderson (1998) and fit all possible parameter combinations, a total of 32 individual models (Table 2). Our purpose in fitting a relatively large set of candidate models was twofold. Including all possible parameter combinations allowed us to (1) find the most parsimonious model, thereby providing the best estimates of survival rates, and (2) investigate the effect that model choice has on our ability to make inferences about factors affecting Peregrine survival. All models were run using Program MARK (White and Burnham 1999).

The fit of these competing probabilistic models was assessed using the information-theoretic approach (Burnham and Anderson 1998). Akiake Information Criteria (AICs; Lebreton et al. 1992) were calculated for each model as: AIC = $-2L$(data | model$_i$) + 2k, where L(data | model$_i$) is the log likelihood of the observed encounter histories, given candidate model i, and k is the number of parameters in the model. Because AICs account for (and therefore penalize for) the number of model parameters, they provide an unbiased estimate of the support of a particular candidate model; the candidate model with the lowest AIC value has the most support from the data. AIC weights were also computed for all candidate models as follows:

TABLE 2. Parameter combinations modeled with Barker model.

Model description	Model name
Basic Barker model	$\phi(.) \ p(.) \ r(.) \ R(.) \ R'(.) \ F(.) \ F'(.)$
Survival	
Stage structured	$\phi(a3\text{-}c/c/c)$
Stage structured with habitat effects for first-year birds	$\phi(a3\text{-}hab/c/c)$
Stage structured with rearing effects for first-year birds	$\phi(a3\text{-}rear/c/c)$
Stage structured with habitat and rearing effects for first-year birds	$\phi(a3\text{-}hab+rear/c/c)$
Recapture	
Trap dependence in recapture	$p(m)$
Stage structured with habitat effects for first-year birds and trap dependence	$p(a2\text{-}hab/m)$
Recovery	
Constant	$r(.)$
Stage structured with habitat effects for first-year birds	$r(a2\text{-}hab/c)$
Resighting	
Constant	$R(.)$
Stage structured with habitat effects for first-year birds	$R(a2\text{-}hab/c)$
Resighting$'$	
Constant	$R'(.)$
Fidelity	
Random emigration	Fixed at 1
Return parameter	
No immigration	Fixed at 0
(4 survival) $\times$ (2 recapture) $\times$ (2 recovery) $\times$ (2 resighting) $\times$ (1 resighting$'$) = 32 models	

Note: Model nomenclature follows the format suggested by Cooch and White (1998). For example, $\phi(a3\text{-}hab+rear/c/c)$ indicates that survival is modeled with three stage classes (first-year, second-year, and adult), with habitat and rearing effects on the first-year survival rate, and a constant second-year and adult survival rate. For the recapture parameter, p, an "m" in the model notation indicates that trap dependence was modeled by fitting a separate recapture rate for birds subsequent to their first recapture.

$$\hat{W}_i = \frac{\exp\left(-\frac{1}{2}\Delta\text{AIC}_i\right)}{\sum\limits_{i=1}^{32} \exp\left(-\frac{1}{2}\Delta\text{AIC}_i\right)}$$

where ΔAIC_i is the difference between the AIC of model$_i$, and the AIC value of the best-fit model (Burnham and Anderson 1998).

Currently there is no straightforward goodness-of-fit test for a model structure as complex as our most highly parameterized model, which would allow detection of any significant lack of fit (overdispersion) between fitted models and the banding data. To assess the potential for overdispersion in the banding data to influence model selection, we made use of the lack-of-fit parameter, $\hat{c}$ (Lebreton et al. 1992). If the data are not overdispersed with respect to the model, $\hat{c} = 1$; values of $\hat{c} > 1$ indicate some source of lack of fit. The $\hat{c}$ parameter, properly estimated, can be incorporated into the AIC calculation, which will favor models with fewer parameters (Lebreton et al. 1992). Thus, large $\hat{c}$ values will alter model selection. Although we were unable to estimate $\hat{c}$ for our best-fit model, we incrementally increased the $\hat{c}$ parameter to find the critical $\hat{c}$ value where our current best-fit model (selected under the assumption of $\hat{c} = 1$) no longer yielded the lowest adjusted AIC value. This critical $\hat{c}$ value was calculated

to provide a measure of the robustness of our model selection to potential overdispersion in the banding data (J. D. Lebreton, *personal communication*).

Because they sum to 1, AIC weights provide a measure of the relative support of the data for each model. We used AIC weights to assess the support of sets of candidate models that differ in the inclusion or exclusion of particular effects of biological interest. This is a robust method, because parameter effects can be scored across all candidate models in which they appear (Burnham and Anderson 1998, Monson et al. 2000). However, in order to compare this method with less comprehensive tests, we also used likelihood ratio tests to ask how different nested model comparisons affected our ability to determine the significance of habitat and rearing effects on first-year survival and on reencounter parameters.

Our final estimates of the mean and variance in each parameter were calculated to account for uncertainty in model selection (Buckland et al. 1997). We first calculated the mean estimate of each parameter as a weighted average of the maximum likelihood estimate (MLE) from each model using AIC weights as the weighting factor. The estimated unconditional variance in the averaged parameter estimate was calculated similarly following Buckland et al. (1997), using the variance of the parameter estimate from each model, cal-

culated using Program MARK (Option 2nd Part; White and Burnham 1999).

Assessing temporal trends in fecundity

In order to assure that our population models were appropriate to each habitat, we estimated habitat-specific fecundity rates from the historical monitoring data. Since the recovery effort began in 1977, nest site surveys have been conducted at many of the known breeding territories in the state. For nests in our study area, wild young were counted by biologists visiting eyries during banding operations or by direct observation. Previous work by the SCPBRG has documented substantial geographical variation in the fecundity of breeding Peregrine Falcons in California, and the degree and persistence of eggshell thinning and levels of DDE, the persistent metabolite of DDT (Walton and Linthicum 1992, Walton 1998, Burns 1998). Previous work has also shown a clear relationship between eggshell thinning rates and reproductive performance in California Peregrines (Peakall and Kiff 1988). We estimated fecundity rates from these data to improve the accuracy of our population models and to connect the variable statewide fecundity rates to our specific habitats of interest (urban and non-urban areas in the mid- and south-coast regions).

