UNIVERSITY OF CALIFORNIA
RIVERSIDE

Effects of Habitat Selection on Avian Population Ecology in Urbanizing Landscapes

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Biology

by

William Bernard Kristan, III

September 2001

Dissertation Committee:
Dr. John T. Rotenberry, Chairperson
Dr. William I. Boarman
Dr. Mary V. Price

The Dissertation of William Bernard Kristan III is approved:

Mary V Price

William Boarman

JT. R

Committee Chairperson

University of California, Riverside

Acknowledgments

Scientists are not known for their eloquent prose, and in this way I am an exemplary scientist. I feel this limitation most keenly when it is time to express my thanks. I apologize to any collaborator, friend, or family member who feels inadequately appreciated after reading this section, for I certainly feel that I can't thank any of you enough.

Each of the members of my dissertation committee were principal investigators on parts of this dissertation, and I worked happily with each of them. John Rotenberry has impressed me with his ability to translate his excellent taste into guidance without condescension. I anticipate that my relationship with John will not change much after I leave, because he already treats me like a colleague. Mary Price has provided a healthy counterpoint to my broad brushed approach, and has widened my perspective. Bill Boarman allowed me to join his Mojave raven project at a time when my original dissertation project was failing. I would not have finished as quickly, or possibly at all, without his intervention. I have enjoyed working with him tremendously, and look forward to our future collaborations.

A large part of the small mammal data used in Chapter 3 was collected by Tony Lynam and his assistants, and he has provided helpful comments on drafts of the manuscript.

My wife, Debbie Kristan, has supported me in every imaginable way, including working as a field assistant on the CSS project. She supports my bizarre work habits when necessary, but together with our children, Nathan and Ian, she also keeps me from

disappearing into my computer.

I have learned a great deal from the collective wisdom of the Biology Department at UCR. My fellow graduate students in the Rotenberry lab have been extremely helpful, particularly Mary Chase, Jamie Rotenberg, Michael Patten, Kris Preston, and Sharon Coe.

The following organizations have provided financial support of parts of this work: USDI National Biological Service, California Department of Fish and Game, USGS Biological Resources Division, and Edwards Air Force Base. The Biology Department provided fellowships and grants at several critical times between 1995 and 2001, including a GAANN Fellowship in 2000-2001.

ABSTRACT OF THE DISSERTATION

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The ability to judge habitat quality when selecting territories is important to individuals, and affects population dynamics. I explored how animals respond to spatial variation in habitat quality, and modeled the consequences to populations of poor habitat choices by individuals.

By treating the attractiveness of the habitat as a seperate quantity from the quality of the habitat I was able to model a range of conditions, from ideal choice of the best habitat (which produces source-sink dynamics) to choice of the poorest habitat (which produces ecological traps). Ecological traps have been detected in natural populations, but their effects have not been modeled. I found that ecological traps promote unstable equilibria, in which an apparently self-sustaining population that is reduced in size can rapidly go extinct because of disproportionate use of poor habitat at small population sizes.

Birds and small mammals choosing habitat near urban-wildland edges in southern Californian coastal sage-scrub have a persistent cue to the presence of increased predator abundance. The vegetation was also different at edges than at interior areas. Changes in

occurrence of some birds were associated with this change in vegetation, whereas other birds and small mammals exhibited direct changes in occurrence that were not explained by their habitat affinities.

Ravens in the west Mojave Desert had greater fledging success near roads and anthropogenic point sources of food and water subsidies (such as landfills, ponds, housing developments, etc.). Nests were clustered near point subsidies but not near roads, and investment in breeding (territory occupancy, breeding initiation, clutch size) was not greater in places where success was more likely. The spatial structure of raven nest site choice and the increased numbers of non-breeding ravens at anthropogenic sites did not prevent areas of high depredation risk from forming around those successful raven nests that were far from roads or subsidies.

Although information is beneficial to animals selecting habitat, it may either be in limited supply or species may lack the capacity to appropriately perceive and respond to information that is present in their environment.

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CHAPTER 1. General Introduction

Animals choose habitat based on environmental cues. Some habitat choices can be based on direct evaluation of an important resource, such as choices of mussel beds by foraging oystercatchers (Stillman et al. 2000). These birds can select foraging areas using visual cues, such as size and density of mussel beds, and decide whether to remain after a choice is made based on direct assessment of the profitability of their foraging. Such a system is rich in information about habitat quality, and close matches between levels of resources that affect individual fitness and distributions of birds should be expected, and have been found (Stillman et al. 2000). Birds are expected to be good at matching their foraging habitat use to variation in food resources because they are mobile and capable of detecting and moving to high-quality habitat, whereas small mammals or other terrestrial vertebrates would both be less able to detect resources at a distance and more restricted in their ability to move to them (Zollner and Lima 1997).

