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Spatial Structure, Dispersal, and Management of a Recovering Raptor Population

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ABSTRACT: The recovery of the peregrine falcon (*Falco peregrinus anatum*) in California has taken place amid strong geographical differences in habitat quality, potentially creating a sink population in the southern coastal habitat and source populations in the northern interior and urban habitats. We analyzed long-term monitoring data to investigate the mechanisms and consequences of spatial structuring for the recovery of this set of nonstable subpopulations. Dispersal rates between habitats were asymmetric, with extremely limited dispersal out of the interior habitat and a strong tendency for birds in the southern coast to disperse to the urban habitats. We used these dispersal estimates and habitat-specific productivity rates to build a set of regional population models that describe population growth within and dispersal between each subpopulation. We tested for the existence of habitat-specific survival and territory acquisition rates by comparing model projections with the number of breeding pairs censused annually in each subpopulation. Our analyses indicate a high rate of survival for interior birds and suggest that both the interior and urban subpopulations were regulated by territory availability over the study period. The inherent spatial structure of this regional peregrine falcon population has had a considerable influence on its recovery and management.

Keywords: asymmetric dispersal, peregrine falcon, population regulation, reintroduction, source-sink, spatial structure.

The recognition that natural populations are often spatially subdivided due to differences in habitat quality has provided numerous insights for population ecology (Holt 1985; Pulliam 1988; Pulliam and Danielson 1991) and evolutionary biology (Morris 1991; McPeek and Holt 1992; Dias 1996). In particular, it is now widely recognized that habitat patchiness may strongly mediate population dynamics when individuals experience steep gradients in habitat quality, resulting in high quality source and low quality sink habitats (Holt 1985; Pulliam 1988; Pulliam and Danielson 1991). Still, the growing number of empirical investigations of the importance and generality of source-sink dynamics in nature (Keddy 1981; Bergerud 1988; Watkinson et al. 1989; Kadmon and Schmida 1990; Diffendorfer et al. 1995; Boughton 2000) include relatively few studies that clearly demonstrate the existence or functioning of source-sink systems in wide-ranging vertebrate populations (Diffendorfer 1998; Gunderson et al. 2001).

While conceptually appealing, a clear dichotomy between source and sink populations connected by dispersal may be rare in nature. The interactions between a stochastic environment, density-dependent factors, and disturbance may produce natural population dynamics that only occasionally conform to a distinct source-sink dichotomy (Thomas et al. 1996). In these more complicated situations, populations may appear as sources at some times and sinks in others (Watkinson and Sutherland 1995; Boughton 1999). Thus, while source-sink models provide a simplified and useful framework for conceptualizing spatial population dynamics, we lack the long-term data needed to carefully test their generality (Watkinson and Sutherland 1995; Dias 1996; Pulliam 1996; Diffendorfer 1998).

In addition to spatially structured habitat quality, dispersal behavior can strongly influence the effect that spatial structure has on regional population dynamics. Thus, a mechanistic understanding of the factors controlling between-patch dispersal is also necessary (Pulliam and Danielson 1991; Diffendorfer 1998; Boughton 2000). In Pulliam's (1988) early investigation of source-sink systems, dispersal was assumed to occur in a nonrandom

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manner, with individuals selecting habitats optimally, based on expected reproductive success. In contrast, Boughton (2000) found support for diffusion-based dispersal in Edith's checkerspot butterfly (*Euphydryas editha*) in the Sierra Nevada Mountains. Theoretical studies suggest that the evolutionarily stable dispersal strategy is inversely related to the carrying capacity of habitat patches (McPeek and Holt 1992); studies on small mammals and collared flycatchers (*Ficedula albicollis*) provide some empirical evidence for this so-called balanced dispersal (Doncaster et al. 1997; Diffendorfer 1998). Alternatively, several authors have suggested that many taxa (especially birds) may use the current distribution of conspecifics to select between habitats of varying quality (Reed and Dobson 1993; Poysa et al. 1998; Lohmus 2001). The lack of a clear, unified understanding of dispersal behavior and habitat selection is particularly problematic, since the manner in which dispersal occurs (or is modeled) will strongly affect the functioning of spatially structured populations and the outcomes of model investigations of spatially complex systems (Kareiva 1990; Pulliam and Danielson 1991).

In addition to their influence on ecological and evolutionary theory, modeling frameworks of spatially structured populations have been widely applied to the study of populations of conservation concern (e.g., Doak 1995; Wennergren et al. 1995; Brawn and Robinson 1996; Gaona et al. 1998). Habitat fragmentation and degradation are presumed to reduce both the connectivity and regional viability of subpopulations, which may impose spatial structure on previously contiguous populations (Fahrig and Merriam 1994). Assessing the viability of such fragmented populations is hindered by our poor understanding of how previously contiguous populations will interact spatially once they become fragmented (Wennergren et al. 1995). Because we still lack large-scale empirical studies, the rich body of theory concerning spatial population dynamics remains disconnected from the management and conservation of populations inhabiting fragmented or degraded habitats (Harrison and Bruna 1999). For endangered populations with complicated source-sink dynamics it becomes essential to base management decisions and viability assessments on habitat-specific demographic rates rather than on potentially misleading indicators such as population counts (van Horne 1983).

In this study, we investigate the patterns, mechanisms, and consequences of spatial structure and dispersal in a nonstable regional population of peregrine falcons (*Falco peregrinus*) in California. Peregrine falcons in California have made a dramatic recovery from the DDT-induced population crash in the 1950s, as they have throughout the world (Hickey 1969; Cade et al. 1988). However, persistent geographical differences in environmental levels of DDE (the persistent metabolite of DDT) exist across the state (Monk et al. 1981; Jarman 1994; Burns 1998). This causes eggshell thinning rates to vary and has led to disparate reproductive performance and rates of population recovery between coastal and interior habitats (Peakall and Kiff 1988; Wootton and Bell 1992; Santa Cruz Predatory Bird Research Group (SCPBRG), unpublished data). Additionally, recent work (Kauffman et al. 2003) has documented a remarkably high population growth rate for urban habitats driven by high survival of first-year birds, and previous modeling suggests potential source-sink dynamics between northern interior and southern coastal subpopulations (Wootton and Bell 1992). Altogether, the extensive demographic information on California peregrines allows us to investigate the effects of these and other sources of habitat-specific demography and dispersal on the dynamics of a regional population consisting of three types of subpopulations that occupy coastal, interior, and urban habitats (fig. 1).

These three subpopulations have also been highly managed by the introduction of hundreds of banded fledglings since 1977 as part of a statewide recovery effort (Linthicum and Walton 1992; Walton 1998). In this study we use these introductions and subsequent population monitoring to understand between-habitat dispersal and the spatial structure of this regional population. Our analyses

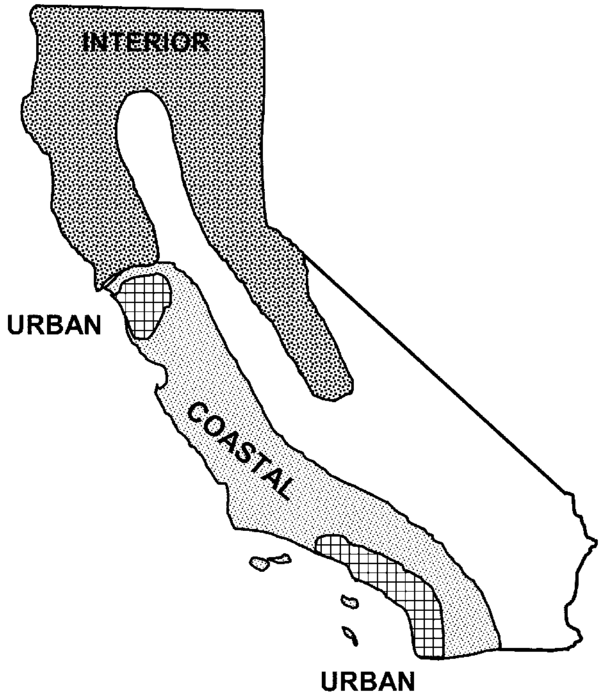

Figure 1: Geographic location of interior, coastal, and urban peregrine falcon habitats in California. Figure redrawn from Kauffman et al. (2003).

suggest clear differences in subpopulation survival rates, between-habitat dispersal, and density-dependent territory acquisition within subpopulations. The spatial structure that we characterize also has important implications for peregrine falcon management efforts and regional population recovery.

