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Stage-structured Matrix Models of Common Ravens (*Corvus corax*) in the West Mojave Desert, CA

U.S. DEPARTMENT OF THE INTERIOR
U.S. GEOLOGICAL SURVEY
WESTERN ECOLOGICAL RESEARCH CENTER

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Abstract

Common Ravens (*Corvus corax*) have dramatically increased in number during the last several decades in the Mojave Desert, in association with human development. Although ravens are a native species, this increase has raised concerns about public health, due to their extensive use of landfills as food sources, and about threats to desert fauna due to raven predation. We developed simple stage-structured demographic models of raven populations, based on seven years of research on the population biology of ravens in the west Mojave Desert. We used these data to estimate fecundity for the population as a whole and by habitat (urban, ecotonal, and desert). Ravens trapped and marked at the Edwards Air Force Base landfill were used to estimate juvenile and non-breeding adult survival probability. Hatch year survival probability was estimated for this population in a published paper (Webb et al. 2004). We found that two unknowns, breeding adult survival probability and transition probabilities between non-breeding adult (“floater”) and breeding adult classes had important effects on estimated population growth rate. The local demographic processes only produced growing populations if breeding adult survival was greater than non-breeding adult survival (estimated to be 0.79). Ravens breeding in “urban” habitats where access to human-provided resources is greatest had greater hatch-year survival and fecundity, and their populations would be stable or growing if breeding adult survival was equal to or greater than non-

breeding adult survival. In contrast, “desert” habitats always produced declining population growth rate estimates. Transition probabilities needed to produce observed ratios of non-breeding to juvenile ravens at landfills were unrealistically high, suggesting that immigration may be important for the dynamics of this population. Recovery times following simulated reductions of either the “landfill” classes (non-breeding adults and juveniles) were shorter than for reductions in the “non-landfill” classes (breeding adults and hatch-year birds). Populations always recovered, even after a 100% removal of breeding ravens, although recovery times could be as great as 20 years. Effectiveness of control actions will depend on timing and intensity of effort, as well as the raven age classes that are targeted.

Introduction

Common Ravens (*Corvus corax*) are generalist scavengers and predators that have flourished in close association with people throughout most their North American range (Boarman and Heinrich 1999, Marzluff and Angell 2005), and in the west ravens are viewed as indicators of human disturbance (Boarman 1993). In the west Mojave Desert, raven populations are tightly associated with sources of human resource subsidies (Knight et al. 1993, Boarman et al. unpubl. data), such as the food they can obtain at landfills (Kristan et al. 2004). Although breeding ravens use and benefit from human resource subsidies (Kristan 2001, Kristan et al. 2004, Webb et al. 2004), large aggregations of ravens at landfills are primarily composed of non-breeding juveniles and adults (Boarman et al. in review). Aggregations of ravens at landfills persist during the breeding season, although breeders spend most of their time in their territories. Breeding adults are more evenly distributed throughout the desert, and are found in large numbers in undeveloped desert, where their reproductive success is poor (Kristan 2001), and post-fledging survival is low (Webb et al. 2004). Ravens at landfills are considered potential disease transmission vectors and in

the Mojave Desert pose a threat to wildlife (Kristan and Boarman 2003); consequently ravens are subject to control actions (Boarman 2003). Because of the ecological differences between non-breeders and breeders, predicting the population dynamics of subsidized populations of ravens in the desert requires a formal population modeling approach. Population models can be used to predict the efficacy of control, as well as the likelihood of inadvertent extirpation of a population by reducing numbers of juveniles and non-breeding adults at landfills.

Stage-based matrix population models provide a means of inferring how populations will change in the future, given a set of demographic rates (Caswell 2001), and have been used successfully to project populations of birds, such as the Semipalmated Sandpiper (Hitchcock and Gratto-Trevor 1997). Matrix models can be used to predict rates of population change (λ), as well as to estimate the relative numbers of individuals that will be present in different classes, such as age or breeding classes (Caswell 2001). Additionally, it is possible to estimate the relative effect of change in each demographic parameter on change in population growth rate, which are called “sensitivities” (if the same absolute amount of change in each parameter is used) or “elasticities” (if the same relative amount of change in each parameter is used) (Caswell 2001). Elasticity analysis can be used to explore the effectiveness of alternative control activities that are focused on particular classes, and elasticities are also useful for identifying the relative importance of unknown parameters, which can help identify data needs for future studies.

Our goal was to use estimated demographic parameters from a seven-year study of a population of ravens in the west Mojave to model raven population dynamics, and predict the response of populations to reductions in either breeding or non-breeding segments of the population. Additionally, we sought to use mismatches between projected population dynamics and the observed behavior of raven populations in the region to identify data needs so that the range of possible responses to management could be reduced in the future.

Methods

Model population

The authors and their colleagues have studied ravens in the West Mojave Desert since 1994. The study population occupies extensive Joshua-tree woodlands, in association with creosotebush (*Larrea tridentata*) and saltbush (*Atriplex* spp.) scrub, on and in the immediate vicinity of Edwards Air Force Base (EAFB), CA. In addition to native desert scrub habitats, several small towns are present in the area: Rosamond, Mojave, North Edwards, and the EAFB cantonment. Towns and associated landfills and sewage ponds provide ravens with a rich assortment of food and water resources. The primary study area encompassed approximately 770 km², within which as many as 168 breeding pairs initiated breeding within a year. More complete descriptions can be found in Kristan and Boarman (2003) and Webb et al. (2004).

We recognized four distinct classes, for which demographic rates were estimated: hatch year (HY), juvenile (J), non-breeding adult (NB) and breeding adult (BR). Hatch year birds included individuals that had successfully fledged, through their first year of life. We did not include a class of nestlings, as their survival was included in our fecundity rate estimates. Ravens were considered juveniles in their second year, after which they became adults. Because there was a large population of non-breeding adults that aggregated at attraction sites (Boarman et al. unpubl. data), it was necessary to have two adult classes. Surviving non-breeders were assumed to be recruited into the population at some hypothetical rate (up to 100% in some models). Additionally, in some models breeding adults were allowed to leave the breeding population and join the non-breeding population. Models that allowed for a multiple-year residence in the non-breeder class, and movement of breeders into the non-breeder class, thus assumed that aggregations of non-breeding adults were “floaters” (Smith 1978).

Demographic data (described below) were collected during portions of the seven-year period, and form the basis for population models. Descriptions of each estimated parameter follow.