Avian foraging decisions may represent the best-case scenario for animals choosing habitat. Breeding site selection is substantially more complicated, because requirements of offspring differ from adults, and change as young develop. Birds may be able to gather a great deal of information at the time that they choose a breeding site, but once they have established a territory their ability to respond to changes in their environment is constrained by the fixed location of the nest. This constraint is strongest for birds that establish multiple-use breeding territories within which they not only must survive, they must also build a nest that is safe from nest predators and forage for food of the right kind and in sufficient quantity to rear young. Much can change between the time that breeding territories are established and offspring disperse from the natal territory. Predator distributions can change, both in response to the distributions of prey and because of predator migratory patterns or periods of activity (e.g. snakes emerging from hibernation). Birds that feed insects to their nestlings in temperate areas must choose territories before insects emerge, but then reproduce most successfully when their chicks reach peak food requirements at the time when insects are most abundant (Blondel et al. 1992). Blondel et al. (1992) found that Blue Tits (*Parus caeruleus*) that fledged in habitats with early insect emergence mis-timed their own broods when they nested in habitats with late insect emergence, whereas birds nesting in the same habitat in which they were fledged had broods that were well timed to peak food availability. In this example the information available regarding the best time to initiate a brood was available to all individuals, but only individuals nesting in habitat similar to their natal habitat were able to capitalize on it. In summary, breeding site selection is a complex forecasting problem, requiring both reliable information in the form of consistent relationships between cues and habitat quality, as well as the perceptual ability of individuals to respond appropriately to the information available.

Predators are important determinants of individual fitness in many species, and predator avoidance behaviors are common. When presented with imminent threat of depredation it is common to see changes in habitat use or decreases in feeding rates (e.g. Longland and Price 1991, Kotler 1997, Lima 1998, Hurly and Oseen 1999, Lima and Bednekoff 1999). When predator distributions are predictable, prey would benefit from avoiding areas of high depredation risk. When the location of individual predators is unpredictable, habitat cues that indicate variation in depredation risk could be used instead of direct assessment of predator distribution. For example, Møller (1988) found that blackbirds (*Turdus merula*) responded more strongly in their nest site choices to habitat features that were associated with decreased numbers of magpies (*Pica pica*), an important nest predator, than to the presence of magpie nests. Information about depredation risk resulted from the habitat associations of the predators, which were capitalized on by the prey.

Habitat selection behavior affects the distribution of individuals among habitats, thereby filtering the environmental conditions to which individuals are exposed. Habitat quality is usually defined as the expected fitness of individuals occupying the habitat (Fretwell and Lucas 1970). Theoretical treatments of the effects of habitat selection on population dynamics have shown potentially large changes in population growth rates and an increase in resistance to extinction from stochastic reductions in population size due to preferential use of good habitat (Pulliam and Danielson 1991, Howe et al. 1991). These theoretical treatments make the simplifying assumption that individuals can judge habitat quality and breed in the best available habitat, an assumption that seems tenuous in light of the complicated and inherently uncertain task faced by animals selecting breeding sites.

A good place to begin searching for cases in which animals are unable to predict habitat quality is in sites altered by anthropogenic activities. Anthropogenic changes to the environment can independently alter the cues to which animals respond and the actual habitat quality. When poor-quality habitats attract individuals they have been called "ecological traps" (Dwernychuk and Boag 1972). The term has been associated with a hypothesized pattern between increased attractiveness of clearcut forest edges to shrub-nesting birds concomitant to increases in abundance of nest predators and nest parasites (Gates and Gysel 1978), but has been applied to a variety of cases in which preferential use of a habitat has been accompanied by reduced breeding success (e.g. Best 1986, Purcell and Verner 1998, Misenhelter and Rotenberry 2000).

Although habitat selection and reproductive success are commonly measured quantities the relationship between them is rarely examined, and yet understanding the distribution and abundance of species inhabiting real-world landscapes will require linking habitat selection behavior with population dynamics (Lima and Zollner 1996). For my dissertation I approached this problem from both theoretical and empirical perspectives. In my first chapter I examined the theoretical concepts by developing population models in which use of habitat is determined by a cue that is separate from the quality of the habitat, and in which the cue can either accurately or inaccurately predict habitat quality. When attractiveness (i.e. the relative preference of individuals for a particular value of a cue) of habitat accurately predicts habitat quality a form of source-sink dynamics results, whereas when the attractiveness of the habitat inaccurately predicts habitat quality an ecological trap results. Differences in the expected distribution and dynamics of populations in these different cases can be compared.

For my second chapter I studied the responses of birds and small mammals to an urban/wildland edge in coastal sage-scrub vegetation to evaluate whether species responded directly to the edge (for example, avoiding the houses and people) or responded to an edge-induced change in the adjacent habitat. This study elaborated on the theoretical chapter by examining different types of information available from one change in the environment, and differences among species in how (or whether) they responded to the information.

For my third chapter I studied the spatial distribution, reproductive investment, and reproductive performance of ravens nesting along an urban/wildland gradient in the Mojave Desert. Whereas the edge study concentrated primarily on the response of species in their natural habitat to introduction of a novel anthropogenic feature, this study examines a species with an essentially commensal relationship with anthropogenic subsidies. The ability of ravens to judge anthropogenically induced variation in habitat quality is examined, as well as the way in which anthropogenic developments express their effects on ravens.

Lastly, given the relationship between ravens and anthropogenic developments, I studied the extent to which the distributions of breeding and non-breeding ravens produce variation in the risk of depredation for raven prey. This study bears both on the potential for urbanizing areas to impact sensitive species far from the actual developments by subsidizing their predators, as well as the degree to which the habitat associations of the predator provide information that can be used by prey in their habitat choices.