Because egg collection and translocation of young birds occurred at urban and rural nest sites suspected to have thin-shelled eggs, the exclusion of these sites from yearly estimates of fecundity would lead to an overestimation of the actual fecundity rate experienced by an average breeding adult. Because of this data limitation, we employed a regression substitution approach (Little and Rubin 1987) to estimate the expected fecundity of each nest where eggs were collected. We used logistic regression to relate eggshell thickness levels to the known fate of all eggs hatched: healthy, broken, or addled in the wild. This relationship was highly significant ($n = 663$, $\chi^2 = 15.27$, df $= 1$, $P < 0.0001$), and provided a reasonable fit to the egg fate data (Pearson goodness of fit, $P = 0.2552$). Thus, we used the fitted logistic regression equation to estimate the expected number of wild young (based on thickness levels of collected eggshells) that would have been produced by managed urban nests had they been left untouched.

From these data, we calculated the mean number of wild young (pre-fledging) produced per breeding pair in both rural and urban habitats. We constrained our fecundity estimates to include only nest locations within the study area delineated by the mark–recapture analysis (Fig. 1). For rural birds, we calculated mean annual fecundity during the period 1981–1999 (n, the number of nests, varied from 5 to 27 over this time period) to account for known time trends in fecundity. We performed a linear regression of year on number of wild young per nest site to test for temporal trends in rural fecundity rates. Because most wild eggs were routinely collected for captive hatching from many urban nest

sites up until 1992, it was only meaningful to estimate urban fecundity during the period 1993–1999 (the number of nests ranges from 8 to 13 over this time period). We used a paired t test to ask if there were consistent differences in the mean number of wild young produced from rural and urban nests over this seven-year period.

In order to bolster our interpretation of habitat-specific fecundity rates, we assessed temporal trends in eggshell thinning rates for both rural and urban birds. For rural birds, we calculated average eggshell thickness during the period 1980–1998 (n, the number of clutches, ranged from 5 to 21 over this time period). We performed a linear regression of year on eggshell thickness to test for temporal trends in eggshell thickness values in rural areas. In urban areas, we were only able to estimate mean thickness values from the years 1989–1998 (the number of clutches ranged from three to 11 over this time period) because of extremely low sample sizes during the 1980s. Again, we used a paired t test to ask if there were consistent differences in mean eggshell thickness values from rural and urban clutches over this nine-year period (the urban sample size was too small for analysis in 1993). We also performed a linear regression of mean eggshell thickness on mean fecundity in the rural habitat for the years 1981–1999.

Estimation of population growth rate

We used a stage-based matrix model (Lefkovitch 1965, Caswell 2001) in order to assess the viability of Peregrine Falcons in California and to understand the population-level consequences of habitat-specific demographic rates. Matrix models combine the survival and fecundity rates of individuals (the matrix elements) to estimate a long-term population growth rate (λ, the dominant eigenvalue; Caswell 2001). Because of their reliance on measured demographic rates instead of population counts, these models provide an appropriate framework to understand population health, not obscured by the historical introduction efforts. We structured our population model to parallel the stage- and habitat-specific survival rates estimated from the mark–recapture analysis; thus, we modeled survival of first-year (classified as either rural or urban natal habitat), second-year, and adult stages. All birds were assumed to breed after completing their second year of life (Fig. 2; Ratcliffe 1980).

We calculated the annual population growth rate, λ, for rural and urban subpopulations separately. For the rural habitat, we separately calculated a different λ_t in each year of the study to understand the effects of the temporal trend in fecundity; calculated in this way, λ_t summarizes habitat quality for a particular set of demographic rates. Uncertainty levels in λ_t values were estimated using the "delta method" (Caswell 2001), assuming no covariance between matrix elements. The variances of fecundity and survival products (top row of the transition matrix) were estimated as the variance of the product of 1000 randomly drawn fecundity and
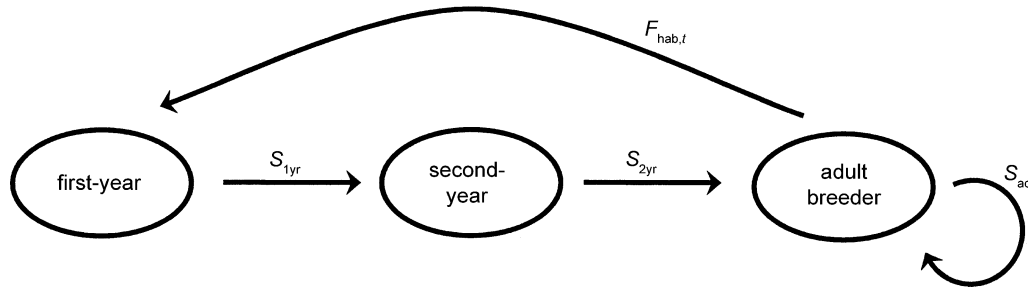
Fig. 2.   Life-cycle graph representing the stage-structured model of Peregrine Falcon population dynamics used in the matrix model analysis. The nodes represent the life stages, and the arrows represent the survival probabilities and fecundity estimates for contributions of one stage to another over a yearly time step.

survival values. Fecundity values were bootstrapped from the yearly monitoring data, and second-year and adult survival values were drawn from a beta distribution (Morris and Doak 2002), with mean and variance estimated from the mark–recapture models.

We also accounted for the effect of temporal variation in fecundity on the population growth rate in both habitats by calculating the temporal average of λ across the years of our study. This average lambda measure was calculated by multiplying all annual transition matrices together, finding the dominant eigenvalue of the product matrix, and then taking the tth root of the dominant eigenvalue as an estimate of the average λ.