Study System

Recovery History and Data

In California, estimates of the historical breeding population (i.e., number of nest sites) of peregrine falcons across the region vary between 120 and 173 pairs (Bond 1946; Jarman 1994; Walton 1998). Surveys conducted by Herman (1971) identified only two breeding pairs and four occupied territories in the state just prior to the banning of DDT in 1972. In 1976, the Santa Cruz Predatory Bird Research Group (SCPBRG) initiated a management program to aid the recovery of peregrine falcons in California. These efforts included placing young fledglings from a captive breeding program in the nests of wild peregrines ("fostering") or prairie falcons (*Falco mexicanus*; "cross-fostering") or releasing them from artificial hack boxes without falcon parents ("hacking"). Wild eggs with thin shells were also salvaged from failing nest sites, hatched and reared in captivity, and released back into the wild population by hacking or fostering. This population management, which occurred from 1977 until 1992 (with some limited hacking post-1992), resulted in the release of approximately 800 birds into the state.

Simultaneous with the recovery effort, a statewide cooperative monitoring program was conducted that censused all known pairs and their young in coastal, interior, and urban habitats. During the reintroduction period, the number of censused pairs occupying territories increased from seven active sites in 1977 to an estimated 140 active aeries by 1997 (Walton 1998). All peregrine falcons released by hacking, fostering, or cross-fostering were given a U.S. Fish and Wildlife Service identification band, and wild young were also banded in the nest. As part of ongoing monitoring efforts, records have been kept of these banded birds since 1976, including annual recaptures each spring along with live resightings and dead recoveries during the rest of the year.

Peregrine Habitat Types and Life History

Aside from the demographic differences that we have already described, the three peregrine habitat types that we recognize vary in several important regards. The interior habitat is relatively undeveloped and has often been considered a stronghold of the regional population. The coastal habitat is more developed and differs from the interior habitat in that most breeding sites are on coastal cliffs. The urban habitats (the metropolitan areas of Los Angeles, San Francisco Bay Area, and San Diego) are different still, with peregrines breeding on artificial structures such as skyscrapers and bridges, an abundance of available prey, and a lack of mammalian predators. Wootton and Bell (1992) first recognized the distinction between interior (their "northern") and coastal (their "southern") habitats. All three habitats are further distinguished by geographic variation in DDE exposure (Monk et al. 1981; Jarman 1994; Burns 1998), which has caused productivity rates to be low in coastal sites, higher in interior sites, and still higher in urban sites where DDE exposure is low (fig. A1 in the appendix in the online edition of the *American Naturalist*).

Biologists typically have recognized three life stages for peregrine falcons: first-year birds (i.e., fledglings), second-year birds, and adult birds older than 2 years (Ratcliffe 1980; Newton 1988; Wootton and Bell 1992). We similarly recognize these three life stages in our analysis, and we note that first-year birds are responsible for the vast majority of dispersal between habitats. Because of territory limitation, some potential breeders (referred to as "floaters") will not breed at the end of their second year, when peregrines typically breed. Such delayed breeding can potentially lead to population regulation (Moffat 1903; Newton 1992; Hunt 1998). Raptor populations may also be regulated by "site dependence," which causes productivity rates to decline as the breeding population increases due to the optimal selection of nest sites of varying quality (Rodenhouse et al. 1997; McPeek et al. 2001). Thus, a recovering population that is regulated by site dependence will experience a decrease in per capita productivity over time (a similar reduction in productivity may result from scramble competition for nonterritorial resources).

The only survival estimates for California peregrines come from Kauffman et al. (2003), who used existing band record data and capture-recapture methods to derive age-specific survival estimates for coastal and urban peregrines (fig. 1). Insufficient capture-recapture data exist to directly estimate survival of interior peregrines, and no prior estimates exist for dispersal rates between the three habitats.

Methods

To fully characterize the spatial structure of California peregrines, we used several different analyses to quantify dispersal between, and population growth within, each habitat. We first estimated dispersal rates between habitats using data on recaptures and resightings of introduced fledglings. We then built regional population models that use these dispersal rates and estimates of annual productivity but make hypothetical characterizations of survival rates and population regulation within subpopulations. For these regional population models we used a model-fitting approach to assess the support for alternative scenarios of subpopulation demography by comparing predicted breeding population trajectories to the observed number of breeding pairs censused each year in each habitat.

Estimating Between-Habitat Natal Dispersal from Banded Birds

We narrowed the problem of characterizing the dynamics of the entire regional population by first estimating four of six separate between-habitat natal dispersal rates using the SCPBRG banding data and a capture-recapture approach. An analysis of this type must be able to estimate the probability of dispersal between habitats while accounting for the chance that some birds may disperse and not be detected. Thus, it is necessary to have some estimate of the reencounter rate in each habitat. For peregrines in coastal and urban habitats in the years 1977–1999, Kauffman et al. (2003) estimated rates of resighting ($R_b = 0.02$) and dead recovery ($r_b = 0.15$) for all birds and stage-specific recapture rates for fledglings ($p_f = 0.03$) and adults ($p_b = 0.07$). Because such estimates of reencounter rates do not exist for the interior habitat, we could not use any direct capture-recapture estimation method to reconstruct natal dispersal rates into the interior habitat. To account for birds that disperse to a nonnatal habitat but die before being reencountered, we use survival estimates from Kauffman et al. (2003).

We used these known reencounter and survival rates and the SCPBRG banding data to separately estimate each habitat-specific natal dispersal rate, $D_{x,y}$, defined as the probability that a bird fledged in natal habitat x disperses to and breeds in nonnatal habitat y. Although there are in fact two physically separated urban habitats (i.e., near the cities of San Francisco and Los Angeles; fig. 1), we treat these areas as one habitat type and estimate the same dispersal rates into and out of both urban habitat areas. The study period for this analysis was spring 1982 to spring 2001. It is easiest to present the diverse array of possible encounter histories for peregrine falcons fledged (wild or hacked) into a given natal habitat x as belonging to two groups: birds reencountered in habitat y after t years and birds never reencountered in habitat y.

Encounter history 1: reencountered in a nonnatal habitat type y. To have this type of encounter history a bird must survive year 1 in habitat x at rate $S_{f,x}$, disperse to nonnatal habitat y with probability $D_{x,y}$, not be recaptured in habitat y the next spring at rate $1 - p_f$, and survive the rest of year 2 without being resighted at rate $S_b(1 - R_b)$. For the next $t - 2$ adult years it must not be recaptured, survive, and not be resighted at rate $(1 - p_b) S_b (1 - R_b)$ before finally being reencountered dead or alive in year t. Thus, the probability of being reencountered in a nonnatal habitat is

$$\Pr(\text{reencountered after year } t > 1) = S_{f,x} D_{x,y} (1 - p_f) S_b (1 - R_b) [(1 - p_b) S_b (1 - R_b)]^{t-2} \theta. \quad (1)$$

The final reencounter (denoted as θ) can occur in three ways: first, escape recapture, die, and be recovered dead in habitat y, in which case $\theta = (1 - p_b)(1 - S_b) r_b$; second, escape recapture, survive, and be resighted alive in habitat y, in which case $\theta = (1 - p_b) S_b R_b$; or, third, be recaptured at the beginning of the year, in which case $\theta = p_b$. (For $t = 1$, eq. [1] reduces to $S_{f,x} D_{x,y} \theta$, with P_f substituted for P_b in θ definitions.) We modeled two survival stages and used rates from Kauffman et al. (2003), which are habitat-specific for first-year but not adult birds. Thus, adult survival, S_b, was 0.86 in all habitats. First-year survival, $S_{f,x}$, was 0.65 for all urban birds and 0.29 for birds fledged in the coastal and interior habitats.