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CHAPTER 2. Sources, Sinks, and Ecological Traps: Effects of Habitat Choice on Population Dynamics

Abstract. Ecological traps, poor-quality habitat that nonetheless attract individuals, have been observed in both natural and human-altered settings. Although they are commonly considered a kind of source-sink system, current source-sink theory does not model maladaptive habitat choice, and therefore cannot accurately represent ecological traps or predict their population-level consequences. I developed models that treat source-sink dynamics and ecological traps as special cases of a single process, in which the attractiveness and quality of the habitat are separate variables that can be either positively or negatively related. As expected, sinks are less detrimental to populations than ecological traps, in which preferential use of poor habitat contributes to extinction risk. Furthermore, ecological traps may be undetected when population sizes are large, and may even appear to be sources, but when populations drop below threshold levels traps may prevent recovery in spite of the presence of high-quality habitat. Conservation biologists do not routinely consider the possibility that apparent sinks are actually traps, but since traps should primarily be associated with the rapidly changing and novel habitat characteristics produced by human activities, ecological traps should be considered an important and potentially widespread conservation issue.

INTRODUCTION

Source-sink dynamics, the idea that populations can persist indefinitely in poor habitat when they receive immigrants from good, productive habitat, has become an important ecological theory. The concept is well grounded theoretically (Shmida and Ellner 1984, Pulliam 1988, Pulliam and Danielson 1991), has found empirical support (Pulliam 1996), and has been identified as one of the mechanistic foundations for landscape ecology (Wiens et al. 1993). Although source-sink dynamics were originally described for plants (Keddy 1982, Watkinson 1985) in which dispersal between source and sink patches was passive, animal-derived models (Pulliam 1988, Pulliam and Danielson 1991) are based on the classic optimal habitat choice models of Fretwell and Lucas (1970) and assume active habitat selection by the organisms. Some of the important population-level predictions derived from source-sink dynamics, such as that sinks can stabilize source population size fluctuations (Howe et al. 1991), depend on individuals accurately judging habitat quality and choosing the best habitat available to them.

However, optimal habitat choice is not always possible. Some habitats attract individuals in spite of being lower in quality than other available habitats, and these habitats have been called "ecological traps" (Dwernychuk and Boag 1972, Gates and Gysel 1978). Although ecological traps have been observed in a variety of settings they have not received the theoretical development that source-sink dynamics has received. The lack of theoretical treatment of ecological traps prevents accurate predictions of the population-level consequences of habitat choices. This can be seen by confusion over the relationship between ecological traps and source-sink systems (Remes 2000), and ecological traps have been called source-sink systems in which the sink looks like a source (e.g. Pulliam 1996). However, an ecological trap can only result when the cues that attract individuals to a habitat become misleading indicators of the quality of the habitat, and since existing source-sink theory has only considered either random habitat occupancy or adaptive habitat choice it is not currently capable of describing ecological traps. In this paper I present a general approach to modeling the effects of habitat choice on population dynamics and habitat occupancy patterns that predicts both source-sink dynamics and ecological traps as special cases. With this framework it is possible to identify the conditions under which habitat choice should benefit or harm populations and the patterns that distinguish sinks from traps. The conservation implications of what may be widespread, pervasive effects of rapid anthropogenic habitat alterations are discussed.

TYPES OF ECOLOGICAL TRAPS

Ecological traps are clearly bad for individual fitness, and it is somewhat counter-intuitive that animals should judge habitat quality so poorly that they would choose to occupy a trap. Although in general ecological traps are produced when habitat attractiveness and habitat quality become uncoupled, this uncoupling could occur in several different ways. The first description of an ecological by Dwernychuk and Boag (1972) reported that ducks that usually nested in association with terns, which provided some protection from predators, sometimes nested in association with gulls, a nest predator. They postulated that the ducks nested near gulls in spite of the risk because they failed to distinguish between gulls and terns.

Another, presumably more common, type of ecological trap is created by rapid changes in the relationship between the attractiveness and quality of habitat (Remes 2000). Most ecological traps are expected to be produced by human activities (Pulliam 1996), such as logging (Gates and Gysel 1978), agriculture (Best 1986), or human-provided resources that are of unexpectedly low quality or are actually toxic (Pierotti and Annett 1990). Additionally, changes that affect the distribution of predator communities independent of the habitat may uncouple the traditional relationship between habitat and risk of depredation, thereby producing a trap (Misenhelter and Rotenberry 2000, Kristan 2001). Thus, some of these changes appear to provide super-normal stimuli that strongly attract individuals to habitat in spite of its poor quality, whereas others are apparently imperceptible changes in quality that occur independently of the habitat. Natural selection may not have had time to adapt populations to anthropogenic disturbances that have only been operating for short periods of time, and populations may go extinct before adaptation occurs.

MODEL MOTIVATION

In natural settings any given measure of habitat is variable. Organisms can respond to variability in their environment either physiologically or behaviorally, and these responses may in turn affect their fitness. Heterogeneous habitat is thus expected to affect the distribution of organisms in the environment or to cause habitat-specific population demography, or both. The demographic effect of habitat heterogeneity will be modified by habitat selection behaviors, because only the subset of habitats that are actually used will affect the population. The extent to which habitat choice can modify population demography will increase with increasing mobility and cognitive ability, and mobile vertebrate populations are particularly likely to be strongly affected by their habitat selection behavior. Given that habitat heterogeneity is ubiquitous, predicting the consequences of this heterogeneity to animal populations requires knowledge of the ways in which individuals respond behaviorally to variation in habitat quality (Smith and Sibly 1985, Anholt 1997).