RESULTS

Model selection

The analysis of a large set of models including different biological effects on survival and reencounter parameters resulted in substantial variability in survival rate estimates. In particular, variability was due to the indirect effects of including habitat on the survival and

reencounter parameters. However, the use of AIC weights to assess model support indicates that the seven best-fit models, which include habitat effects on first-year survival, recovery, and resighting parameters, have 92% of the support of the data. Our best-fit model was retained in all model selection runs with $\hat{c}$ values ≤ 2.45; thus, our model inferences are robust in the case of moderate levels of overdispersion in the banding data. The full set of candidate models tested is given in the Appendix.

Although we fit all model combinations to gauge the strength of habitat effects, in many modeling scenarios it is not practical to fit models containing all potential parameter combinations. An alternative approach often used is to perform likelihood ratio tests between only two models, which differ in the inclusion of an effect of interest (Lebreton et al. 1992). To explore the robustness of this approach, we compared the fit of pairs of nested models and found that habitat effects did not improve model fit when incorporated into the recapture parameter (Fig. 3). However, almost all model contrasts
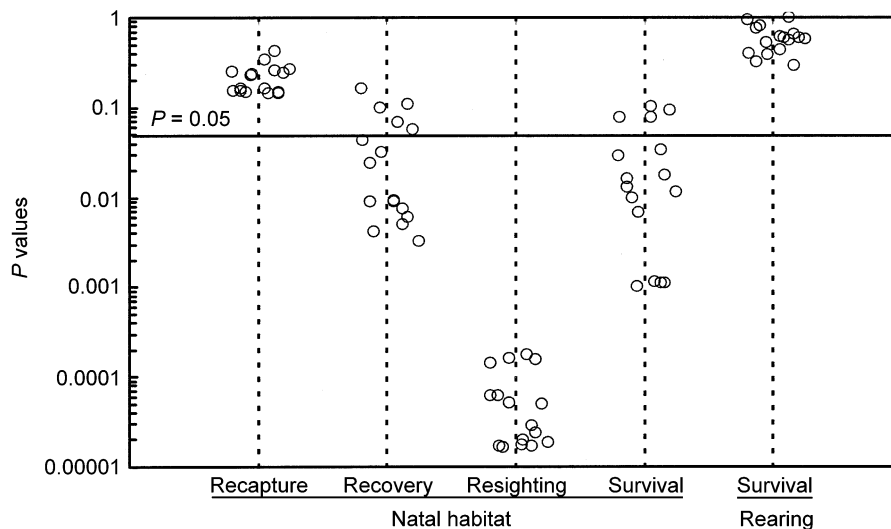

Fig. 3.   Significance of natal habitat and rearing effects on survival and reencounter parameters, with P values (note log scale) shown for likelihood ratio tests between all combinations of nested models that could be used to test the significance of a habitat or rearing effect on survival and reencounter rates.

TABLE 3. Survival estimates of Peregrine Falcons in California. Maximum likelihood estimates (MLE) of survival parameters and their standard errors from the best-fit model are shown, along with the weighted-average estimate of each MLE and its associated standard error.

Parameter	From best-fit model		From model averaging	
	MLE	MLE SE	Ave MLE	Ave SE
S_{1yr}	0.3327	0.0588	0.3760	0.0762
$S_{1yr(rural)}$	0.2708	0.0504	0.2780	0.0545
$S_{1yr(urban)}$	0.6437	0.1466	0.6500	0.1471
$S_{1yr(rural-hack)}$	0.2322	0.0724	0.2405	0.0780
$S_{1yr(rural-rear)}$	0.2794	0.0523	0.2850	0.0554
S_{2yr}	0.8701	0.0605	0.8606	0.0661
S_{ad}	0.8623	0.0243	0.8588	0.0250

Note: Subscripts denote stage class, habitat, and rearing method, following the general format of $S_{stage\ class(habitat-rearing\ method)}$.

indicated a significant effect of habitat on recovery rate (the exceptions being five model comparisons between models that did not include habitat in the survival parameter). Including habitat effects in the resighting parameter made the largest improvement to model fit: all pairwise comparisons of models that varied only in their inclusion of habitat effects on the resighting parameter were highly significant. We found a significant effect of habitat on first-year survival for all but four comparisons. The four model comparisons that did not indicate a significant habitat effect were between models that had virtually no support of the data (based on AIC weights), due to the exclusion of the habitat effect in the resighting parameter. The inclusion of rearing effects on survival did not improve model fit. Overall, these results suggest that limited likelihood ratio tests would usually, but not always, correctly identify the most important factors to include in a model.

Survival estimates

Adult and second-year survival estimates did not differ and were estimated at 0.86 ± 0.03 (mean ± 1 SE) and 0.86 ± 0.07, respectively. The survival rate for first-year birds was estimated for five different first-year groups: all first-year birds, rural first-year birds, urban first-year birds, rural-hacked first-year birds, and rural-reared first-year birds. The pooled estimate of first-year bird survival, regardless of habitat, was estimated at 0.33 ± 0.08. First-year birds fledged in urban areas had a survival rate of 0.65 ± 0.15, more than twice the survival of birds fledged into rural areas, 0.28 ± 0.06. In rural habitats, hacked birds known to reach independence had an annual survival rate of 0.24 ± 0.08, whereas the annual survival estimate for wild-reared birds, which includes pre-dispersal mortality, was 0.29 ± 0.06. Survival estimates are summarized in Table 3 as the MLE from the best-fit model, as well as the MLE weighted average from all models.