Fecundity

Estimates of fecundity rates (f) were obtained from reproductive monitoring of the study population between 1996 and 2000 (Kristan and Boarman, unpubl. data). The only reproductive class in our models was the BR individuals, and thus we had only one class-specific fecundity estimate. The breeding population (i.e. the number of individuals in the BR class) was defined as all pairs that moved out into breeding territories in the spring, whether they laid eggs or not. Fecundity was thus estimated as one-half of the average fledging success for territories that were occupied during each season (Table 1).

Fledging success varies among years and among habitats for desert ravens (Kristan 2001, Kristan and Boarman, unpubl. data). We estimated average fecundity among years, and concentrated on differences in fecundity among sites. Ravens that nest near urban areas have a greater incidence of trash in their pellets, indicating greater consumption of human-provided foods, and these ravens have increased fledging success (Kristan et al. 2004). Furthermore, the small landfills on the study area were associated with nearby towns. Ravens select breeding sites that are near towns, landfills, and other sources of trash, and we should expect that ravens would exhibit “site dependent” population dynamics (Rodenhouse et al. 1997). Site-dependent regulation refers to a pattern of consistent occupancy of high-quality habitat, and use of low-quality habitat at large population sizes when high-quality habitat is unavailable. Although correctly considered a form of density-dependence, the quality of occupied territories does not decline with increasing density in site-dependence. Thus, an overall estimated decline in population size could indicate “overpopulation” of high-quality habitat. Ravens would then use low-quality desert habitat as high-quality urban habitat is filled and additional ravens are excluded due to territorial behavior.

Because of the patchy availability of urban habitat in our study area, territories could be classified as “urban” (those that fell entirely within towns), “ecotonal” (those that included both desert and urban habitat within their territories) and “desert” (those that contained only desert habitat). Fledging success was calculated separately for each habitat type for models that explored the importance of urban resource subsidies on population dynamics.

Survival probabilities

Survival probabilities were estimated for marked ravens. Ravens were trapped using cannon nets at bait stations, in 1994, 1995, 1996, 1997, and 1999 at the EAFB landfill. All captured ravens were marked with patagial markers, and a subset of trapped ravens was fitted with radio transmitters at each capture event. Ravens were re-sighted during weekly surveys of attraction sites throughout the region (Boarman et al. unpubl. data), and during weekly radio tracking, resulting in 174 capture histories that could be used for survival analysis, of which 84 had live radio transmitters during at least part of their capture history. Marks faded and became illegible on ravens trapped in 1994, and they were dropped from survival analysis.

We modeled survival probabilities (s) for three age classes: HY, J, and NB. Few breeding adults were trapped at the landfill, and because they nested in the vicinity of the landfill, rather than being distributed across the study area, we could not be certain that they were representative of the breeding population as a whole; we therefore could not estimate s_{BR} from our capture data. Survival probabilities will be subscripted by age class throughout (e.g. hatch-year survival will be s_{HY}).

Survival analysis was done using program MARK (White and Burnham 1999), using a recaptures-only model. Survival and recapture probabilities are estimated in MARK simultaneously using a maximum likelihood approach, and the best-supported model for a set of capture histories is selected using information-theoretic techniques (Burnham and Anderson 1998). Because recapture probabilities were expected to be sensitive both to age (because of possible age-related differences

in movements) and marking method, heterogeneity in recapture probabilities (p_i 's) was explored in detail. Survival probabilities were modeled as age- and year-dependent, and these models were compared to reduced models in which survival probability was constant across ages, across years, or both. Although the survival models are able to account for failure to detect live birds during surveys, they cannot account for permanent emigration from the population, which would falsely appear to be mortalities. Consequently our numbers are likely to be conservative estimates of true survival parameters.

Although we modeled s_{HY} from our landfill data so that we could explore age-specific variation in survival among years, we had reason to suspect that our estimates were not indicative of first year survival in ravens. Webb et al. (2004) studied first year survival in the same population, but marked chicks still in nests in 1999 and 2000. They found that post-fledging survival was lower in first-year birds than in second- or third-year birds, but this effect was primarily due to high mortalities prior to departure from the natal territory. Once fledglings left the natal territory and joined aggregations of ravens, such as at the EAFB landfill, survival probability was substantially increased. Consequently, we estimated first year survival using the product of two survival estimates from Webb et al. (2004): (1) survival after fledging but before departure from the natal territory, and (2) survival after departure through the first year (Table 1).

We could not be certain that survival probabilities obtained from landfill birds was representative of the breeding population because of the small number of ravens trapped at the landfill that proved to be breeding birds. Breeding ravens experience the increased demands of reproduction (which tend to reduce adult survival), but are also territorial and can defend food sources (which would tend to increase adult survival). Estimates of breeding adult raven survival probability in the Olympic Peninsula of Washington varied by habitat type, but never exceeded 78% (J.M. Marzluff and E. Neatherlin, unpubl. data). Lacking an obvious survival advantage or

disadvantage for breeders based on first principles, we modeled a range of hypothetical survival probabilities for the adult breeding population.

Although we did not have empirical estimates for s_{BR} or for transition probabilities among breeding and non-breeding adult classes, we were able to use survey data (Boarman et al. unpubl. data) to help bound the plausible range of values for these parameters. The age class composition of ravens trapped at the EAFB landfill gave us an estimate of the ratio of adult to juvenile ravens in the non-breeding NB/J = 1.28). For a given adult survival probability, it was possible to find combinations of transition probabilities for entry of non-breeders into the breeding population and of breeders into the non-breeding population that produced a ratio of NB/J of 1.28 in the model's stable age distribution. These values were found numerically by selecting hypothetical values for s_{BR} and one of the transition probabilities and solving for the other. This process allowed us to explore the range of transition probabilities that were likely to occur under the assumption that the populations were at stable age distribution and that there was either no immigration or that the pool of immigrants had the same ratio of NB/J as was produced by intrinsic growth processes.

Population models

Although we were able to use empirical estimates for many demographic parameters (Table 2, Results), we lacked estimates for s_{BR} and transition probabilities between NB and BR. Multiple models were constructed that contained a range of parameter values, so that the dependence of population dynamics on unknown parameters could be evaluated.