Habitat choice is assumed to be an evolved behavior, and therefore under normal circumstances should be adaptive (Cody 1985, Sibly and Smith 1985, Morrison et al. 1992), in the sense that individuals should only exhibit habitat preference when they are able to accurately judge habitat quality, and should prefer the best habitat. This assumption has been the basis of existing source-sink models, in which habitat quality is defined explicitly as the expected (i.e. mean) Darwinian fitness of individuals occupying the habitat, and in which animals choose the habitat with the highest quality. However, this assumption poorly represents the habitat selection process because expected fitness cannot be judged directly by organisms. Factors that are closely related to fitness, such as the distribution of predators or abundance of resources, may be uninformative to animals choosing habitat because the fitness consequence of a habitat choice is not realized for some time, and it is possible for the conditions that existed when a habitat choice was made to change in unpredictable or unexpected ways. Even apparently obvious, persistent features of habitats, such as proximity to predators, either may not be perceived as threats or may be poor predictors of quality compared to other cues in the environment over evolutionary time scales (Møller 1988). Because of the constraints on individuals' abilities to assess expected fitness, habitat must be selected based on cues in the environment such as the structure or floristic composition of vegetation that are correlated with important determinants of expected fitness (e.g. depredation risk or food levels). Because habitat is chosen based on environmental cues rather than direct assessment of habitat quality the relationship between cues and their expected fitness benefits may change, which can cause individuals to choose habitat poorly. Under these circumstances a rigid requirement that individuals choose optimal habitat will make source-sink models predict population dynamics poorly.

A more accurate representation of the habitat choice process can be constructed by treating the "attractiveness" of the habitat (i.e. the relative preference of an individual for for a particular habitat) and the "quality" of the habitat (i.e. the expected fitness of individuals occupying the habitat) as different variables whose relationship can be changed.

IDEAL HABITAT CHOICE

MODEL STRUCTURE

The model has three components: the relative frequency distribution f(x) of territories possessing the value x of a habitat variable X, a fitness function g(x) relating the habitat variable to the expected fitness of individuals that occupy the habitat (the quality of the habitat), and a function h(x) describing the degree of preference for particular values of the habitat variable (the habitat's attractiveness). Fretwell and Lucas' (1970) "ideal despotic" habitat choice assumes that territorial individuals have complete information about the quality of all available sites and choose the best site that is not already occupied. The assumption of complete knowledge of the quality of all sites is the "ideal" assumption. In its simplest form density effects are solely produced by use of lower-quality territories as population size increases, but territory quality is fixed and is not affected by density. My models employ a similar "ideal" assumption, but rather than complete information about habitat quality (g(x)) individuals have complete information about the attractiveness of the habitat (h(x)). Therefore, the only information available to individuals about the quality of the habitat is through the environmental cues represented by h(x).

Source-sink models, having developed from metapopulation patch choice models, encourage thinking about patches with sources and sinks as discrete geographic places that contain subpopulations. However, the habitat within these geographic locations will generally also be heterogeneous, and this within-patch heterogeneity may be sufficiently great that identification of patches becomes arbitrary. If patch structure is not a necessary condition for the important predictions of source-sink theory to hold, then insistence on patch structure may unnecessarily complicate identification of sources and sinks in natural populations. Consequently my models will use continuous variables to represent habitat gradients rather than discrete habitat types.

For any given distribution of the habitat variable X, the proportion of the territories occupied between any two values a and b of X is:

$$p = \int_a^b f(x)dx \tag{1}$$

The model assumes that all individuals prefer the same habitat (a particular value of X), that habitat is limited in abundance, and individuals use the most attractive habitat that is unoccupied. The endpoints of the used habitat (a and b) are defined by the attractiveness of the habitat, and habitat is occupied from the most attractive to the least attractive. If the attractiveness function h(x) is unimodal, then the endpoints of the occupied habitat will have equal attractiveness, so that h(a)=h(b). The occupied habitat can be converted to a probability distribution, which by definition is:

$$z(x) = \frac{f(x)}{\int_a^b f(x)dx} \tag{2}$$

and the mean attractiveness for the habitat used is:

$$\overline{h} = \int_a^b h(x)z(x)dx \tag{3}$$

For a given population size, the habitat used will have the highest average attractiveness.

A perfect correlation between attractiveness and quality can be enforced by establishing a linear relationship between quality g(x) and attractiveness h(x):

$$g(x) = v + \omega h(x) \tag{4}$$

To simplify examination of the effects of habitat choice on population dynamics I have adopted the convention of interpreting the fitness function as the expected growth rate of a population using habitat X=x, so that g(x) can be considered synonymous with λ the population growth rate. The sign of w determines whether the model results in a source-sink system (w is positive) or an ecological trap (w is negative), provided that λ crosses 1.0 (that is, both source and either sink or trap habitats exist within the population). The coefficient v determines either the maximum or minimum expected fitness.