Eggshell thinning and habitat-specific fecundity

Fecundity rates of breeding Peregrines in rural habitats have increased linearly since 1981 ($F_{1, 279} = 14.20$,

$r^2 = 0.0486$, $P < 0.0002$; Fig. 4A), a trend that presumably is due to a concurrent increase in eggshell thickness measures over the same time period ($F_{1, 204} = 8.658$, $r^2 = 0.041$, $P < 0.004$; Fig. 4B). Surprisingly, a regression of mean eggshell thickness on mean fecundity in the rural habitat was not significant ($F_{1,17} = 2.09$, $r^2 = 0.1154$, $P < 0.1678$). Comparisons of these two important fecundity measures between habitat types were also significant. The number of wild young produced by urban breeders was consistently higher than that found for rural breeders ($t = -4.827$, df = 6, $P < 0.003$; Fig. 4A). Likewise, eggshell thickness levels in urban clutches have been consistently higher than those of rural clutches ($t = -11.069$, df = 8, $P < 0.001$; Fig. 4B).

Matrix model analysis

Incorporating habitat-specific survival and fecundity rates into population models reveals substantial differences in the population growth rates for Peregrines in rural and urban habitats. In rural habitats, the population growth rate from the matrix model varied over the study period from a low of $\lambda = 0.90 \pm 0.10$ (mean ± 1 SE) to a high of $\lambda = 1.06 \pm 0.10$, with a general
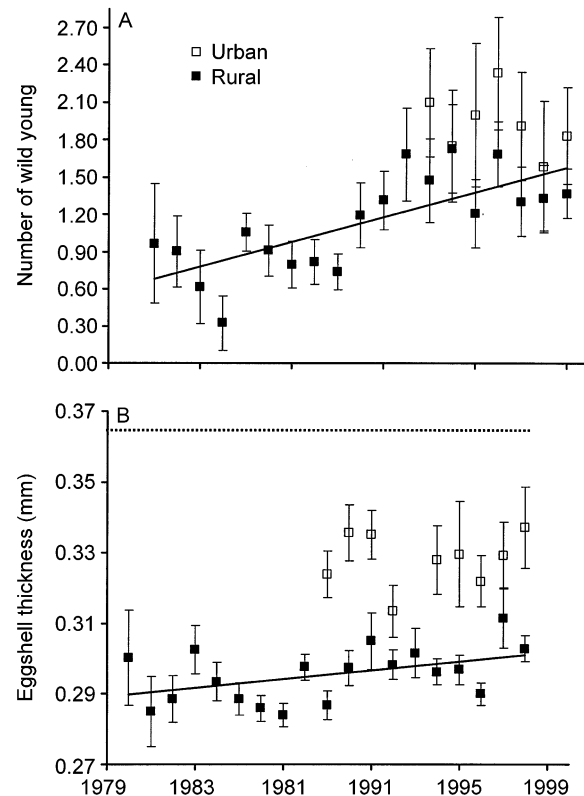

FIG. 4. (A) The number of pre-fledging Peregrine Falcon young per nest in rural and urban habitats in the mid- and south-coast regions of California. (B) Eggshell thickness values for Peregrine Falcons from rural and urban habitats. The dotted line denotes the pre-DDT average thickness of 0.365 mm.

FIG. 5. Annual population growth rates for Peregrine Falcons in rural habitats of mid- and south-coast California. Year-to-year variation is due to the incorporation of increasing annual fecundity estimates from field monitoring; all survival rates are held constant. The dotted line denotes $\lambda = 1$, indicative of a stable population.
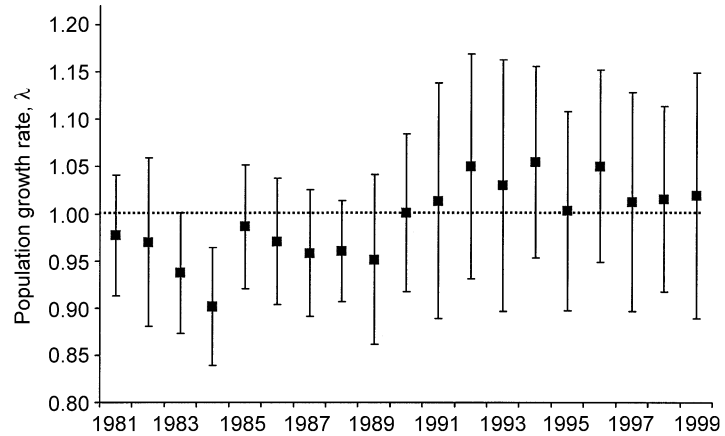
increase through time driven by the temporal trend in fecundity (Fig. 5). Based on these results, the long-term theoretical population growth rate in rural areas was <1 throughout the period 1981–1990, becoming >1 in years subsequent to 1990. However, the temporally averaged population growth rate was estimated as $\lambda = 0.993$ in the rural areas, indicating a declining population, on average, over the entire study period. The population growth rate in the urban habitat averaged from 1993 to 1999 was calculated as $\lambda = 1.280$.

DISCUSSION

Our work represents a novel and useful application of mark–recapture models to the monitoring and management of endangered species, where constraints often prevent traditional experimental design. For the Peregrine Falcon in California, our demographic analysis has allowed a deeper appreciation of the demographic contribution of introduced birds, as well as the importance of spatial structure in this recovering population. Most importantly, our approach has allowed an assessment of Peregrine Falcon population health in the rural habitat that is not confounded by the sustained

introduction program. We will discuss some of these issues in further detail.

Survival rates from opportunistic data

Our maximum likelihood estimates of first-year, second-year, and adult survival rates are the first ever reported for Peregrine Falcons in the western United States. Our estimate of adult survival (0.86 ± 0.03) is comparable to published survival estimates of other Peregrine Falcon populations (Table 4). Our survival estimate for rural first-year birds (0.28 ± 0.05) is lower than most published estimates, whereas our urban first-year bird estimate (0.65 ± 0.15) is considerably higher; first-year survival pooled over both habitats, however, is quite comparable to existing estimates (Table 4).

Overall, the Barker model provided a robust framework for modeling Peregrine Falcon survival rates based on a very disparate set of data. Our ability to make estimates of first-year, second-year, and adult survival and to distinguish first-year survival for habitats and rearing effects is most likely due to the model's inclusion of the three different sources of information (recapture, recoveries, and resightings). Because the

TABLE 4. Comparison of estimated survival rates for Peregrine Falcons in mid- and south-coast California with other studies of Peregrine Falcon demography worldwide.