A first set of models (“average habitat” models) was constructed to explore the population dynamic properties of west Mojave ravens, beginning with a model that used observed point estimates for each parameter, for which an estimate was available. In the average habitat models, we assumed that all surviving NB ravens became breeders after one year (thus the probability of transition from NB to BR was set to 1.0). Lacking an estimate for s_{BR} , we set $s_{BR} = s_{NB}$ (and thus,

equal to s_j ; see “Results, Survival probabilities” below). Population growth rate and elasticities for model parameters were calculated for this model. Parameters were then varied across a range from 20% decrease to 20% increase, so that the combination of parameters that produce an overall population growth could be identified. The results of this first set provided an assessment of the robustness of conclusions that could be drawn given the uncertainties in parameter values.

Next, a set of models was constructed to explore the effects of anthropogenic resource subsidies on raven population growth (“subsidy” models). Known effects of human subsidies on fledging success (Kristan 2001) and first-year survival (Webb et al. 2004) were used to parameterize models for the “urban”, “ecotonal” and “desert” ravens. These models, like the average habitat models, assumed that all birds moved into the breeding adult class after one year as a non-breeding adult. Because ravens move to non-breeding aggregations as HY individuals, we assumed that J and NB individuals were part of the same non-breeding population, and thus s_j and s_{NB} were set to the same, empirically estimated value for all habitats.

A second set of subsidy models was constructed to explore the importance of the unknown relationship between breeding and non-breeding segments of the population (“floater” models). Because the subsidized segment of the population has the greatest growth rates, and is most likely to contribute to a floater population, models were parameterized with the “urban” s_{HY} , s_j , and f values. For these models we assumed that s_{BR} would be at least as high as s_j , and thus s_{BR} was varied from the estimated value of s_j up to 120% of s_j . For each value of s_{BR} , transition probabilities were varied across the range that resulted in the observed ratio of NB/J of 1.28.

The ability of a raven population to recover after a control action is taken depends on the nature and duration of the action. Short-term, one-time reductions in raven population size at an attraction site is expected to have no lasting impact on intrinsic survival and fecundity rates, and can be modeled as a change in the population vector (i.e. the vector representing the number of

individuals in each age class) rather than the projection matrix (i.e. the matrix containing demographic rates). Although no change in growth rate occurs when the population vector is changed, it is possible to have temporary decline in numbers as a shortage of new recruits prevents replacement of lost breeders, and such declines can cause an extinction event in a population with a $\lambda > 1.0$ (if the population size declines below 2.0 we would consider the population extinct). We simulated reductions in raven numbers due to control actions at landfills in the spring, when breeding birds and hatch-year birds would be largely unaffected, and control actions aimed at breeders and nestlings, which would leave non-breeders and juveniles largely unaffected. For simplicity, therefore, we considered the J and NB classes to be the ones affected by actions at the landfill, and HY and BR classes to be the ones affected by actions at breeding territories. Reductions were varied from 20% to 100%, and population size was projected until it either recovered to its pre-reduction size (100 individuals), or went extinct. The alternative strategy, of permanently reducing survival or fecundity, was not specifically modeled, but any strategy that reduces growth rate to less than 1.0 would be expected to result in the eventual extinction of the population. It was therefore possible to evaluate how much change in demographic rates would be needed to drive this population to extinction by observing which combinations of parameter values resulted in growth rates less than 1.0. We evaluated recovery time using subsidy models.

Because recovery time depends on unknown parameters (such as s_{BR}), we once again selected different parameter values to explore the range of likely outcomes. However, only values of s_{BR} that produced a growing population within urban habitats were used, because populations would not recover at all otherwise. This represents a mild assumption, essentially equivalent to assuming that at least some of the growth in population size in the desert is attributable to local recruitment rather than immigration. The parameter s_{BR} was assumed to be the same in all habitat types. Breeding adult survival probability was selected in two ways: (1) by setting the weighted

average growth rate across all habitats to 1.0 (weighted by the number of territories found in urban, ecotonal, and desert habitats), and (2) by setting the growth rate in ecotonal habitats to 1.0. All models used measured values for f , s_j , and s_{NB} . All non-breeders became adults after one year, and no breeders became floaters.

Results

Survival probabilities

Both wing-tagged and radio-tagged ravens were recorded during the study. Models that distinguished between marking methods had little statistical support, and thus resightings of ravens with different mark types were combined for survival analysis. Although there was strong support for annual variation in either survival probability or resighting probability (but not both), there was no evidence of age-specific survival in ravens trapped at the EAFB landfill (Table 2). Statistical support for each survival model was assessed by comparing their Akaike's Information Criterion (AIC) values (Burnham and Anderson 1998); the model with the smallest AIC is the best supported. Differences in AIC values (ΔAIC) of 4.0 or more between models indicates a substantial difference in support. The best-supported model that included age-specific survival had a ΔAIC of 4.11, indicating poor relative support. The survival probability estimate from the model with annual variation in resighting probability but constant survival was 0.794 (95% C.I. = 0.748 – 0.834). This value was used as the “estimated” value for s_j and s_{NB} in all population models.

Average habitat models

Models based on the estimates of s_{HY} , s_j , s_{NB} and f , and assuming that $s_{BR} = s_{NB}$ yielded a population growth rate of $\lambda = 0.89$, indicating a population that is declining by 11% per year. Of the models that used $\pm 20\%$ deviations from estimated values, the only models that reached or

exceeded a growth rate of 1.0 were those with a 20% increase in adult survival (Table 3).

Increasing all other parameters by 20% while holding adult survival at the point estimate value of 0.8 still resulted in a declining population ($\lambda = 0.95$). In contrast, increasing s_{BR} to 0.96 resulted in a growing population in all but the model with the lowest values of all other parameters. The stable age distribution of average habitat models was dominated by BR (53.3%) and HY (33.3%) birds. Holding all parameters at their empirically-estimated values, the survival s_{BR} needed for the population to be stable was 0.932. Population growth was most strongly affected by s_{BR} (elasticity of 68%, indicating that 68% of the variation in growth rate is attributable to this parameter). Survival in all other classes and fecundity all had identical, low elasticities (8%).

Subsidy models

Fledging success and hatch-year survival both benefit from human-provided resources. With these benefits, and assuming no survival advantage for breeding adults, populations in urban areas were stable ($\lambda = 1.00$), whereas ravens in ecotonal or desert areas had declining populations ($\lambda = 0.91$ and 0.89 respectively, if s_{HY} was assumed equal, but 0.94 and 0.85 respectively if s_{HY} was assumed greater in ecotonal areas; Table 4). Assuming a greater survival probability for breeding ravens in all habitats raised growth rate to the point that models in all habitats had growth rates greater than 1.0, except for nests in desert areas when HY survival was assumed to be lower than in ecotonal areas.