MODEL PARAMETERIZATION

Although a variety of functions could be used, I've chosen to use probability density functions with simple parametric forms for f(x) and h(x). No particular function for the distribution of a habitat variable in the environment is expected to be universal, but asymmetry is an interesting common condition. A particularly simple asymmetrical distribution is the exponential:

$$f(x) = \frac{1}{\theta} e^{-\frac{x}{\theta}} \tag{5}$$

The parameter θ is the mean of the habitat distribution. I used a fixed habitat distribution for all models, with θ set at a value of 5 (Figure 2.1A). The proportion of territories occupied between any two values a and b of X is found by integrating the habitat function:

$$p = \int_a^b f(x)dx = e^{-\frac{a}{\theta}} - e^{-\frac{b}{\theta}} \tag{6}$$

Changes in habitat occupancy as population size changes are expressed as changes in the positions of a and b.

The habitat that is actually occupied (i.e. the positions of a and b) is determined by the attractiveness of the habitat, h(x) (Figure 1B). The values of h(x) were interpreted as the relative attractiveness of territories with habitat X=x, and determined the order in which the territories were used. I used a unimodal form of the gamma probability density function for h(x) with:

$$h(x) = \frac{x}{\phi^2 e^{\frac{x}{\phi}}} \tag{7}$$

The parameter ϕ defines the modal value of h(x), which is the position of the most attractive habitat. This function was chosen because it is bounded at 0 and it allowed me to easily change the position of the most attractive habitat by varying the value of ϕ. The habitat used at a given population size was found first by solving equation 6 for b, yielding the relationship between the upper and lower endpoints of the habitat used at a given population size, then finding the values of a and b that have equal attractiveness. The endpoints of the occupied habitat at a given population size are related by:

$$b = -ln(e^{-\frac{a}{\theta}} - p)\theta \tag{8}$$

The endpoints used will have equal attractiveness, h(a)=h(b):

$$\frac{a}{\phi^2 e^{\frac{a}{\phi}}} = \frac{b}{\phi^2 e^{\frac{b}{\phi}}} \tag{9}$$

Substituting equation 8 for b in equation 9 yields:

$$\frac{a}{\phi^2 e^{\frac{a}{\phi}}} = \frac{-ln(e^{-\frac{a}{\theta}} - p)\theta}{\phi^2 e^{-ln(e^{-\frac{a}{\theta}} - p)\theta/\phi}} \tag{10}$$

The value of a that satisfies this relationship was found iteratively. This procedure can be viewed graphically (Figure 2.1C) by moving a horizontal line up or down along the attractiveness curve h(x) to define an area of a given population size under the habitat curve f(x) constrained to have endpoints of equal attractiveness. Using h(x) in this way imposes a settling order within the habitat as population size increases, and only the most attractive habitats are used at a given population size.

The mean value of X for the occupied habitat is, by definition:

$$\overline{f} = \int_a^b x \frac{\left(\frac{1}{\theta} e^{-\frac{x}{\theta}}\right)}{e^{-\frac{a}{\theta}} - e^{-\frac{b}{\theta}}} dx \tag{11}$$

Given the habitat occupied, the mean attractiveness is:

$$\overline{h} = \int_a^b \left(\frac{x}{\phi^2 e^{\frac{x}{\phi}}}\right) \left(\frac{\left(\frac{1}{\theta} e^{-\frac{x}{\theta}}\right)}{e^{-\frac{a}{\theta}} - e^{-\frac{b}{\theta}}}\right) dx \tag{12}$$

The mean fitness, and thus the growth rate for the population, is:

$$\overline{g} = \lambda = v + \omega \overline{h} \tag{13}$$

The parameters v and w determine the minimum or maximum mean fitness, and the relationship between attractiveness and fitness (either positive or negative), respectively.

MODEL VARIATIONS

The effects of preference for relatively common vs. relatively rare habitat was modeled by varying the value of ϕ (the position of the most attractive habitat) between 1 and 5. Differences between sinks and traps were modeled by changing the sign of w. Values of v and w were chosen so that the population growth rate at saturation (i.e. the growth rate when all territories were occupied) was the same for sinks and traps for a given value of ϕ. The effects of differences in saturated growth rate upon the growth rate at particular population sizes were explored by setting the saturated population growth rate to 0.95, 1.0, and 1.05.

MODEL OUTPUT

These models address the effects of habitat selection behavior on the distribution of organisms, and the effects of habitat choice on their population dynamics. For each variation in the model structure at a given population size, I explored the expected pattern of distribution of the population within the habitat (the upper and lower bounds of occupied habitat, a and b in equation 6), the mean of the occupied habitat (equation 11) the proportion of source habitat that was occupied (i.e. occupied source habitat/total source habitat), and the proportion of the occupied habitat that was source habitat (i.e. habitat occupied that is source habitat/total occupied habitat, see appendix for equations used for the latter two variables), as well as the growth rate for the population as a whole (equation 13).

PROBABILISTIC HABITAT CHOICE

MODEL STRUCTURE

Real animals do not exhibit ideal habitat choice. Among other constraints, individuals do not have complete information about their environment at any given time, cannot forecast conditions at a future time with certainty, and do not have equal access to all possible sites. Alternatively, habitat preference may vary individually, which may result in different habitat choices among individuals presented with equivalent alternatives. Although these two alternatives are distinct processes they would produce similar patterns of habitat occupancy, and consequently would have similar effects on population dynamics. Instead of modeling these factors individually I constructed a model in which the pattern of occupancy at a given population size is expressed as a distribution rather than as a linear ranking.