Source	Region	Survival		
		First-year	Second-year	Adult
This study	California	0.38 ± 0.08	0.86 ± 0.05	0.85 ± 0.02
	California rural	0.28 ± 0.04		
	California urban	0.65 ± 0.15		
Enderson (1969)	North America	0.3		
Enderson (1969)	eastern N. America			0.75
Mebs (1971)	Finland	0.29		0.81
Mebs (1971)	Germany	0.44		0.72
Lindberg (1977)	Sweden	0.41		0.68
Newton and Mearns (1988)	Scotland	0.44		0.91
Tordoff and Redig (1997)	midwestern USA	0.16†		0.86
Enderson and Craig (1988)	Colorado			0.79
Nelson (1988)	British Columbia			0.68
Olsen and Olsen (1988)	southeast Australia			0.95

† Minimum estimate.

original monitoring program was not designed as a mark–recapture study, it is unlikely that we would have been able to derive sound estimates of survival for this managed population of falcons based on traditional mark–recapture models alone.

Our results also provide insight regarding the appropriateness and usefulness of carefully assessing optimal model complexity. In our suite of mark–recapture models, the inclusion of additional biological realism (mainly habitat effects) had a net positive effect on model fit and, thus, on the accuracy of estimated survival rates. We certainly would have arrived at biased survival estimates if we had not included habitat effects in the reencounter parameters, potentially masking the real differences in habitat-specific survival rates. It is likely that similar posthoc formulations of mark–recapture studies based on long-term monitoring data will have similar complications. For many endangered species (including the Peregrine Falcon), monitoring data are not collected with future data analysis in mind, but for a more general, ongoing assessment of management success. Thus, careful testing of habitat-specific recapture, resighting, and recovery rates may be important in studies like this one that seek to glean survival information out of disparate data sets.

Equivalence of second-year and adult survival

Results from the mark–recapture analysis show no difference between second-year and adult survivorship. The equivalence of the survival rates for these two seemingly different stage classes could arise for two different reasons. First, the advantages and disadvantages associated with nonbreeding vs. breeding may be comparable, thus conferring similar survival rates. Second, in this recovering population, most second-year birds may quickly recruit to suitable breeding territories, thereby experiencing the higher survival rate conferred by holding territory.

Breeding Peregrines nest on cliffs and similar sites, and have a high fidelity to nesting territories (Ratcliffe 1993). The establishment of a suitable and familiar territory, which is used for many consecutive years, may lower mortality risks (Ratcliffe 1980). By comparison, nonbreeding, second-year birds lack the protection and safety of a familiar territory and may risk death or injury as they test the occupancy of existing territories and move through unfamiliar areas (Ratcliffe 1980, Tordoff and Redig 1997). By this reasoning, there should be a survival advantage for adult birds, which typically recruit to a territory and establish a pair bond, over second-year birds, which may spend much or all of the second year of life searching for a territory and a mate (Ratcliffe 1993). Indeed, second-year survival has been estimated to be substantially lower than adult survival in other raptor studies (Mead 1969, Newton 1979).

Alternatively, Hunt (1998) has suggested that breeding pairs may have a higher mortality rate than non-breeding birds because of the risks associated with defending a territory and raising a brood. Increased brood size has been shown to increase mortality among Peregrine breeders (Nelson 1988). Higher survival rates for nonbreeders were documented for a raptor population in Prince William Sound, Alaska, USA, where subadult Bald Eagle (*Haliaeetus leucocephalus*) survival was estimated at 95% compared to 88% survival for adult birds and 71% for first-year birds (Bowman et al. 1995). The similarity of our survival estimates for second-year and adult birds may reflect a balance between the risks associated with breeding and the benefits of holding territory.

Alternatively, second-year birds in this recovering population may have recruited to breeding territories because of an abundance of readily available and suitable territories after the population crash. In a stable population, failure of most second-year birds to recruit to a breeding territory is more likely, based on suitable nest availability, rather than on physiological inability to breed (Hunt 1988, Newton and Mearns 1988, Ratcliffe 1993). In this growing population, with many suitable breeding territories, it is possible that second-year birds recruited to breeding territories or simply suffered very little from competition, and therefore experienced mortality risks similar to those of adult birds (Hunt 1988, Newton and Mearns 1988).

Habitat effects: rural vs. urban

Our analysis indicates that Peregrines fledged into the urban environments of California (mainly the San Francisco Bay Area and Los Angeles) have a much greater chance of surviving their first year of life than do birds fledged along the rural coastline and inland areas of southern and central coastal California (0.65 ± 0.15 vs. 0.28 ± 0.05, respectively). Urban areas have been identified as a valuable habitat resource for Peregrines in other parts of the country, notably the East Coast and Midwest (Cade and Bird 1990, Tordoff and Redig 1997). Such dramatic survival differences for first-year birds have not yet been recorded because previous analyses were unable to separate the masking effect of increased reencounter rates in urban areas from the real differences in survival between urban and rural Peregrine populations.

In their review, Cade and Bird (1990) found that urban areas are suitable for Peregrines because cities are generally devoid of natural predators, provide an abundant prey base of Rock Doves (*Columba livia*) and other avian species, and offer suitable nesting habitat in the form of skyscrapers and bridges. Documented hazards to young fledglings first learning to fly include plate glass windows, electrical wires, and busy streets. These researchers and others (Bell et al. 1996) found that bridges are particularly dangerous eyrie sites, because fledglings may land in the water on their first flight and drown.

We found a remarkably high survival rate of first-year Peregrines in urban habitats, and our work suggests, more generally, that urban areas provide Peregrines, even fledglings, with a usable and safe habitat. Our estimate of urban first-year survival is probably slightly biased toward overestimation because the SCPBRG actively removed fledglings from known problem eyries in urban settings to be released at hacksites on the coast. This careful management strategy may have prevented some first-year fatalities from occurring in urban areas, thereby artificially inflating urban survival rates. Still, the large difference in urban vs. rural first-year survival that we found is unlikely to result solely from this potential bias.