The greatest differences in stable age distributions occurred between urban birds and desert birds in the J, NB, and BR age classes (Table 5). Lack of J and NB birds in the declining desert populations produced very few non-breeding adults (3.7%).

Floater models

Floater models were based on “urban” subsidy models, with the addition of movement between the NB and BR classes. All models in which there was no assumed survival advantage of breeding predicted declining populations if a floater population was present. When, for comparison, all non-breeders became breeders after one year, with no movement of breeders into the non-breeder population, then populations in urban areas were stable (the “urban” subsidy model). When breeding ravens were assumed to have greater survival than non-breeders populations could grow in the presence of a floater population, provided that NB individuals became BR at twice the rate than the converse (Table 6). The proportion of the population in NB and J age classes (i.e. ravens at the landfill) was greatest when BR survival was at 0.8 and the proportion of BR ravens entering the NB class equaled the proportion of NB ravens entering the BR class (Table 7). Increased s_{BR} and uneven exchange between NB and BR classes reduced the proportion at the landfill, but even this reduced proportion was higher than in the average habitat models in which NB became BR after a year and no floaters were produced at all (Table 5). Floater models therefore had the greatest relative number of non-breeding individuals of all the models considered, and thus predict the largest population at landfills and other attraction sites for a given breeding population size. Numbers of non-breeding adults exceeded the number of breeders in several models (Table 7), although none of the models with more non-breeding adults than breeding adults had population growth rates that exceeded 1.0 (Table 6).

Ravens captured at the EAFB landfill were 56.8% adults and 43.2% juveniles (hatch-year ravens were rarely caught), for a ratio of 1.28 adults per juvenile in the non-breeding population. Using the ratio of NB/J ravens to constrain the transition probabilities between the NB and BR classes shows that, for a given s_{BR} , between 0 and 18% of breeding adults are expected to enter the non-breeding population in any given year (Figure 1). The range of possible transition probabilities

from NB to BR classes is broader, ranging from 0.43 to 1.0. Greater s_{BR} led to different relationships between entry into and movement out of the breeding population (Figure 1). If no breeders become floaters, then increasing adult survival probability leads to increased recruitment into the breeding population. In contrast, if the probability that a breeder becomes a floater is at 0.15, then increasing survival probability leads to a decreased proportion of NB individuals that move into the BR class.

Recovery time

The basic model used to estimate the effects of population reductions on time to recovery was a subsidy model that used “urban” parameters for s_{HY} , s_{NB} , and f . When the overall population across the three habitat types was assumed to be stable, $s_{BR} = 0.949$ and $\lambda_{urban} = 1.099$. Populations recovered to pre-removal size after two years with up to 40% one-time removal of non-breeders, and took six years with 100% removal of non-breeders (Figure 2). Breeding population size did not decline at all until 100% of the non-breeders were removed, and then breeding population size declined from 38 to 34 individuals before recovering. When breeding adults and hatch-year birds were targeted, recovery times were longer, taking up to 13 years to reach pre-removal numbers with 100% removal of breeders and hatch-year birds. When ecotonal habitat was considered to be stable, rather than the entire population across all three habitats, s_{BR} declined to 0.881, and $\lambda_{urban} = 1.052$. The same general patterns of recovery times were seen with this projection matrix, but declines in the breeding population with 100% removal of non-breeders was greater (from 38 to 29), and recovery times were greater, taking up to 22 years to reach pre-removal numbers with 100% removal of breeders and hatch-year birds (Figure 3).

Discussion

Detailed prediction of raven population dynamics from our models is complicated by the presence of several important unknowns. Ravens in the Mojave Desert increased dramatically since 1968 (Boarman and Berry 1995), and large aggregations of them can be found consistently at attraction sites, such as landfills (Boarman et al. unpubl. data). Use of human-provided foods and nest substrates in urban areas increases fledging success (Kristan 2001) and post-fledging survival (Webb et al. 2004). In spite of the overwhelming impression that this collection of observations leaves that raven populations are exploding in the region, our data provide only weak evidence that local resource subsidies are driving the increase, and in fact the population as a whole would be rapidly declining based on our empirical estimates of demographic rates. However, our population models are most sensitive to changes in breeding adult survival, a parameter for which we do not have an empirical estimate. When we assume that breeding survival is 20% higher than juvenile survival, populations in urban areas grow explosively, but when we use the very conservative assumption that breeding adult survival equals juvenile survival these same populations are stable. Such great importance of an unknown parameter is problematic.

A second important unknown is the degree of exchange between breeding and non-breeding adult segments of the population. Population growth is not as sensitive to the parameters that model this process, but without empirical estimates of them it is difficult to know whether local productivity can explain the presence of large aggregations of ravens at attraction sites. Our data suggests that juveniles flow into the non-breeding population, but we have little information about the rate of recruitment from the non-breeding population into the breeding population. Fledglings from nests in the study area join aggregations of ravens in their first year (Webb 2001), and most ravens trapped and marked at the EAFB landfill moved between several attraction sites within the study area (Boarman et al. unpubl. data). Movement among attraction sites becomes less likely as

distance between them decreases (Boarman et al. unpubl. data). These patterns suggest that once ravens are part of the population in our study area they tend to remain there. We also had only five individuals trapped between 1995 and 1999 enter the breeding population, suggesting that rates of transition from NB to BR are low, in contrast to the high numbers suggested by Figure 1. To explain the large aggregations of ravens at attraction sites only with local population dynamics, high adult survival probabilities lead to the most realistic transition probabilities, provided that breeders commonly become floaters. Individuals that fail to reproduce may become floaters in the hope of acquiring better breeding habitat later, and a more complex set of models that link urban, ecotonal, and desert segments of the population may be better able to account for floaters. A large immigration rate into the area may help explain the large population of non-breeders, and if immigrants are more often adults than juveniles then lower transition probabilities may become plausible. However, additional field work would be needed to confirm these predictions, and to assess whether large-scale immigration into the area occurs.