The probabilistic models are structurally similar to the ideal models. I used the same habitat distribution ($f(x)$), but used a preference function ($h(x)$) that related the probability of a territory being occupied at a particular population size to the habitat variable X. Since the probability that territories are occupied is related both to the habitat and to the population size, whereas habitat quality only depended on the value of X, it was not possible to simply use treat preference and quality as linear functions of one another, and I used a fixed function of habitat to represent habitat quality (g(x)). This had the disadvantage of breaking the perfect linear correlation between preference and quality, but by using functions with the same shape I was able to maintain a perfect rank correlation between them.

MODEL PARAMETERIZATION

I used a logistic equation, commonly used as a resource selection function in field studies, that described the probability that a territory will be used at a given population size (Figure 2.2A-C). Thus, any habitat with a non-zero probability of use can be occupied simultaneously, but with differing proportions of the available territories within the habitats used. The interpretation of this is either that the preferred habitat differs among individuals, or that the most attractive habitat is not always used because of constraints on the search ability of the individuals. The equation for the selection function is:

$$h(x) = \frac{1}{1 + e^{\beta_1 + \beta_2 x}} \tag{14}$$

The function used for fitness, g(x), was a linear function of a logistic equation:

$$g(x) = \upsilon + \omega \left(\frac{1}{1 + e^{\beta\prime_1 + \beta\prime_2 x}} \right) \tag{15}$$

evaluated for two sets of parameters: one in which fitness increased with increasing values of the habitat variable x, and one in which fitness decreased with increasing values of the habitat variable. The parameters of g(x) were selected so that the population growth rate was 1.0 when all territories were occupied for both sets of parameters.

To determine the relative number of territories occupied at a given habitat value x, I multiplied the logistic selection function h(x) by the distribution function f(x) for the habitat variable (θ=5). This distribution of occupied territories was converted to a probability distribution, and mean growth rate was calculated:

$$\bar{g} = \lambda = \int_0^\infty g(x) \left(\frac{h(x)f(x)}{\int_0^\infty h(x)f(x)dx} \right) dx \qquad (16)$$

This equation was solved numerically.

MODEL VARIATIONS

Effects of variation in the strength of preference for habitat were modeled by changing the magnitude of β'_1 (ie the steepness of the slope at the inflection point) and the effects of preference for common or rare habitat was examined by changing the end of the habitat distribution that was preferred (determined by the sign of β'_2). The effects of changes in population size were modeled by changing the position of the inflection point (determined by β'_1) to change the amount of the habitat that was occupied for a given strength of preference. I modeled five variations in model conditions (Figure 2.2): strong preference for uncommon habitat, moderate preference for uncommon habitat, no habitat preference, moderate preference for common habitat, and strong preference for common habitat. Each of these variations was modeled for populations that occupied 10%, 30%, 50%, 70% and 90% (10%, 50%, and 90% shown in Figure 2.2) of the available territories.

MODEL OUTPUT

For each variation in model conditions and population sizes I measured the growth rate for the population as a whole (equation 16), and the proportion of source habitat occupied, and the proportion of occupied habitat that is source (see Appendix for equations for the latter two variables)).

RESULTS

IDEAL HABITAT CHOICE

Consistent with classical ideal despotic models (Fretwell and Lucas 1970) less-attractive habitats were used with increasing population size (Figure 2.3). If the preferred habitat is not at the mean of the habitat distribution ($\phi \neq \theta$) the mean of the habitat used is only near the preferred habitat (ϕ) at small population sizes, but moves toward the mean of the habitat distribution ($\theta = 5$ for these models) as population size increases (Figure 2.3).

Habitat choice is beneficial in source-sink systems, but detrimental in ecological traps. Mean population growth rates are highest at small population sizes for source-sink systems, but lowest at small population sizes for ecological traps (Figure 2.4). Different saturated population growth rates produced parallel results, as can be seen in Figure 2.4 A-C. For each saturated growth rate, a horizontal line is placed at $\lambda = 1.0$. With a saturated growth rate of 1.0, ecological trap populations never achieved positive growth rates, even though some of the habitat occupied was source habitat (Figure 2.4A). When the total amount of source habitat is reduced, thereby reducing saturated population growth rate to 0.95 (Figure 2.4C), source-sink systems have higher growth rates than ecological trap systems, but choice of the best habitat does not always produce mean population growth over 1.0 for source-sink systems (i.e. those with the most attractive habitat at X=3). When the the total amount of source habitat is increased, thereby increasing saturated population growth rate to 1.05 (Figure 2.4B), all of the trap populations could grow. However, models with the most attractive habitat at $X < 3$ only had $\lambda>1.0$ at large population sizes. Under these conditions ecological traps would be prone to unstable equilibria because decreases in population size would result in growth rates less than 1.0, and the populations would be unable to recover.

The proportion of source habitat occupied increased with increasing population size with both source-sink systems and traps, but started high and increased to saturation in source-sink systems, and started at 0 and only increased after populations were large enough to fill all of the habitat with growth rates less than 1.0 in traps (Figure 2.5). Expressed alternatively, at small population sizes all of the occupied habitat was source in source-sink systems but none of the occupied habitat was source in ecological traps (Figure 2.6).