Encounter history 2: never reencountered in nonnatal habitat type y. To have the second encounter history a bird can either (1) die its first year; (2) survive its first year but not disperse to habitat y; (3) survive its first year, disperse to habitat y, survive the rest of the study period, and escape detection in all years; or (4) survive its first year, disperse to habitat y, die prior to the end of the study (within t years), escape detection all years while alive, and not be recovered dead. This fourth case depicts many possible unknown fates (i.e., die after year $i = 1, 2 \ldots t$ and not be recovered), the probability of which is the sum of the probabilities of dying in any year i between dispersal and the end of the study. Thus, for an individual bird, the probability of never being reencountered in a nonnatal habitat is the sum of the following mutually exclusive probabilities:

$$\begin{aligned}
&(1)\ \Pr(\text{die in first year}) = (1 - S_{f,x});\\
&(2)\ \Pr(\text{survive year 1, do not disperse to habitat } y) = \\
&\quad S_{f,x}(1 - D_{x,y});\\
&(3)\ \Pr(\text{survive year 1, disperse to habitat } y, \text{ survive}\\
&\quad t \text{ years without reencounter}) = \\
&\quad S_{f,x} D_{x,y} (1 - p_f) S_b (1 - R_b) [(1 - p_b) S_b (1 - R_b)]^{t-1};\\
&(4)\ \Pr(\text{survive year 1, disperse, die within } t \text{ years,}\\
&\quad \text{no recovery}) = \sum_{i=1}^{t} \{S_{f,x} D_{x,y} (1 - p_f) [S_b (1 - R_b)(1 - p_b)]^{i-1} d\\
&\quad (1 - S_b)(1 - r_b)\}.
\end{aligned} \quad (2)$$

Table 1: Definitions and sources for parameters used in the natal dispersal model and regional population model of peregrine falcon recovery in California

Parameter	Description
Fixed parameters:	
From Kauffman et al. (2003); SEs in parentheses:	
$S_{\mathrm{fh,c}} = .24(.08)$	Survival of first-year hacked birds in coastal habitats
$S_{\mathrm{fw,c}} = .29(.06)$	Survival of first-year wild-fledged birds in coastal habitats
$S_{\mathrm{f,u}} = .65(.15)$	Survival of first-year hacked and wild-fledged urban birds
$S_{\mathrm{nb,c}} = .86(.07)$	Survival of nonbreeding birds in coastal habitat
$S_{\mathrm{b,c}} = .86(.03)$	Survival of adults in coastal habitat
From annual nest monitoring regression:	
$F_{\mathrm{t,i}}$	Time-varying, per capita productivity in interior habitat
$F_{\mathrm{t,c}}$	Time-varying, per capita productivity in coastal habitat
$F_{\mathrm{t,u}}$	Time-varying, per capita productivity in urban habitat
Fitted parameters:	
Natal dispersal model:[a]	
$D_{\mathrm{u,c}}$	Per capita dispersal from urban to coastal habitats
$D_{\mathrm{i,c}}$	Per capita dispersal from interior to coastal habitats
$D_{\mathrm{c,u}}$	Per capita dispersal from coastal to urban habitats
$D_{\mathrm{i,u}}$	Per capita dispersal from interior to urban habitats
Regional population model:	
Survival:	
$S_{\mathrm{b,i}}$	Survival of adults in interior habitat
$S_{\mathrm{f,i}}$	Survival of first-year birds in interior habitat
$S_{\mathrm{b,u}}$	Survival of adults in urban habitat
Territory acquisition:	
$x_{0,\mathrm{i}}$ and $x_{1,\mathrm{i}}$	Logit function coefficients for the interior subpopulation
$x_{0,\mathrm{c}}$ and $x_{1,\mathrm{c}}$	Logit function coefficients for the coastal subpopulation
$x_{0,\mathrm{u}}$ and $x_{1,\mathrm{u}}$	Logit function coefficients for the urban subpopulation
Natal dispersal:	
$D_{\mathrm{u,i}}$	Per capita dispersal from urban to interior habitats
$D_{\mathrm{c,i}}$	Per capita dispersal from coastal to interior habitats

[a] Once these dispersal estimates were estimated in the natal dispersal model, they were used as fixed parameters in the regional population model.

We found maximum likelihood estimates for each habitat-specific dispersal rate, $D_{\mathrm{x,y}}$, by minimizing the sum of the negative log-likelihood of the encounter history for each bird using the likelihood calculation:

$$\mathrm{L}(D_{\mathrm{x,y}}|\text{banding data}) = -\sum_{k=1}^{n} \ln\left[\Pr(\text{encounter history}_k|D_{\mathrm{x,y}})\right], \tag{3}$$

where $\Pr(\text{encounter history}_k|D_{\mathrm{x,y}})$ is the binomial probability of the encounter history observed for bird k (using eqq. [1] or [2] above) of n total birds banded in natal habitat x, given a modeled dispersal rate, $D_{\mathrm{x,y}}$. We estimated confidence limits for maximum likelihood dispersal estimates using likelihood profiles (Hilborn and Mangel 1997). The SCPBRG data are sufficient to allow estimation of four of the six natal dispersal probabilities (table 1), and we estimated the two remaining dispersal rates into the interior habitat, $D_{\mathrm{c,i}}$ and $D_{\mathrm{u,i}}$, as part of the fitting of each regional population model as described below.

Regional Population Model

To characterize subpopulation demography and spatial structure, we next developed a suite of regional population models that describe population growth within, and natal dispersal between, all three subpopulations. Our models pose alternative hypothetical characterizations of subpopulation growth and regulation, allowing us to make inferences about the underlying spatial structure of the regional peregrine falcon population. Each regional population model has three components: habitat-specific survival and productivity that govern internal dynamics of each subpopulation, a territory acquisition function that controls the transition from floater to breeder (sensu Brown 1969), and natal dispersal between subpopulations.

Internal dynamics. To model the internal dynamics of each subpopulation, we use a postbreeding census with three stage classes: first-year birds that are 0 years old, N_f; nonbreeders that are 1 year old or older, N_{nb}; and breeding adults that are 2 years old or older, N_b. In each year, we keep track of the number of wild-reared fledglings, N_{fw}, the number of hacked fledglings, N_{fh}, and the number of fledglings fostered and cross-fostered, N_{ffos}. The resulting stage-based matrix model (Lefkovitch 1965; Caswell 2001), including introductions, is

$$\begin{bmatrix} N_{fw} \\ N_{fh} \\ N_{nb} \\ N_b \end{bmatrix}_{t+1} = \left(\begin{bmatrix} 0 & 0 & S_{nb}F_t P_{N_{b,t}} & S_b F_t \\ 0 & 0 & 0 & 0 \\ S_{fw} & S_{fh} & S_{nb}(1 - P_{N_{b,t}}) & 0 \\ 0 & 0 & S_{nb}P_{N_{b,t}} & S_b \end{bmatrix}_t \times \begin{bmatrix} N_{fw} \\ N_{fh} \\ N_{nb} \\ N_b \end{bmatrix}_t \right) + \begin{bmatrix} N_{ffos} \\ N_{fh} \\ 0 \\ 0 \end{bmatrix}_{t+1} . \quad (4)$$

Survival probabilities are S_{fw}, S_{fh}, S_{nb}, and S_b for wild (or fostered) first-year birds, hacked first-year birds, nonbreeding birds, and breeding adults, respectively. A time-varying habitat-specific productivity rate, F_t, denotes the estimated number of female fledglings produced per breeding adult. We account for the historical introductions by adding to the population vector the known number of fledglings introduced into each subpopulation annually by hacking, N_{fh}, and by fostering or cross-fostering methods, N_{ffos}. In a similar way, we account for the number of managed nest sites each year (nest sites where SCPBRG collected thin eggs) by preventing an equivalent number of pairs from breeding in the model. To investigate the relationship between territory occupancy and acquisition, we model the probability of a nonbreeder acquiring a territory, $P_{N_{b,t}}$, as a logistic function dependent on the number of breeders at time t:

$$P_{N_{b,t}} = \frac{\exp(x_0 + x_1 N_{b,t})}{1 + \exp(x_0 + x_1 N_{b,t})}, \quad (5)$$

where x_0 and x_1 are shape-fitting parameters and subscripts denote that P is a function of N_b at time t. This allows a range of relationships between the current number of breeders and the probability of acquiring a breeding territory, including the special case where $P_{N_{b,t}} = 1$ for all breeding population sizes (i.e., no floaters and no density dependence).