Survival analysis showed that resighting probabilities did not differ between wing-tagged and radio-tagged individuals, and that survival probability did not differ by age. The usual benefit of radio-telemetry for resighting animals was not found in our data set for several reasons. First, ravens in our population aggregated at a small number of locations with food or water resources, and moved primarily between them (Boarman et al. unpubl. data). Second, although radio-tagged ravens may have been easier to locate initially, they were usually found with other ravens, and all marked ravens were recorded. Third, a “resighting” was recorded for any raven that was seen at least once during a one year period; although radio-tagged ravens may have been seen more frequently within a year, most ravens that stayed in the area were seen at least once per year.

The lack of difference in survival probability among ages is not surprising, given that ravens were all trapped at a superabundant food source, the EAFB landfill. Webb et al. (2004)

found that once hatch-year birds joined aggregations at landfills their survival probabilities increased to 0.82, which is very similar to our estimate of 0.79. Ravens in these groups are exposed to similar ecological conditions and are shielded from food limitations, such that we were unable to detect differences in survival probability among age classes.

Given the strong habitat quality gradient created in the study area by introducing human-provided resources to an otherwise inhospitable environment it is not surprising that urban-nesting ravens exhibit increasing population growth. Ravens aggregate their nests near towns, landfills, sewage ponds, and other sources of human resources (Kristan 2001). Nests are re-used between breeding seasons, and are more consistently occupied over time near attraction sites than they are in open desert. That a gradient in fledging success and pre-departure survival can be detected (Kristan 2001, Webb et al. 2004) indicates that density-dependence is not equalizing habitat quality (as occurs in an ideal-free population, Fretwell and Lucas 1970), but rather that ravens are obtaining and defending superior territories in urban areas, and as population size increases a greater number of ravens are forced into poor-quality desert habitat (as occurs in an ideal-despotic population [Fretwell and Lucas 1970], or in “site-dependence” [Rodenhouse et al. 1997]). Because low-quality habitat has a growth rate less than 1.0, high-quality habitat has a growth rate greater than 1.0, and ravens select high-quality habitat, our study site can be considered a source-sink system (Pulliam and Danielson 1991, Kristan 2003). Population growth rates will be higher than indicated by the average habitat models because of the preferential use of high-quality habitat (Kristan 2003). A similar pattern has been described for crows that use human-provided resources at campgrounds in the Olympic Peninsula of Washington (Neatherlin and Marzluff 2004).

Provided that the breeding population is not impacted, temporary reductions in the non-breeding segment of the population should have very little effect on population persistence. Breeding raven numbers decline after a large reduction in non-breeding individuals because more

breeding adults are dying than are being recruited into the population, and in very small populations this could cause the loss of adult breeders; this would be seen in a simulation model as the number of BR individuals dropping below 2.0 individuals. However, in the relatively small population size of 100 used in our simulated removals, breeding adult numbers declined from 38 to 29 under the most extreme case of 100% removal of J and NB individuals with s_{BR} of 0.88, and this population recovered after nine years. In contrast, if removal is targeted at the breeding segment of the population, then recovery is much slower and total population size declines while non-breeding individuals move into the breeding population. However, we caution that our models provide a less realistic simulation of removal of breeders, because in real populations floaters would be expected to occupy breeding vacancies quickly. Consequently, recovery times are expected to be greatly reduced when breeders are removed, and the population would quickly come to resemble the models of reduced NB and J classes rather than HY and BR classes.

Recovery-time estimates are based on the assumption that there is no immigration into the population. Ignoring immigration makes these calculations conservative relative to extinction probability, because vacancies in both the breeding and non-breeding segments of the population would be filled both by local recruitment and by immigrants, thereby reducing the likelihood of extinction. Emigration out of the population was also not modeled, but we found a very low rate of departure from the population over six years of radio-tracking (Boarman et al. unpubl. data). Overwhelmingly, ravens trapped at the EAFB landfill stayed in the immediate vicinity, or moved to a handful of other attraction sites that were all within the broad study area. This extensive use of a limited set of locations accounts for the lack of difference in resighting probabilities between wing-tagged and radio-tagged ravens. Although radio-tagged ravens were easier to locate initially, once located any wing-tagged ravens found were also recorded, and over the course of a year radio-

tagged ravens led us to nearly all of the wing-tagged ravens (resighting probabilities ranged from 0.90 to 0.97).

Data needs

Breeding adult survival probability was the parameter that had the greatest effect on population growth rate in our models, but we currently lack an empirical estimate for it. We also lack transition probability estimates between breeding and non-breeding segments of the population, which have less effect on population growth in an unmanaged population, but which would affect recovery times after control activities. Finally, we assumed in all models that there was no immigration from outside the population. For example, comparisons of stable age distributions against observed age class distributions at the EAFB landfill assume that immigration has no effect on the observed ratio of non-breeding adults to juveniles. The minimum rate of recruitment of non-breeders into the breeding population that reproduced the observed NB/J ratio was quite high (the smallest proportion of NB that needed to become BR each year was 0.43). However, during intensive nest searching between 1996 to 2000, we only found five marked individuals breeding on the study area. Disproportionate immigration of different age classes could produce the observed NB/J ratio, and still allow a low rate of recruitment of NB individuals into the BR class. Alternatively, ravens are thought to periodically skip breeding for a year, and this behavior is more common in ravens following reproductive failure (Boarman and Heinrich 1999). We know that reproductive success is greater both in urban areas and near roads, and reproductive failures are most common in undeveloped desert (Kristan 2001). With a more realistic, perhaps even spatially-explicit, model of this population the need to invoke large amounts of adult-biased immigration into the population may be eliminated, but empirical estimates of immigration would be preferable.

Even without additional data, a spatially-explicit simulation model would allow us to incorporate more of our raven data. For example, we currently have only used data from marked ravens to estimate survival probability, yet we also know a great deal about their movement patterns, and they do not move across the desert at random (Boarman et al. unpubl. data). If we incorporated movement patterns among attraction sites, we could refine our estimates of the transition probabilities and breeding adult survival probabilities needed to produce ratios of non-breeding to juvenile ravens observed at particular locations. Withey and Marzluff (2005) used this approach to explore the importance of migration from exurban areas for the population dynamics of urban American Crows.