PROBABILISTIC HABITAT CHOICE

With ideal assumptions relaxed, the probabilistic model yielded qualitatively similar results to the ideal habitat choice model. In source-sink systems habitat choice increased mean population growth rate, whereas in ecological traps habitat choice decreased mean population growth rate (Figure 2.7). Strong habitat preference increased the proportion of source habitat occupied at small population sizes in source-sink habitats, but not in ecological traps (Figure 2.8). The proportion of occupied habitat that is source approaches 1.0 at small population sizes in source-sink systems, but approaches zero in ecological traps (Figure 2.9). As with the ideal models, increased population size decreased mean growth rate in the source-sink systems as habitat of decreasing quality was used, but increased mean growth rate in ecological traps as higher quality habitat was used.

DISCUSSION

UNCOUPLING ATTRACTIVENESS AND QUALITY

Although previous models demonstrated effects of habitat choice on population dynamics, their assumptions implicitly treated habitat attractiveness and habitat quality as the same quantity. Because of this it was not possible to produce ecological traps with previous models, and analyses were limited to comparing adaptive habitat choice with random habitat use. Animals must use cues to select habitat and then discover the fitness consequences of their choice. This constraint means that the currently accepted range of possible effects of habitat choice on population dynamics must be broadened to admit the possibility of ecological traps. By treating habitat attractiveness and habitat quality as different variables this model unifies source-sink theory with the idea of an ecological trap, and highlights the importance of understanding the habitat selection process in determining population trajectories.

CONTINUOUS VARIATION, PSEUDO-SINKS AND PSEUDO-SOURCES

I modeled population dynamics using continuous variation in habitat rather than the discrete patch structure frequently used in source-sink models (Pulliam 1989, Pulliam and Danielson 1991). Habitat gradients produce effects similar to classical source-sink dynamics, particularly that sink habitats can be occupied indefinitely, thereby increasing overall population size and promoting persistence. Habitat can exhibit a gradient structure at a variety of scales, from within-patch to landscape. Imposing a patch structure on a gradient in the landscape, or on patches with substantial within-patch variation in quality, may create a pseudo-sink (Watkinson and Sutherland 1995). Pseudo-sinks are patches in which density-dependence reduces the population growth rate to less than 1.0 at large population sizes, but at smaller populations the growth rates increase sufficiently that the population is actually self-sustaining. My models produce pseudo-sinks when the best habitat within an area has an expected growth rate greater than 1.0, but the population exhibits a mean growth rate less than 1.0 because of density-dependent use of poor habitat. Additionally, my models showed that populations can produce "pseudo-sources" in the presence of ecological traps. Pseudo-sources exhibit a mean growth rate greater than 1.0 when population sizes are large, but at smaller population sizes the growth rate declines below 1.0 (Figure 2.4). These population structures demonstrate the importance of considering both heterogeneity in habitat quality and how individuals choose habitat when assessing the value of habitat for a species.

OCCUPANCY PATTERNS

At small population sizes, the range of habitat used was small and close to the preferred value (Figure 2.3). As population sizes increase, the range of habitats used increased. This pattern has often been observed in bird populations, has been termed the "buffer effect" (Brown 1969, Krebs 1971), and is a common feature of habitat selection models (Fretwell and Lucas 1979, Rosenzweig 1981).

The mean of the used habitat draws away from the preferred value and moves toward the mean of the habitat distribution as population size increases (Figure 2.3). Although this pattern is produced by the particular functions chosen, it is expected to be a very general result because only a limited number of combinations of habitat distributions and preference functions would position the mean of used habitats at the preferred habitat value for all population sizes. For example, if preference was unimodal and symmetrical, combined with a habitat distribution that was uniform (or at least symmetrical with the preferred habitat at the mean of the distribution of habitats), then the preferred habitat would fall at the mean of the used habitats at all population sizes. Given that these conditions will rarely be met, the mean of used habitat should be considered a poor estimate of the preferred habitat.

EFFECTS OF HABITAT SELECTION ON POPULATION GROWTH

Selectivity for habitat is beneficial to individual fitness and increases population growth if animals are able to choose habitat accurately, particularly when the best habitat is rare (Figure 2.4, 2.7). However, whereas habitat choice is expected to ameliorate the effects of habitat heterogeneity on population growth if habitat quality can be judged accurately, habitat choice should amplify the detrimental effects of low-quality habitat if habitat quality is judged inaccurately.

Populations occupying landscapes that include ecological traps exhibit inverse density-dependence, because better habitat is used as population size increases. As a result, it is possible for population growth rates to exceed 1.0 if the amount of trap habitat is small compared to the amount of source habitat, producing pseudo-source populations. Although these models do not include stochastic effects, it is clear that if pseudo-source populations are reduced to the point that population growth is less than 1.0 then the trap habitat should push the population to extinction. Population decreases in source-sink systems would be less dangerous, because the remaining individuals would occupy the best habitat available, which would speed recovery (Howe et al. 1991). Therefore, whereas source-sink systems would promote stable equilibria, ecological traps would promote unstable equilibria and population extinction.

IDENTIFYING PATHOLOGICAL HABITAT CHOICE

Typically, attempts to classify sources and sinks have been based solely upon the performance of individuals or populations within habitat patches, but the nature of the response of the animals to variation in habitat quality and the effects of within-patch variation in quality are seldom addressed (e.g. Knight et al. 1988, Beshkarev et al. 1994, Donovan et al. 1995b, Paradis 1995, Skupski 1995, Hatchwell et al. 1996, Ellison and Van Riper 1998). For species that are able to actively choose habitat, it is not possible to accurately predict the consequences of changes in habitat without understanding both how the species behaviorally responds to the change and the consequences of their response. For example, the predicted magnitude of the detrimental effects of changes in land use on an endangered species will be very different if they are able to perceive the reduced habitat quality and avoid it, if they fail to recognize the change, or if they are actually attracted to it. Models of real populations produced to date have not considered the possibility that low-quality habitats are actually ecological traps rather than sinks, and consequently may have over-estimated the prospects for population persistence (e.g. Doak 1995, Donovan et al. 1995a, Gaona et al. 1998).