Equations (4) and (5) describe a general model of internal subpopulation dynamics so that the parameters in these equations have no habitat subscript. However, in our regional population models these parameters have habitat subscripts because most fixed demographic rates were habitat specific (table 1), and fitted parameters were either habitat specific or equal across habitats depending on the structure of each alternative model. This full 12 × 12 matrix also includes the six-directional, habitat-specific dispersal rates that connect our three subpopulation models ("Twelve-Stage Regional Population Model" in the appendix). Because of the small numbers of peregrines in both urban habitats, we model their dynamics as one urban subpopulation with consistent internal dynamics and habitat-specific dispersal. Natal dispersal rates between habitats are constant through time, and we assume that subsequent movements (i.e., breeding dispersal) do not result in additional between-habitat dispersal.

Alternative Forms of Regional Population Models

We developed a comprehensive set of regional population models that varied in their characterization of survival and population regulation as either homogenous or heterogeneous across subpopulations. All alternative models were consistent, however, in their use of reintroduction and egg manipulation data, their inclusion of natal dispersal between all habitats, and their use of time-varying productivity estimates.

Because previous studies have strongly suggested that the interior (Wootton and Bell 1992) and urban birds (Kauffman et al. 2003) have higher survival rates than coastal birds, we sought to test these assertions. To test for survival rate differences, we first built a baseline set of models with homogenous survival rates across subpopulations. These rates were fixed at the Kauffman et al. (2003) coastal survival estimates (table 1). Next, we built variants of these baseline models that fit distinct survival rates for the interior and urban subpopulations. Thus we considered four different model forms for survival: first, homogenous survival rates for all subpopulations fixed at the coastal rates; second, fitted urban survival rates ($S_{b,u}$); third, fitted interior survival rates ($S_{f,i}$ and $S_{b,i}$); and fourth, fitted survival rates in both urban and interior subpopulations. For urban and interior habitats, survival of nonbreeders was assumed to be equal to that of breeders (Kauffman et al. 2003). In all models, we assumed that the baseline survival estimates are appropriate for the coastal subpopulation and did not fit additional survival rates for this habitat.

To test for different territory acquisition patterns between subpopulations, we used three alternative functions to characterize the relationship between territory acquisition and breeding population size (i.e., the functional relationship of $P_{N_{\mathrm{b,t}}}$ in eq. [5]): all nonbreeders acquire a territory at the end of their second year ($P_{N_{\mathrm{b,t}}} = 1$); a constant fraction of nonbreeders acquire a territory at the end of their second year ($P_{N_{\mathrm{b,t}}} < 1$ but constant; x_0 varies but $x_1 = 0$); or the fraction of nonbreeders that acquire a territory is dependent on the size of the current breeding population (both x_0 and x_1 vary). We applied these three functions separately to each of the three subpopulations, yielding 27 model forms (3 interior × 3 coastal × 3 urban). Because we include field estimates of productivity trends in each habitat (F_{t} in eq. [4]; calculated from fig. A1), high statistical support for models with regulated territory acquisition would suggest the functioning of this regulatory mechanism in addition to any effects of site-dependent regulation on observed productivity rates.

Habitat-specific survival rates will interact with population regulation to determine the projected number of breeding pairs in each subpopulation (on which model selection is based). Thus, we considered a total of 108 regional population models that included all possible combinations of habitat-specific survival and territory acquisition forms for each subpopulation (four model forms for survival crossed with 27 model forms for territory acquisition).

Fitting Regional Population Models to Annual Censuses

Our approach to fitting the regional population models was to use existing independent estimates of demographic and dispersal rates and then to fit the remaining unknown parameters. Fixed parameters in the model included baseline survival estimates from Kauffman et al. (2003), four dispersal estimates from our capture-recapture analysis (see the section "Estimating Between-Habitat Natal Dispersal from Banded Birds"), and annual habitat-specific productivity trends from nest monitoring data (see fig. A1). We found best-fit estimates of the remaining survival, dispersal, and territory acquisition parameters by fitting the regional population models to the annual census of breeding pairs (see table 1 for a list of fitted parameters).

Field data for this model-fitting analysis come from the statewide monitoring program in 1980–1992 that censused the number of known pairs in all three habitats (urban and coastal habitats were monitored until 1999). We used maximum likelihood and Akaike Information Criterion (AIC) techniques (Edwards 1992; Hilborn and Mangel 1997; Burnham and Anderson 2002) to assess the support from the breeding pair census data for each alternative model and to estimate best-fit parameters. In the language of model selection, we chose the model and parameter values that reduced the variation between the model predictions and the observed number of adult breeders. The total negative log-likelihood of model i is the sum of each of T yearly negative log-likelihoods in each of the three habitats given the number of breeding adults ($N_{\mathrm{b,m,t}}$) censused in each habitat m and year t:

$$\mathrm{L}(\mathrm{model}_i|\text{all census data}) = \sum_{m=1}^{3}\sum_{t=1}^{T}\mathrm{L}(\mathrm{model}_i|N_{\mathrm{b,m,t}}). \tag{6}$$

For census data for a given habitat m in year t, the negative log-likelihood of model i is

$$\mathrm{L}(\mathrm{model}_i|N_{\mathrm{b,m,t}}) = -\ln\left[\Pr\left(N_{\mathrm{b,m,t}}|\mathrm{model}_i\right)\right], \tag{7}$$

where $\Pr(N_{\mathrm{b,m,t}}|\mathrm{model}_i)$ is the probability of observing the censused number of breeding adults in habitat m for year t given the parameter values and spatial structure explicit in model i. We assumed normally distributed within-year observation errors and no process error, resulting in (Hilborn and Mangel 1997)

$$\mathrm{L}(\mathrm{model}_i|N_{\mathrm{b,m,t}}) = \log(\sigma) + \frac{1}{2}\log(2\pi) + \frac{(N_{\mathrm{b,m,t}} - N_{\mathrm{b,m,t[pred]}})^2}{2\sigma^2}, \tag{8}$$

where $N_{\mathrm{b,m,t(pred)}}$ is the number of breeders predicted by model i to be in habitat m at time t, and σ^2 is the fitted variance. Best-fit parameters of alternative models were obtained using the nonlinear solver NPSOL in the TOMLAB optimization environment (Holmstrom 1999). All optimizations were implemented in MATLAB (version 6.0.0.88, release 12, Mathworks, Natick, Mass.). The time span for which we were able to fit the regional population models was 1980–1992 in the interior habitat and 1982–1999 in the urban and coastal habitats.

We calculated an AIC value for each alternative model i as $\mathrm{AIC}_i = 2\mathrm{L}_{\mathrm{model}_i} + 2p_i$, where p_i is the number of parameters in model i. To compare the relative support between models, we calculated the AIC weight, $\hat{w}_i$, of each model as

$$\hat{\mathrm{w}}_i = -\frac{\exp^{(-[1/2]\Delta\mathrm{AIC}_i)}}{\sum_{i=1}^{108}\exp^{(-[1/2]\Delta\mathrm{AIC}_i)}}, \tag{9}$$

where $\Delta\mathrm{AIC}_i$ is the difference in AIC value between model i and the model with the lowest AIC (i.e., the best-fitting model; Burnham and Anderson 2002). All 108 AIC weights sum to 1 and thus estimate the proportional support of the data for each candidate model. We assessed the support of distinct model components (which may exist across a family of models) by summing the AIC weights of all models that include the component of interest (Burnham and Anderson 2002). For example, to assess the support for the existence of distinct survival rates for the interior habitat, we summed the AIC weights of all 54 models that fit a distinct survival rate for that habitat. We calculated final parameter estimates as weighted averages (using AIC weights) of all models that fit a given parameter (Burnham and Anderson 2002). We estimated one-dimensional 95% confidence limits for each fitted parameter in the best-fit model using the likelihood profile method of Hilborn and Mangel (1997). Because of their strongly interactive effects on model fit, we modified these methods to estimate a two-dimensional 95% confidence bound for the parameters x_0 and x_1 in the territory acquisition function (eq. [5]) and then graphed $P_{N_{b,t}}$ within these limits for observed values of $N_{b,t}$ in each habitat.