Rearing effects: hacked vs. wild-reared survival

We quantified differences in first-year survival between wild-reared fledglings and hacked fledglings in rural areas. For hacked birds, the annual survival rate presented here describes the probability of surviving for the remainder of the year after successful dispersal from the hack site, whereas the survival rate for wild-reared birds includes the pre-dispersal dependence period. To make the survival estimates of the two groups comparable, we need to consider pre-dispersal mortality rates for wild-reared young. The pre-dispersal mortality rate for wild raptor fledglings has been well documented for a variety of other species, and ranges from 11% to 31% (Kochert 1976, 1977, Konrad and Gilmer 1986, Bustamante 1993, Kenward et al. 1993, Varland et al. 1993, McFadzen and Marzluff 1996). The most comprehensive of these studies (McFadzen and Marzluff 1996) found that Prairie Falcon fledglings experienced 31% mortality during the fledging dependence period ($n = 152$ radio-tagged birds) in southern Idaho. Prairie Falcons are similar to Peregrine Falcons in many aspects of their life history and probably provide a good comparison with Peregrine Falcon fledgling pre-dispersal mortality. Assuming 31% mortality during the fledging dependence stage, the survival of wild Peregrines during the postdispersal stage would be 42% $[0.29 = (0.31)(0.42)]$. Our survival estimate for hacked young during the postdispersal stage was only 24%. The substantial difference between these two estimates suggests a clear survival disadvantage for hacked young after successful dispersal. Even if we assume a low pre-dispersal mortality rate of 11% (Kochert 1977), the difference between postdispersal survival for hacked and wild-reared young would still be meaningful at 24% for hacked young vs. 32% for wild-reared first-year birds.

Hacking has been widely acknowledged as a useful and successful tool in the reintroductions of raptors (Sherrod and Cade 1978, Newton 1979) and was certainly instrumental in the California reintroduction effort (Walton and Thelander 1988). However, the apparent reduced survival rate of hacked first-year birds after their successful introduction indicates that longer term effects are associated with the reintroduction method. Our analysis suggests that an examination of the efficacy of hacking (and other reintroduction efforts) should include a measure of the survival of released young, even after apparent introduction success. In a study similar to ours, Sarrazin et al. (1994) found lower survival rates of Griffin Vultures (*Gyps fulvus fulvus*) in the first year of their release into a recovering population, compared to naturally fledged individuals. In populations with a substantial input of introduced individuals, estimating differences in survival and other demographic rates for the introduced population may be crucial to accurately model overall population dynamics (Armstrong and Ewen 2001).

Population growth and recovery

Population growth rates calculated from habitat-specific matrix models revealed substantial differences in the performance of urban and rural subpopulations. The urban population is estimated to grow at 29% per year, a remarkable rate of growth for any raptor species. This extraordinary performance is occurring adjacent to the rural population, which, without the introductions, would have had declining population growth throughout the 1980s before becoming self-sustaining after 1989. However, detailed monitoring throughout the 1980s has documented the recovery of a breeding population (33 pairs in 1998; SCPBRG, *unpublished data*) to the same rural areas where we have estimated a declining rate of growth. This recovery trend, coupled with the known survival of hacked and fostered young, provides a clear indication of the importance of reintroductions into the rural habitats of the mid- and south-coast regions. Thus, the south-coast population appears to have recovered, based on annual population censuses. However, true demographic amelioration and an increasing rate of population growth were out of step with this management-induced recovery, and may have only recently been obtained (Fig. 5).

Given the exceptional performance in urban areas, it is tempting to suggest that these sources also may have contributed dispersers to the sink habitat along the rural coastline. Los Angeles and San Francisco are easily within dispersal range of areas such as the Big Sur Coast and the Channel Islands, regions with the highest remaining DDE levels. Although banding data confirm that dispersal between urban and rural areas does occur, movement out of the urban habitats into rural habitats has been observed only rarely. For example, we know of 15 birds that fledged or were hacked from rural habitats and were later found (usually breeding) in urban areas. By contrast, no rural breeders have been identified as originating from an urban area. However, the urban population was fairly small throughout the 1980s (ranging from two to six breeding pairs), making it unlikely that limited dispersal from urban sources had much of an influence on the rural recovery. Observed movements from rural to urban areas suggest

that Peregrines may be selecting urban areas based on higher prey abundance, higher density of breeding birds, or a general tendency to disperse from inland to coastal sites (Siemens 1993). However, as urban densities increase, the habitat quality (as perceived by dispersing Peregrines) may decline and dispersal out of these areas may become more common (Pulliam 1988).

The results of this study, indicating that substantial differences exist in the theoretical population growth rate of rural and urban subpopulations, provide a timely account of spatial structuring during the recovery of both a wild and managed population. Several authors have recently noted the paucity of strong empirical evidence of source–sink dynamics (Diffendorfer 1998, Gundersen et al. 2001), even while theoretical interest in the subject has remained high ever since Pulliam's (1988) paper on the potential for such structured populations to persist. In this system, the sink habitat was ephemeral, created by a transient environmental contaminant (DDT). This drastically reduced fecundity (causing the initial crash in the 1950s), but then was ameliorated over the course of the recovery (Figs. 4 and 5).