Management implications

Although firm conclusions about the population dynamics of ravens cannot be drawn without additional information about important unknown parameters, it is clear that human-provided food and water help maintain ravens in the desert. Short-duration attempts to control non-breeding ravens at large, conspicuous aggregations do not pose substantial risk of inadvertent population extirpation, provided that the breeding segment of the population is not affected. Conversely, removing ravens at large aggregations without also removing breeding ravens is unlikely to control their numbers for very long. Changes in survival probabilities or fecundities represent long-term efforts. If the goal is to reduce the size of raven populations permanently, then a combination of control methods aimed at both breeding and non-breeding ravens may be necessary (Boarman 2003).

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Table 1. Values for fecundity estimates and hatch-year survival used in demographic models.

Fecundity¹		Hatch-year Survival²	
Overall	0.56	Overall	0.19
Urban	0.78	Urban	0.40
Ecotonal	0.62	Ecotonal	0.20-0.30
Desert	0.47	Desert	0.10-0.20

¹Kristan et al. unpubl. data.

²Webb et al. 2004.

Table 2. Statistical support for raven survival models of the capture histories of ravens trapped at the EAFB landfill. Subscripts indicate that parameters (p = resighting probability, s = survival probability) were allowed to vary by the subscripted variable (year, age or both). The best-supported models (with the lowest ΔAICc) include annual variation in survival probability or resighting probability, but not both.

Model	AICc	ΔAICc	Weights	Likelihood	Parameters	Deviance
p, s _{year}	580.8	0.0	0.41	1.00	6	92.80
p _{year} , s	581.0	0.2	0.37	0.90	6	93.01
p _{year} , s _{year}	583.4	2.6	0.11	0.28	9	89.14
p _{year} , s _{age}	584.9	4.1	0.05	0.13	8	92.72
p, s _{age, year}	586.2	5.4	0.03	0.07	12	85.66
p _{year, age} , s	586.9	6.1	0.02	0.05	12	86.38
p, s _{age}	592.8	12.0	0.00	0.00	4	108.87
p _{age} , s _{year, age}	594.7	13.9	0.00	0.00	16	85.56
p _{year, age} , s _{year, age}	604.3	23.6	0.00	0.00	24	77.55

Table 3. Population growth rate estimates for average habitat models. Parameters are fecundity (f), hatch-year survival (s_{HY}), breeding adult survival (s_{BR}), and juvenile and non-breeding survival (s_J, s_{NB}). Middle values in the range for f , s_{HY} , $s_{J,NB}$ are estimated values. Population growth is only stable or growing when breeding adult survival probability is greater than non-breeding adult and juvenile survival probability.

f	s_{HY}	$s_{J,NB} =$	$s_{BR} = 0.64$			$s_{BR} = 0.80$			$s_{BR} = 0.96$		
			0.64	0.80	0.96	0.64	0.80	0.96	0.64	0.80	0.96
0.46	0.03		0.66	0.67	0.67	0.81	0.82	0.82	0.97	0.97	0.97
	0.19		0.73	0.76	0.80	0.86	0.88	0.91	1.00	1.01	1.03
	0.35		0.78	0.82	0.87	0.89	0.93	0.96	1.02	1.05	1.08
0.56	0.03		0.66	0.67	0.69	0.81	0.82	0.83	0.97	0.97	0.98
	0.19		0.75	0.78	0.82	0.87	0.89	0.89	1.00	1.02	1.05
	0.35		0.80	0.85	0.89	0.91	0.95	0.99	1.03	1.06	1.10
0.67	0.03		0.67	0.68	0.69	0.81	0.82	0.83	0.97	0.97	0.98
	0.19		0.76	0.80	0.84	0.88	0.91	0.94	1.01	1.03	1.06
	0.35		0.82	0.87	0.92	0.92	0.92	1.01	1.04	1.08	1.11

Table 4. Growth rates of populations in urban, ecotonal, and desert habitats. Urban habitat models differ only in assumed adult breeding survival probability. Ecotonal and desert habitats additionally differ in whether hatch-year survival is assumed to be equal in both habitats, or greater in ecotonal habitat than in desert habitat. Parameters are fecundity (f), hatch-year survival (s_{HY}), breeding adult survival (s_{BR}), and juvenile and non-breeding survival (s_J, s_{NB}).

f	s_{HY}	s_J	s_{NB}	s_{BR}	λ
Urban					
0.78	0.40	0.80	0.80	0.80	1.00
0.78	0.40	0.80	0.80	0.96	1.11
Ecotonal					
0.62	0.20	0.80	0.80	0.80	0.91
0.62	0.30	0.80	0.80	0.80	0.94
0.62	0.20	0.80	0.80	0.96	1.03
0.62	0.30	0.80	0.80	0.96	1.06
Desert					
0.47	0.20	0.80	0.80	0.80	0.89
0.47	0.10	0.80	0.80	0.80	0.85
0.47	0.20	0.80	0.80	0.96	1.02
0.47	0.10	0.80	0.80	0.96	0.99

Table 5. Stable age distributions for average habitat and subsidy models. Breeding adults are expected to make up the greatest fraction of the population, particularly in desert habitat.

Age class	Average habitat	Subsidy models				
		Urban	Ecotonal $s_{HY} = 0.2$	Ecotonal $s_{HY} = 0.3$	Desert $s_{HY} = 0.2$	Desert $s_{HY} = 0.1$
HY	33.3%	33.3%	34.8%	32.2%	30.2%	32.9%
J	7.1%	13.3%	7.7%	10.2%	6.8%	3.9%
NB	6.3%	10.7%	6.8%	8.7%	6.1%	3.7%
BR	53.3%	42.7%	50.8%	48.9%	56.9%	59.5%
Landfill ¹	13.4%	24.0%	14.4%	18.9%	12.9%	7.6%
Non-landfill ²	86.6%	76.0%	85.6 %	81.1%	87.1%	92.4%

¹ Sum of J and NB classes, which are the classes using the landfill during the breeding season.

² Sum of HY and BR classes, which are the classes on breeding territories during the breeding season.

Table 6. Effects of transition probabilities (t) from NB to BR (t_{NBBR}), and from BR to NB

(t_{BRNB}), on population growth rate. Transition probabilities from NB to BR were: Small = 0.1, Medium = 0.25, Large = 0.5. For “balanced” models the transition probabilities for BR to NB were the same as these, and for “unbalanced” exchange transition from BR to NB was ½ of these rates. Transition probabilities within a class (t_{BRBR} and t_{NBNB}) are the joint probability of surviving and staying within the class, whereas transition between classes (t_{JNB} , t_{NBBR} , t_{BRNB}) are the joint probabilities of surviving and moving into a new class. The sum of the probability of survival and remaining in the same age class and the probability of survival and transitioning into another equals the overall survival probability (e.g. t_{NBNB} + t_{NBBR} = 0.8 in all models).