Finally, we used the AIC-weighted parameter estimates to calculate the annual population growth rate, λ, for each habitat in each year. Using the observed number of breeding pairs to hold $P_{N_{b,t}}$ constant for each year, we calculated λ as the dominant eigenvalue of each subpopulation matrix, providing an estimate of population growth that is independent of the management intervention. This also allowed us to discern whether habitats were sources or sinks and how this characterization was maintained (or not) throughout the recovery due to density-dependent effects on territory acquisition and habitat-specific productivity trends.

Evaluating the Effects of Management

Once we had characterized subpopulation survival, territory acquisition, and dispersal by fitting the regional population models, we assessed how this spatial structure mediated the effectiveness of the management intervention. Because the SCPBRG removed eggs primarily from failing nests, the use of average productivity rates from monitored nests (which were used in the model fitting) would overestimate the productivity of breeders in an unmanaged scenario. To make a proper assessment, we estimated what habitat-specific productivity rates would have been if the egg collection effort had not occurred, using a previously derived relationship between eggshell thickness and egg fate (see Kauffman et al. 2003 for details). Using these adjusted productivity estimates, we ran our best-fit regional population model as a population projection without introductions or egg manipulations. This allowed us to characterize the expected recovery rate of each subpopulation in the absence of all management efforts, allowing for dispersal between habitats.

Table 2: Model selection results for 108 regional population models

Model component	Relative support (total AIC weights) Interior	Coastal	Urban
Survival:			
Habitat-specific survival rates	1.0000	…	.2781
Homogenous survival rates	.0000	…	.7219
Territory acquisition:			
Density-dependent territory acquisition	.9909	.1012	.8778
Constant territory acquisition	.0024	.2484	.1163
Territory acquisition probability = 1	.0066	.6504	.0059

Note: Akaike Information Criterion (AIC) weights presented are summed across all models that include the given model component. "Habitat-specific survival rates" refers to the set of models that fit distinct survival rates for either the interior or urban habitat (survival rates were never fitted for the coastal habitat). "Homogenous survival rates" refers to the set of models where each habitat had its survival rates fixed at the coastal values given in table 1. Note that AIC weights sum to 1 within each model component contrast (i.e., survival and territory acquisition in the interior habitat). Model components with total AIC weight scores near unity have strong support from the data.

Results

Between-Habitat Natal Dispersal

Most observed natal dispersal events were recorded for birds moving into urban habitats from the coastal habitat. The per capita dispersal rate and 95% confidence intervals from coastal to urban habitats was estimated at $D_{c,u} = 0.154$ (0.090, 0.243), whereas the best-fit dispersal rate from the urban to coastal habitat was $D_{u,c} = 0.047$ (0.003, 0.198). In contrast to the dispersal from coastal to urban habitats, very few birds moved out of the interior habitat to breed in either of the other habitats; dispersal estimates of interior birds into both urban ($D_{i,u} = 0.012$ [0.002, 0.036]) and coastal habitats ($D_{i,c} = 0.006$ [0, 0.025]) were near 0. The weighted maximum likelihood estimates for dispersal of fledglings from the coastal habitat to the interior habitat (fit in the regional population model) were also near 0 ($D_{c,i} < 0.0001$ [0, 0.010]). The estimated dispersal rate of urban birds moving into the interior habitat was much higher ($D_{u,i} = 0.226$ [0, 0.435]), although confidence intervals for this estimate are wide.

Subpopulation Growth and Regulation

While we did not find clear support for any one regional population model, several model components had overwhelming support based on AIC weights. In particular, all models that included habitat-specific interior survival rates

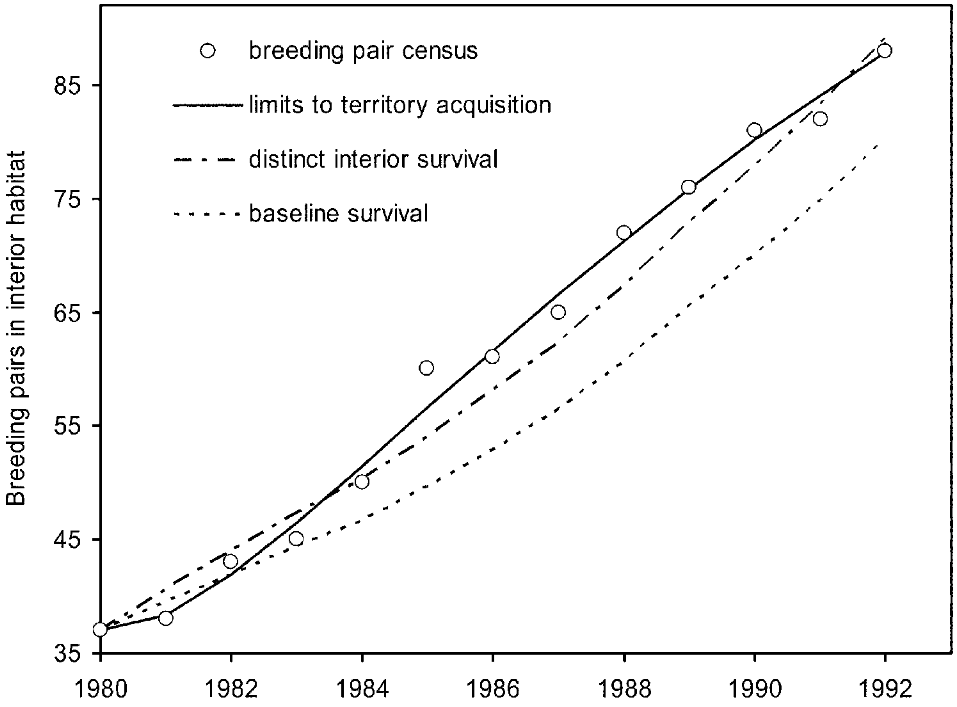

Figure 2: Evidence for distinct survival rates and density-dependent territory acquisition in the interior subpopulation. The population trajectory produced by the baseline survival model (*dotted line*), which uses coastal survival rates, provides a poor fit to the observed recovery of breeding pairs to the interior habitat. A companion model to the baseline model that differs only in its inclusion of distinct interior survival rates (*dotted and dashed line*) provides a significantly better fit to the data. The best-fitting model of interior subpopulation growth (*solid line*) includes density-dependent territory acquisition as well as distinct survival and has overwhelming support of the breeding pair census data.

and density-dependent territory acquisition in the interior and urban subpopulations had high relative support from the breeding pair census data (total AIC weights = 1.000, 0.9909, 0.8778, respectively; table 2). There was relatively little support for density-dependent territory acquisition in the coastal subpopulation (total AIC weights = 0.1012). Thus, the spatial structure characterized by our model-fitting approach is that of robust but regulated growth in the interior and urban subpopulations and slow growth in the coastal subpopulation where there is no evidence of limits to territory acquisition over the period of data collection.

One of the clearest results of the model selection was the difference between the estimated survival rates in the two nonurban habitats (interior and coastal). Allowing distinct interior survival rates made the strongest improvement to model fit (table 2; fig. 2). The maximum likelihood estimates (and 95% C.I.) for interior adult and first-year survival were 0.99 (0.81–1.0) and 0.45 (0.26–1.0), respectively. (We imposed a biological limit of 0.45 on this parameter in our model fitting.) These rates are markedly higher than survival rates in the coastal habitat (0.86 and 0.29). Because first-year and adult survival rates interact to influence growth of the interior subpopulation, we were unable to tease these estimates apart when calculating confidence intervals using likelihood profiles (while allowing all other parameters to fit to their new best-fit values). However, models that assumed the same survival rates in interior and coastal habitats (i.e., when neither $S_{\mathrm{b,i}}$ nor $S_{\mathrm{f,i}}$ are fitted) had essentially no support based on AIC weights (table 2). In the urban habitat, statistical support for baseline (coastal) survival rates was considerably higher than the support for distinct survival rates (total AIC weights = 0.7219 and 0.2781, respectively).