Numerous theoretical studies have investigated the importance of source–sink gradients, as a particular form of spatial structure, for population dynamics (Pulliam 1988, Pulliam and Danielson 1991, Watkinson and Sutherland 1995). In general, theoretical source–sink studies have highlighted the importance of studying the linkage of subdivided populations by dispersal (Kareiva 1990). More particularly, investigators have suggested that source–sink dynamics may be important in maintaining metapopulations (Crone et al. 2001), assessing viability of endangered populations (Doak and Mills 1994, Fahrig and Merriam 1994, Mace and Waller 1998), and planning effective monitoring of population trends (Doak 1995, Brawn and Robinson 1996). For Peregrine Falcons in California, we have shown habitat-specific differences in estimated population growth, but the factors controlling movement of individuals between these two habitats remain poorly understood. Based on the observed tendency of Peregrine Falcons to move from rural sink habitat to urban source habitat, it seems unlikely that classic source–sink dynamics (sensu Pulliam 1988) facilitated the recovery of the species in this portion of its former range.

Literature Cited

Armstrong, D. P., and J. G. Ewen. 2001. Assessing the value of follow-up translocations: a case study using New Zealand robins. Biological Conservation **101**:239–247.

Barclay, J. H., and T. J. Cade. 1983. Restoration of the peregrine falcon in the Eastern United States. Bird Conservation **1**:1–40.

Barker, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics **53**:666–677.

Barker, R. J. 1999. Joint analysis of mark–recapture, resighting and ring-recovery data with age-dependence and marking-effect. Bird Study **46**:S82–S91.

Bell, D. A., D. P. Gregoire, and B. J. Walton. 1996. Bridge use by peregrine falcons in the San Francisco Bay area. Pages 15–24 *in* D. M. Bird, D. E. Varland, and J. J. Negro, editors. Raptors in human landscapes: adaptations to built and cultivated environments. Academic Press, San Diego, California, USA.

Bond, R. M. 1946. The peregrine population of western North America. Condor **48**:101–116.

Bowman, T. D., P. F. Schempf, and J. A. Bernatowicz. 1995. Bald eagle survival and population dynamics in Alaska after the Exxon Valdez oil spill. Journal of Wildlife Management **59**:317–324.

Brawn, J. D., and S. K. Robinson. 1996. Source–sink population dynamics may complicate the interpretation of long-term census data. Ecology **77**:3–12.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. Biometrics **53**:603–618.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burns, S. A. 1998. Organochlorine compounds in peregrine falcon (*Falco peregrinus*) in three regions of the United States. Thesis. University of California, Davis, California, USA.

Bustamante, J. 1993. Post-fledging dependence period and development of flight and hunting behaviour in the Red Kite (*Milvus milvus*). Bird Study **40**:181–188.

Cade, T. J., and D. M. Bird. 1990. Peregrine falcons (*Falco peregrinus*) nesting in an urban environment: a review. Canadian Field-Naturalist **104**:209–218.

Cade, T. J., J. H. Enderson, L. F. Kiff, and C. M. White. 1997. Are there enough good data to justify de-listing the American peregrine falcon? Wildlife Society Bulletin **25**:1–12.

Cade, T. J., M. Martell, P. Redig, G. Septon, and H. B. Tordoff. 1996. Peregrine falcons in urban North America. Pages 3–13 *in* D. M. Bird, D. E. Varland, and J. J. Negro, editors. Raptors in human landscapes: adaptations to built and cultivated environments. Academic Press, San Diego, California, USA.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.

Cooch, E., and G. White. 1998. Using MARK—a gentle introduction. [Online, URL: ⟨http://www.phidot.org/software/mark/docs/book/⟩.]

Crone, E. E., D. F. Doak, and J. Pokki. 2001. Ecological influences on the dynamics of a field vole metapopulation. Ecology **82**:831–843.

Diffendorfer, J. 1998. Testing models of source–sink dynamics and balanced dispersal. Oikos **81**:417–433.

Doak, D. F. 1995. Source–sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conservation Biology **9**:1370–1379.

Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. Ecology **75**:615–626.

Enderson, J. H. 1969. Peregrine and prairie falcon life tables based on band-recovery data. Pages 505–509 *in* J. J. Hickey, editor. Peregrine falcon populations: their management and recovery. University of Wisconsin Press, Madison, Wisconsin, USA.

Enderson, J. H., and G. R. Craig. 1988. Population turnover in Colorado peregrines. Pages 685–688 *in* T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Boise, Idaho, USA.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology **8**:50–59.

Federal Register. 1999. Endangered and threatened wildlife and plants; final rule to remove the American Peregrine Falcon from the federal list of endangered and threatened wildlife, and to remove the similarity of appearance provision for free-flying peregrines in the conterminous United States; final rule. Federal Register **64**:46541–46558.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts, USA.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science **245**:477–480.

Gundersen, G., E. Johannesen, H. P. Andreassen, and R. A. Ims. 2001. Source–sink dynamics: how sinks affect demography of sources. Ecology Letters **4**:14–21.

Hall, A. J., B. J. McConnell, and R. J. Barker. 2001. Factors affecting first-year survival in gray seals and their implications for life history strategy. Journal of Animal Ecology **70**:138–149.

Herman, S. G. 1971. The peregrine falcon decline in California. II. Breeding status in 1970. American Birds **25**:818–820.

Hunt, G. 1988. The natural regulation of peregrine falcon populations. Pages 667–676 *in* T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Boise, Idaho, USA.

Hunt, G. 1998. Raptor floaters at Moffat's equilibrium. Oikos **82**:191–197.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London B, Biological Sciences **330**:175–190.

Kendall, B. E., O. N. Bjornstad, J. Bascompte, T. H. Keitt, and W. F. Fagan. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. American Naturalist **155**:628–636.

Kenward, R. E., V. Marcstrom, and M. Karblom. 1993. Post-nestling behaviour in goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest-switching. Animal Behaviour **46**:371–378.

Kochert, M. N. 1976. Reproductive performance, food habits, and population dynamics of raptors. Pages 1–56 *in* Snake River Birds of Prey Research Project, Annual Report 1976. U.S. Department of the Interior, Bureau of Land Management, Boise, Idaho, USA.

Kochert, M. N. 1977. Reproductive performance, food habits, and population dynamics of raptors. Pages 1–39 *in* Snake River Birds of Prey Research Project, Annual Report 1977. U.S. Department of the Interior, Bureau of Land Management, Boise, Idaho, USA.