Model	f^1	s_{HY}^2	t_{JNB}	t_{NBNB}	t_{BRNB}	t_{NBBR}	t_{BRBR}	λ
$s_{\text{BR}}^3 = 0.80$								
Small balanced	0.78	0.40	0.80	0.72	0.08	0.08	0.72	0.90
Medium balanced	0.78	0.40	0.80	0.60	0.20	0.20	0.60	0.92
Large balanced	0.78	0.40	0.80	0.40	0.40	0.40	0.40	0.93
Small unbalanced	0.78	0.40	0.80	0.72	0.04	0.08	0.76	0.91
Medium unbalanced	0.78	0.40	0.80	0.60	0.10	0.20	0.70	0.93
Large unbalanced	0.78	0.40	0.80	0.40	0.20	0.40	0.60	0.95
$s_{\text{BR}} = 0.96$								
Small balanced	0.78	0.40	0.80	0.72	0.10	0.08	0.86	0.97
Medium balanced	0.78	0.40	0.80	0.60	0.24	0.20	0.72	0.98
Large balanced	0.78	0.40	0.80	0.40	0.48	0.40	0.48	0.98
Small unbalanced	0.78	0.40	0.80	0.72	0.05	0.08	0.91	1.00
Medium unbalanced	0.78	0.40	0.80	0.60	0.12	0.20	0.84	1.01
Large unbalanced	0.78	0.40	0.80	0.40	0.24	0.40	0.72	1.03

¹Fecundity

²Hatch-year survival probability

³Survival probability for breeding ravens

Table 7. Stable age distribution of "floater" models. "Balanced exchange" means that an equal proportion of non-breeding adults (NB) became breeding adults (BR) as BR became NB. "Unbalanced exchange" means that twice the proportion of NB became BR as BR became NB.

Age class	$s_{BR} = 0.80$		$s_{BR} = 0.96$	
	Balanced exchange	Unbalanced exchange	Balanced exchange	Unbalanced exchange
Hatch year	22.4%	24.9%	23.1%	26.1%
Juvenile	9.8%	10.7%	9.5%	10.3%
NB	41.5%	34.6%	38.2%	29.7%
BR	26.3%	29.8%	29.2%	34.0%
Landfill ¹	51.3%	45.3%	47.7%	40.0%
Non-landfill ²	48.7%	54.7%	52.3%	60.0%

¹ Sum of J and NB classes, which are the classes using the landfill during the breeding season.

² Sum of HY and BR classes, which are the classes on breeding territories during the breeding season.

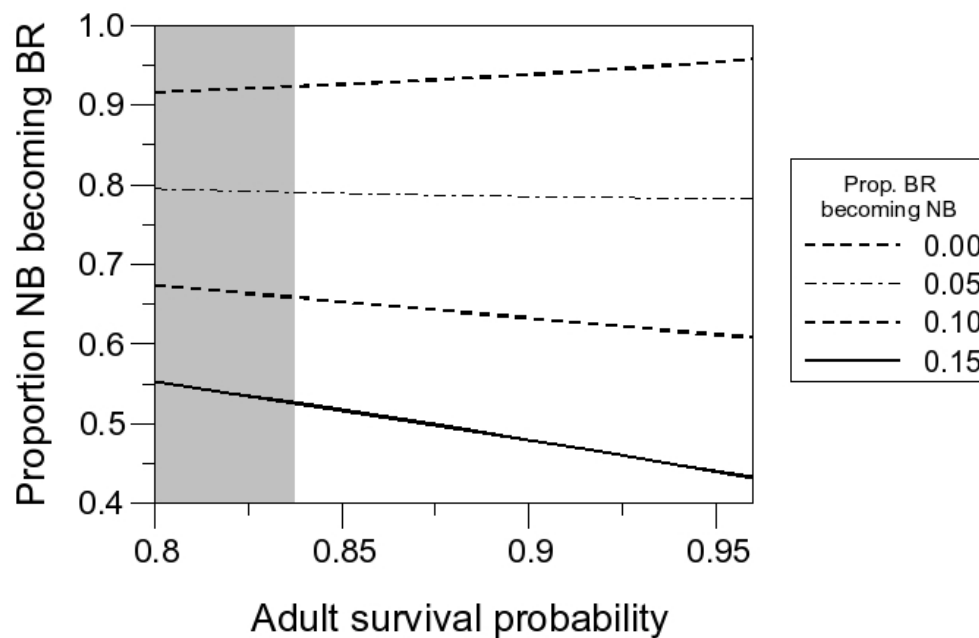


Figure 1. Combinations of s_{BR} , and transition probabilities from NB to BR, and BR to NB classes that produce a ratio of NB/J of 1.28, as observed at the EAFB landfill during raven surveys conducted from 1994 to 2000 (Boarman et al. unpubl. data). The gray region indicates s_{BR} values that result in a declining population.