Density-dependent territory acquisition strongly improved model fit when included in the interior and urban subpopulations (table 2; figs. 2, 3). For the coastal subpopulation, there was three times more support for the alternative hypothesis that the territory acquisition probability was constant and equal to 1 (i.e., all second-year birds breed; total AIC weight = 0.6504) than for the hypothesis that this rate was constant and <1 (total AIC weight = 0.2484). For the interior subpopulation, model results suggest that territory acquisition was controlled by breeding population throughout our study period (fig. 4), although confidence intervals are wide. The probability of

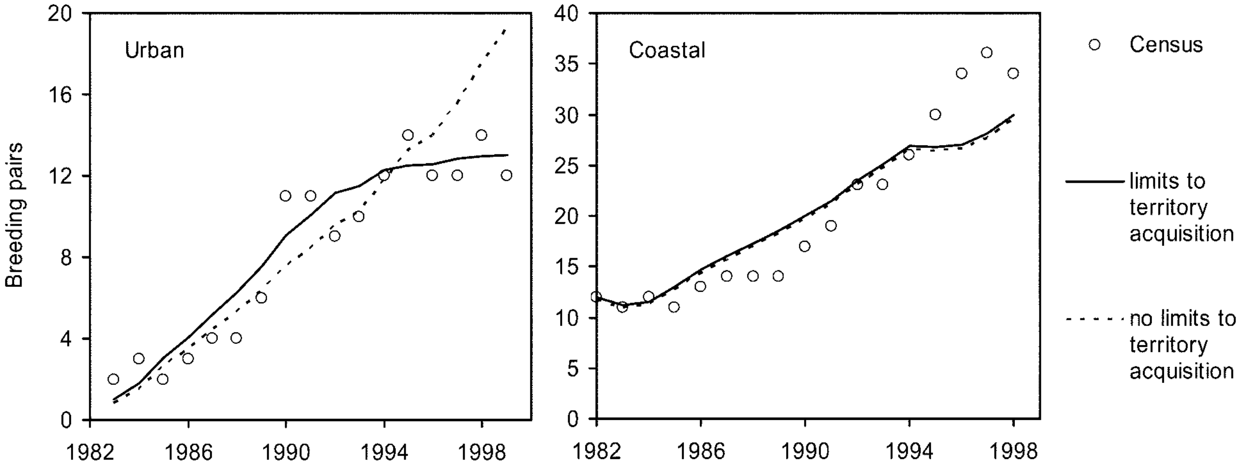

Figure 3: Effect of density-dependent territory acquisition in the urban and coastal subpopulations. The best-fit model is plotted for each subpopulation (urban = *solid line*, coastal = *dotted line*), along with the one nested model that is identical to the best-fit, except for the inclusion (coastal) or exclusion (urban) of density-dependent territory acquisition. Density-dependent territory acquisition best explains the growth of the urban subpopulation, but not in the slowly recovering coastal subpopulation.

recruiting to a breeding territory declined as the number of occupied territories increased from 37 in 1980 to 88 in 1992 (see arrows in fig. 4). Because of the limits to territory acquisition imposed by territory saturation, model projections suggest that by the early 1990s as many as 200 floating females may have been present in the interior habitat (fig. 5). For the urban habitat, the growth of the breeding population appeared to level out at approximately 12 territories and the floater population increased rapidly after limited breeding sites became saturated (figs. 4, 5). Thus, the three peregrine habitat types are predicted to have dramatically disparate stage structures (fig. 5) because of differences in intrinsic subpopulation growth and in the number (and saturation) of available breeding sites between habitats.

Trends in Population Growth Rates

Trends in annual population growth rate (λ) revealed the changing quality of each habitat due to ameliorating productivity rates and population regulation via territory limitation. Due to a reduction in eggshell thinning, and thus increased productivity, the coastal habitat showed a steady increase in λ over the study period (fig. 6). These calculations suggest that the coastal subpopulation was a sink until the early 1990s, after which productivity was high enough to sustain this subpopulation. However, our calculations showed a declining λ for interior birds as their subpopulation recovered (fig. 6). This was driven by the observed decline in the average productivity rate per year (fig. A1), and an increasing proportion of nonbreeding floaters each year (fig. 5). The decline of λ to near 1 toward the end of the study period suggests that this subpopulation may now be limited by territory availability. In the urban habitat, λ increased steadily with improved productivity rates (fig. A1) from a low of 0.86 in 1983 to a high of 1.19 in 1989. However, the estimated λ fluctuates widely (including estimates of $\lambda \approx 1$; fig. 6) after 1989 due to the abrupt relationship between territory acquisition probability and breeding population size (near $n = 11$ breeding pairs; fig. 4) and a limited number of urban breeding territories.

Effects of Management

Because of the strong habitat-specific differences in population growth, regulation, and dispersal, these three subpopulations were differentially affected by the historical introductions (fig. 7). Most remarkable was the response of the coastal subpopulation to the various management efforts. Our regional population projection, which excludes the historical introductions, indicates that in the absence of management the coastal subpopulation would have failed or been very slow to recover (fig. 7), with its recovery driven solely by dispersal from the interior and (eventually) the urban subpopulation. The rapid recovery of the coastal subpopulation that actually came about was due almost entirely to directed management efforts.

The recovery of breeding pairs in the interior subpopulation, however, was more pronounced than the coastal habitat and was largely independent of the management intervention. The regional population projection suggests

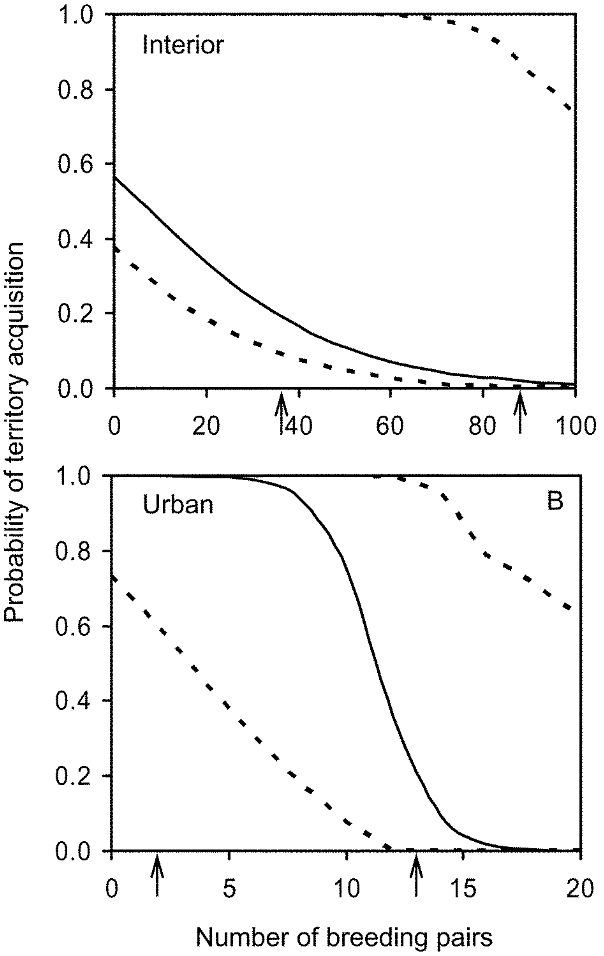

Figure 4: Density-dependent territory acquisition probabilities for the interior and urban subpopulations. Solid lines show predictions from the best-fit logistic function; dotted lines are 95% likelihood profile confidence limits. Arrows indicate the limits of the observed breeding population size for each subpopulation.

that, by the late 1980s, the reintroduction of birds into the more productive interior habitat was only responsible for increasing the breeding population by approximately five or six breeding pairs beyond what might have been expected from a natural recovery process (fig. 7). The effect of management was also apparent in the urban subpopulation. Without management intervention, the urban population growth is predicted to have lagged behind observed numbers until the mid-1990s (fig. 7). This was an unexpected result, since the management intervention that occurred in the urban habitats resulted in a net loss of young birds; only a limited number of introductions occurred ($n = 18$) compared with a large number of egg collections ($n = 59$) and translocations of urban young ($n = 81$) to the coastal habitat.