Konrad, P. M., and D. S. Gilmer. 1986. Post fledging behavior of ferruginous hawks in North Dakota. Raptor Research **20**:35–39.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist **142**:911–927.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs **62**:67–118.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics **21**:1–18.

Lindberg, P. 1977. The peregrine falcon in Sweden. Pages 329–338 *in* R. D. Chancellor, editor. Proceedings of the ICBP World Conference on Birds of Prey. International Council for Bird Preservation, London, UK.

Little, R. J. A., and D. B. Rubin. 1987. Statistical analysis with missing data. John Wiley, New York, New York, USA.

Mace, R. D., and J. S. Waller. 1998. Demography and population trend on grizzly bears in the Swan Mountains, Montana. Conservation Biology **12**:1005–1016.

McFadzen, M. E., and J. M. Marzluff. 1996. Mortality of Prairie Falcons during the fledgling-dependence period. Condor **98**:791–800.

Mead, C. J. 1969. Ringed peregrines in Great Britain. Pages 385–390 *in* J. J. Hickey, editor. Peregrine falcon populations: their management and recovery. University of Wisconsin Press, Madison, Wisconsin, USA.

Mebs, T. 1971. Todesursachen und mortalitatsraten beim wanderfalken (*Falco peregrinus*) nach den wiederfunden deutscher und finnischer ringvogel. Die Vogelwarte **26**:98–105.

Millsap, B. A., P. L. Kennedy, M. A. Byrd, G. Court, J. H. Enderson, and R. N. Rosenfield. 1998. Review of the proposal to de-list the American peregrine falcon. Wildlife Society Bulletin **26**:522–538.

Monson, D. H., D. F. Doak, B. E. Ballachey, A. Johnson, and J. L. Bodkin. 2000. Long-term impacts of the Exxon Valdez oil spill on sea otters, assessed through age-dependent mortality patterns. Proceedings of the National Academy of Sciences (USA) **97**:6562–6567.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Nelson, R. W. 1988. Do large natural broods increase mortality of parent peregrine falcons? Pages 719–728 *in* T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Boise, Idaho, USA.

Newton, I. 1979. Population ecology of raptors. T. and A. D. Poyser, London, UK.

Newton, I., and R. Mearns. 1988. Population ecology of peregrines in Scotland. Pages 651–666 *in* T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Boise, Idaho, USA.

Olsen, P. D., and J. Olsen. 1988. Breeding of the peregrine falcon (*Falco peregrinus*): I. weather, nest spacing and territory occupancy. Emu **88**:195–201.

Peakall, D. B., and L. F. Kiff. 1988. DDE contamination in peregrines and American kestrels and its effect on reproduction. Pages 337–350 *in* T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Boise, Idaho, USA.

Pradel, R. 1993. Flexibility in survival analysis from recapture data: handling trap-dependence. Pages 29–38 *in* J.-D. Lebreton and Ph. M. North, editors. Marked individuals in

the study of bird populations. Birkhauser Verlag, Boston, Massachusetts, USA.

Pulliam, R. H. 1988. Source, sinks and population regulations. American Naturalist **132**:652–661.

Pulliam, R. H., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist **137**:S51–S66.

Ratcliffe, D. A. 1980. The peregrine falcon. Buteo Books, Vermillion, South Dakota, USA.

Ratcliffe, D. A. 1993. The peregrine falcon. Second edition. Academic Press, San Diego, California, USA.

Sandland, R. L., and G. P. Kirkwood. 1981. Estimation of survival in marked populations with possibly dependent sighting probabilities. Biometrika **68**:531–541.

Sarrazin, F., C. Bagnolini, J. L. Pinna, E. Danchin, and J. Clobert. 1994. High survival estimates of Griffon vultures (*Gyps fulvus fulvus*) in a reintroduced population. Auk **111**: 853–862.

Sarrazin, F., and R. Barbault. 1996. Reintroduction: challenges and lessons for basic ecology. Trends in Ecology and Evolution **11**:474–478.

Sherrod, S. K., and T. J. Cade. 1978. Release of peregrine falcons by hacking. Pages 121–136 *in* T. A. Geer, editor. Birds of prey management techniques. British Falconers' Club, Oxford, UK.

Siemens, M. C. 1993. An analysis of peregrine falcon movements in California as revealed by band recovery data. Thesis. University of California, Santa Cruz, California, USA.

Tordoff, H. B., and P. T. Redig. 1997. Midwest peregrine falcon demography, 1982–1995. Journal of Raptor Research **31**:339–346.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893–901.

Varland, D. E., E. E. Klass, and T. M. Loughin. 1993. Use of habitat and perches, causes of mortality and time until dispersal in post-fledging American Kestrels. Journal of Field Ornithology **64**:169–178.

Walton, B. J. 1998. California peregrine falcon implementation plan, pre-1988 season update. Santa Cruz Predatory Bird Research Group, Santa Cruz, California, USA.

Walton, B. J., and J. Linthicum. 1992. Peregrine falcon monitoring, nest management, hack site, and cross-fostering efforts. Santa Cruz Predatory Bird Research Group, Santa Cruz, California, USA.

Walton, B. J., and C. G. Thelander. 1988. Peregrine falcon management efforts in California, Oregon, Washington, and Nevada. Pages 587–598 *in* T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Boise, Idaho, USA.

Watkinson, A. R., and W. J. Sutherland. 1995. Sources, sinks and pseudo-sinks. Journal of Animal Ecology **64**:126–130.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimates from populations of marked animals. Bird Study **46**:S120–S138.

Wootton, J. T., and D. A. Bell. 1992. A metapopulation model of the Peregrine Falcon in California: viability and management strategies. Ecological Applications **2**:307–321.

APPENDIX

A table presenting mark–recapture models of Peregrine Falcons ranked by their AIC weights is available in ESA's Electronic Data Archive: *Ecological Archives* A013-026-A1.