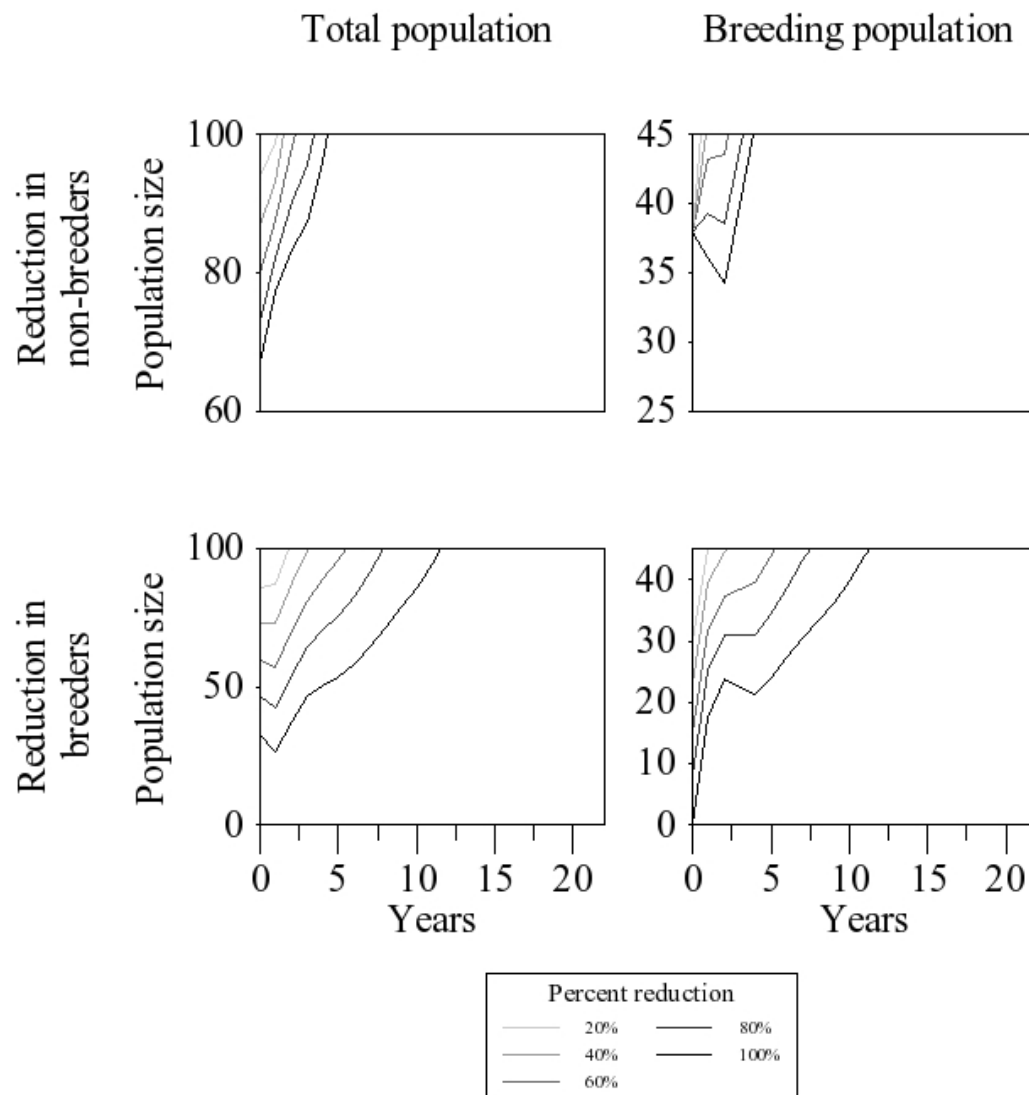


Figure 2. Recovery of raven populations following removal of either non-breeding or breeding classes. Adult survival probability ($s_{BR} = 0.949$) was selected to produce a stable population across all three habitats (urban, ecotonal, desert).

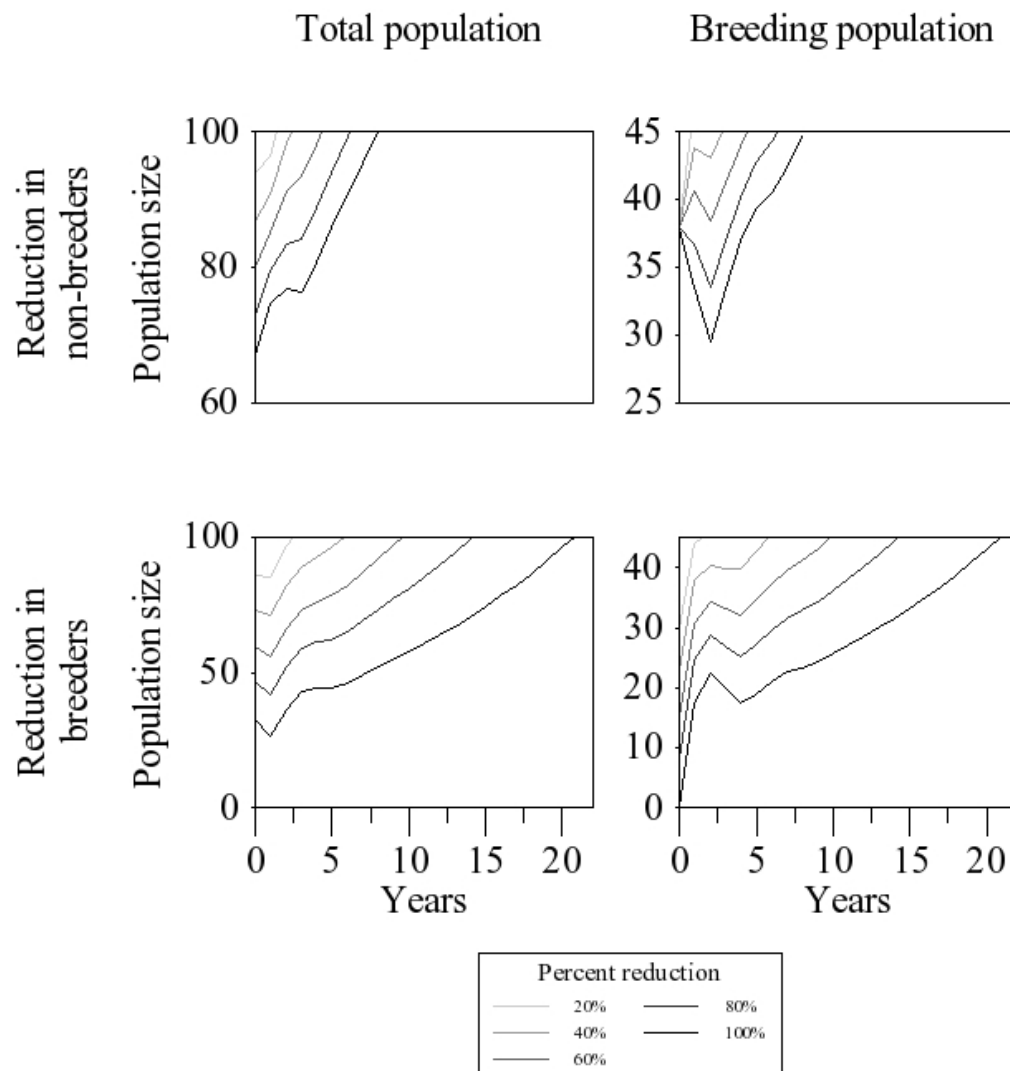


Figure 3. Recovery of raven populations following removal of either non-breeding or breeding classes. Adult survival probability was selected so that ecotonal habitats were stable ($s_{BR} = 0.881$).