Discussion

Our results support the existence of distinct demographic differences between three separate peregrine falcon habitats in California and confirm the general spatial structure first put forth for this regional population by Wootton and Bell (1992). This spatially structured regional population is characterized by an interior subpopulation that, when the recovery began, supported a high population growth rate, an urban subpopulation with a high potential for population growth, and a coastal subpopulation that was a sink throughout more than half of our study period. The interior subpopulation recovered quite rapidly, and the urban subpopulation was able to establish and grow despite persistent collection of eggs and removal of wild young. By contrast, the coastal subpopulation—although it was unable to sustain itself—experienced a robust recovery due to a consistent and well-coordinated management program that introduced hundreds of young birds into coastal breeding areas.

Our analyses indicate that subpopulation growth and performance of California peregrines was asynchronous because these habitats are asymmetrically connected by dispersal. Individuals in the largest and most productive habitat—the interior—show little propensity for dispersal to the coastal or urban habitat (both $D_{\mathrm{i,u}}$ and $D_{\mathrm{i,c}}$ were near 0). Birds from the coastal habitat appear to disperse rarely to the interior population, but disperse to the urban habitats with higher probability ($D_{\mathrm{c,u}} = 0.154$). While the urban subpopulation was largely founded by and has received a fair percentage of its breeders from the coastal subpopulation, the existing evidence only weakly supports movement from urban sources to the coastal subpopulation (only one bird has been observed to make this transition). Thus, this system is characterized by asymmetric dispersal rates between habitats, in addition to strong differences in habitat-specific demography.

This analysis provides a useful examination of the effects of asymmetric dispersal behavior on population dynamics of a spatially structured population that, because of the population crash and subsequent recovery, is not at an equilibrium condition. Nonequilibrium dynamics are likely to be common for many species of conservation concern, as well as many unmanaged populations that experience periodic disturbances. Disparate subpopulation densities resulting from habitat-specific population recovery rates may result in dispersal behavior that is different than the optimal behavior expected for stable populations (Pulliam and Danielson 1991). In this study, demographic differences produced remarkably varying population trajectories and stage structure between subpopulations, which potentially affected observed dispersal patterns. In particular, the interior subpopulation rapidly recovered and began to fill up existing

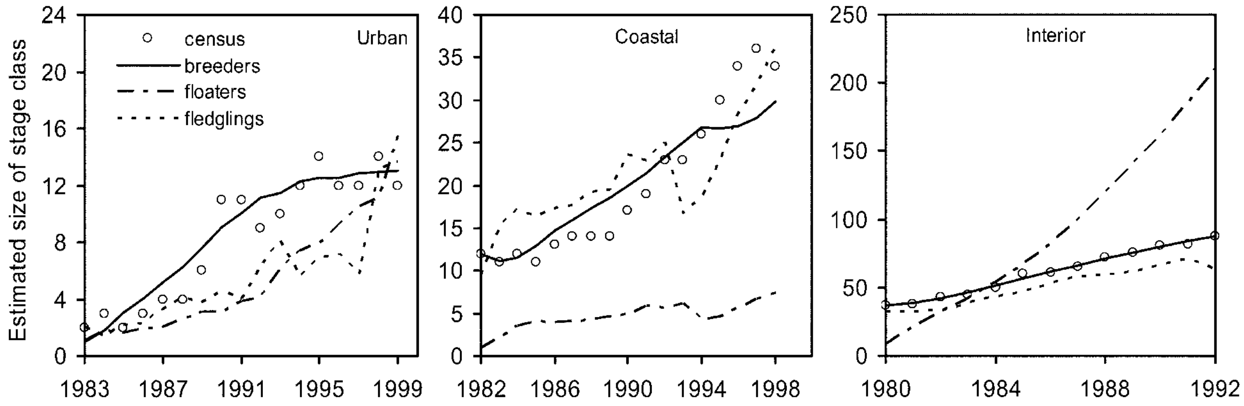

Figure 5: Habitat-specific demography creates disparate projected stage structures for recovering peregrine falcon subpopulations in interior, coastal, and urban habitats of California. All projections are based on the best-fit regional population model.

suitable territories leading to the early development of a floater population. During this same time, many historical nest sites remained empty in the coastal habitat, even though these sites must have appeared desirable to a dispersing bird (and were, in fact, high-quality sites after 1990, once annual productivity increased to a level where $\lambda > 1$). It has been widely assumed that dispersing individuals are capable of selecting the habitat that best insures their fitness (Pulliam 1988; Pulliam and Danielson 1991; McPeek and Holt 1992; Doncaster et al. 1997; Diffendorfer 1998). However, based on band recoveries, dispersers from the interior habitat were very uncommon in the coastal habitat despite the fact that they were abundant and would have to wait years to acquire a breeding site in their natal habitat. At the same time, birds from the coastal habitat appear to be selecting urban nest sites (15 coastal birds were observed making this transition, and confidence limits for $D_{c,u}$ are relatively narrow). Below we explore several possible explanations for these trends.

Some bird species may have the ability to select habitat based on proximate indicators of habitat quality such as breeding success. Wiklund (1996) has shown that breeding merlins (*Falco columbarius*) with historically poor reproductive success have higher breeding dispersal distances than more successful breeders. Similarly, a number of bird species have been shown to select habitat based on the reproductive performance of conspecifics (Danchin et al. 1998; Brown et al. 2000). If peregrine falcons select habitat in this way, it would help explain why urban and interior birds did not disperse to coastal breeding territories—where nest failure was common—during the 1980s (fig. A1). A second possible explanation that addresses why birds did not disperse out of the interior habitat (and why coastal birds dispersed to urban habitats) is habitat selection through conspecific attraction (e.g., Muller et al. 1997; Hanley et al. 1999). For peregrine populations, which are known historically for their remarkable stability (Ratcliffe 1980), and where floaters must replace breeders to acquire a territory, conspecific attraction may be an optimal strategy for selecting a breeding habitat. A third explanation for the limited dispersal between the coastal and interior habitats is the geographic distance between these two habitats. Young birds probably face energetic limitations when searching for vacant breeding sites (Orians and Wittenberger 1991), and historically stable populations may not be adapted for such long-distance natal dispersal. Interior birds would have to sample an enormous area to discover, select, and recruit to the cliff habitats of the southern coast. That we found the highest dispersal estimates from coastal to nearby urban sites also supports the notion of spatial limits to effective dispersal.

In addition to asymmetric dispersal, the strength and timing of subpopulation regulation varied between habitats due to the number of available breeding sites in, and intrinsic growth rate of, each subpopulation type. The long-term data set analyzed here has allowed us to understand critical temporal dynamics of this spatially structured population, namely, territory limitation in the interior and urban habitat and ameliorating demographic rates in the coastal habitat. Many authors have acknowledged the importance of these temporal effects, especially in source-sink systems (Pulliam and Danielson 1991; Watkinson and Sutherland 1995; Pulliam 1996), but empirical examples remain rare (but see Thomas et al. 1996). While our model fitting found strong support for limits to population growth in the interior subpopulation, one caveat is warranted. Although we cannot quantify the potential bias, we suspect that in the early years annual population monitoring may have underestimated the size of the interior subpopulation due to the inability to find all breeding territories. If this was a large bias, it would exacerbate

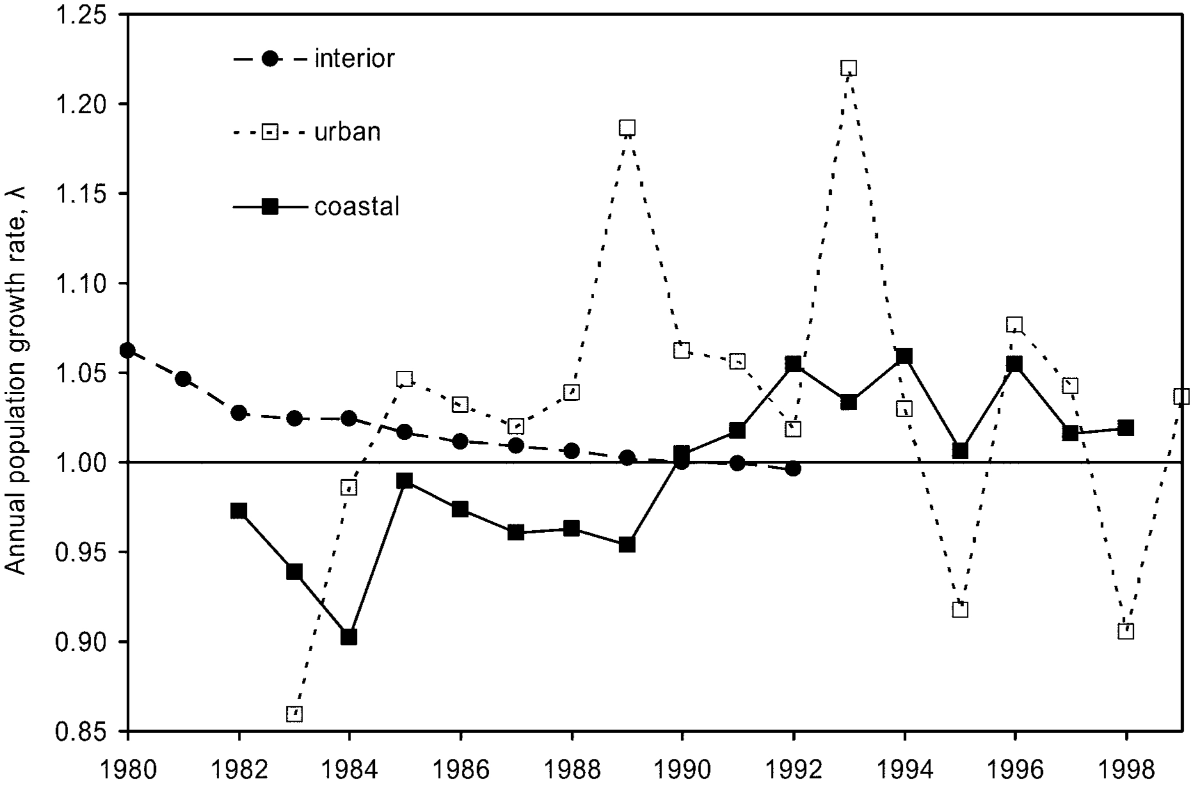

Figure 6: Trends in analytical population growth rate (λ) for three peregrine falcon subpopulations in California. Estimated λ declines through time in the interior subpopulation due to declining productivity rates and limited breeding territories but increases in the coastal subpopulation due to DDT dissipation that has resulted in increasing productivity rates. Territory acquisition rates do not change throughout the recovery of the coastal subpopulation. Dotted line indicates a stable population growth rate (λ = 1).

the trend of population regulation that we detected in the breeding pair census data.

It is important to note that we also included the declining productivity trend of interior birds (fig. A1) in all regional models. Whether this decline in productivity is due to increasing floater pressure or the temporal (and optimal) selection of increasingly poorer quality nest sites as the population increased—so-called site-dependent regulation (Rodenhouse et al. 1997)—is unknown. What is clear is that if site-dependent regulation is the cause of the productivity decline, it was not sufficient to bring about the population regulation observed in the breeding pair census data. Instead, the mechanism of territory saturation and the development of a floater population (i.e., delayed breeding of adults) was necessary to explain the observed decline in growth rate of the interior subpopulation. The regulation of bird populations by territory limitation has been known for some time (Moffat 1903; Brown 1969; Hunt 1998) and is now widely supported by experimental studies (reviewed in Newton 1992). However, its influence on the dynamics of a recovering population has rarely been documented (Newton 1979, 1998).

Together, asymmetrical dispersal rates and habitat-specific demography have had large impacts on the dynamics of this spatially structured population and its management. In particular, it is evident that a lack of immigration from the urban and interior source habitats made artificial augmentation of the coastal sink habitat critical for recovery of that subpopulation. This differs from the results of earlier modeling efforts by Wootton and Bell (1992), which suggested that management efforts (introductions) should be focused on the more productive interior source population. Lacking the additional 10 years of data we now have, Wootton and Bell (1992) assumed a symmetrical per capita dispersal rate of 0.27 (as compared with our estimate of 0.006 for $D_{i,c}$). With this high rate of dispersal, their model suggested that birds introduced in the northern interior would eventually produce young that would naturally emigrate to and sustain the coastal subpopulation. By incorporating empirical data on dispersal into our modeling analysis, we find

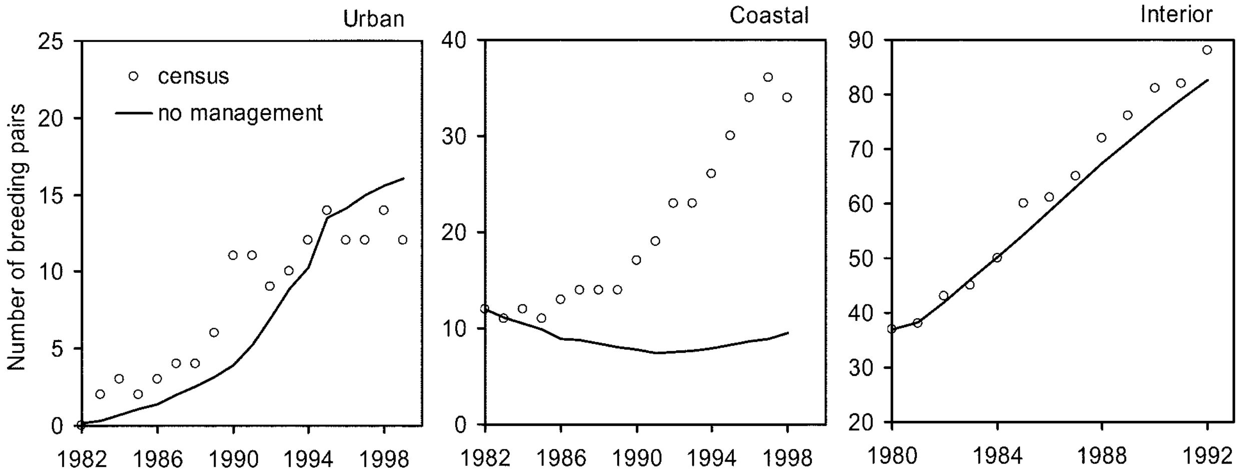

Figure 7: Effect of management on population recovery of peregrine falcons in urban, coastal, and interior habitats of California. The observed number of breeding pairs (*open circles*) is shown in each habitat along with the subpopulation recovery that would have occurred under a "no management" scenario (*solid line*) if no eggs were collected and no fledglings were introduced into any habitats.

that this was unlikely to have been an effective management strategy because interior birds have largely remained in their natal habitat.

The growth of a breeding population in the urban habitats also underscores how strong habitat differences and asymmetric dispersal behavior can mediate management efforts. In the urban habitat, historical management efforts should have reduced subpopulation growth in comparison to an unmanaged scenario because these efforts resulted in a large net reduction in urban young through both egg collecting and translocation of urban birds to the coastal habitat. However, the overall result of management efforts in these adjacent habitats was to increase the growth rate of the urban subpopulation. This occurred because the direct negative effects of management on the urban subpopulation (egg collection and removal of young) were outweighed by the indirect positive effects that resulted from the augmentation of the coastal subpopulation and the subsequent dispersal of those introduced birds to urban habitats (fig. 7). These insights into the management of California peregrines underscore the need to understand the natural history of movement and dispersal and their incorporation into spatial models of species viability (Wennergren et al. 1995).

Our analysis illustrates the necessity of understanding spatial structure and its effects on managed populations of conservation concern. Because we treated the three habitat types separately, it is clear that the coastal subpopulation was a sink throughout much of the recovery and that management intervention played a critical role in facilitating its recovery. Only by fully characterizing the habitat-specific demography of the two other habitat types (which were much more productive) were we able to disentangle the effects of the historical introductions from natural immigration from source populations. Similarly, this study highlights the importance of understanding habitat-specific demographic rates rather than population counts alone (van Horne 1983). Population monitoring of the peregrine falcon recovery in California has been better than for most endangered species, but still a reliance on population trends alone without additional estimation of demographic rates would yield a misleading diagnosis of the health of the coastal subpopulation throughout the 1980s. Analyses of this kind can provide scientific guidance on how best to target management efforts and also how to determine when a cessation of management is warranted.

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