Conclusions about ecological traps should be drawn cautiously, particularly in natural predator-prey systems such as the duck-gull system described by Dwernychuk and Boag (1972). For example, Wheelwright et al. (1997) found that Savannah Sparrows that nested near relatively ineffective predators (gulls) were protected from effective predators (crows), although sparrows nesting away from both predators were the most successful. In this natural population, apparent cases of maladaptive habitat choice (nesting near gulls) may actually prove to be choice of the best habitat from a set of poor choices. Thus, while it is possible for ecological traps to exist within natural systems, it is likely that upon close inspection many apparent traps will prove to be sinks.

It is far more plausible that ecological traps could be created in anthropogenically-altered landscapes. Kristan (2001) found evidence that developed edges act as an ecological trap for small mammals. Misenhelter and Rotenberry (2000) found a negative relationship between habitat choice (attractiveness) and the consequences of the choice (habitat quality) in Sage Sparrows in contiguous patches of coastal sage scrub habitat that are subject to invasive exotic plants and altered predator communities. In both cases, ecological traps were created by processes that originated from outside of the study areas.

It is therefore important to consider not only the local impacts of management activities, but the potential consequences to the conservation value of adjacent protected lands.

My models show that distinguishing between sinks and traps requires knowledge of habitat choice, and that demographic measures alone are not sufficient. However, it is important to note that it is possible to have positive correlations between the attractiveness and quality of habitat without growth rate exceeding 1.0, and negative relationships between attractiveness and quality without growth rate dropping below 1.0 (Figure 2.4). The traditional definition of source (i.e. growth rates exceeding 1.0) is still required to distinguish sources from sinks or traps, and the correlation between attractiveness and quality is required to further distinguish between sinks and traps.

Imposing boundaries on gradient habitats can be misleading, and an alternative approach to identifying sources and sinks is suggested by my models. It is possible to evaluate the expected growth rate of a population within small areas, preferably the least indivisible unit such as the breeding territory. At this scale, population growth rate and individual fitness nearly converge (McGraw and Caswell 1996). Each territory could be scored by whether it exceeds values of fecundity or survivorship required to produce a net surplus of recruits. It would then be possible to spatially cluster these source territories into larger units, which would then form the source patches. Such a bottom-up approach would avoid many of the current problems of classifying sources and sinks.

ACKNOWLEDGEMENTS

This project benefitted from discussions and advice from John T. Rotenberry. I wish to

thank F. Bashey, W. Boarman, M. Bryant, S. Coe, D. Kristan, M. Patten, K. Preston, M. V. Price, J. Rotenberg, J. Rotenberry, and W. Webb for reviewing drafts of this manuscript.

APPENDIX

To find the proportion of source habitat occupied and the proportion of occupied habitat that is source, I first identified which habitat was source habitat. Source habitat is found by solving for the points on the fitness function that equal 1.0. The proportion of the habitat that is a source is the area under the habitat distribution f(x) in which fitness g(x) is greater than 1.0. For a source-sink system, the proportion of source habitat that is occupied is the proportion of the source habitat that falls between a and b:

$$p_{so} = \frac{p}{e^{-\frac{l}{\theta}} - e^{-\frac{u}{\theta}}} \qquad p_{so} \leq 1$$

with l and u representing the lower and upper values of the habitat variable that are source habitat. For an ecological trap system, the equation is:

$$p_{so} = \frac{\left(e^{-\frac{a}{\theta}} - e^{-\frac{l}{\theta}}\right) + \left(e^{-\frac{u}{\theta}} - e^{-\frac{b}{\theta}}\right)}{e^{0} - e^{-\frac{l}{\theta}} + e^{-\frac{u}{\theta}}}$$

Similarly, the proportion of occupied habitat that is source habitat can be computed. This value is the area under the habitat distribution that is occupied (falls between a and b, and has expected fitness g(x) greater than 1.0. For source-sink systems, the equation is:

$$p_{os} = \frac{e^{-\frac{l}{\theta}} - e^{-\frac{u}{\theta}}}{p} \qquad p_{os} \leq 1$$

For ecological traps the equation is:

$$p_{os} = \frac{\left(e^{-\frac{a}{\theta}} - e^{-\frac{l}{\theta}}\right) + \left(e^{-\frac{u}{\theta}} - e^{-\frac{b}{\theta}}\right)}{p}$$

Similar calculations were used to find the proportion of source habitat occupied and proportion of occupied habitat that was source for models with a distribution of attractiveness. The proportion of source habitat occupied was:

$$p_{so} = \int h(x) f(x) dx$$

integrated either from 0 to u (when g(x) was a declining function of x) or from l to infinity (when g(x) was an increasing function of x). The proportion of occupied habitat that is source was:

$$p_{os} = \frac{p_{so}}{\int_0^{\infty} h(x) f(x) dx}$$

These quantities were calculated numerically.

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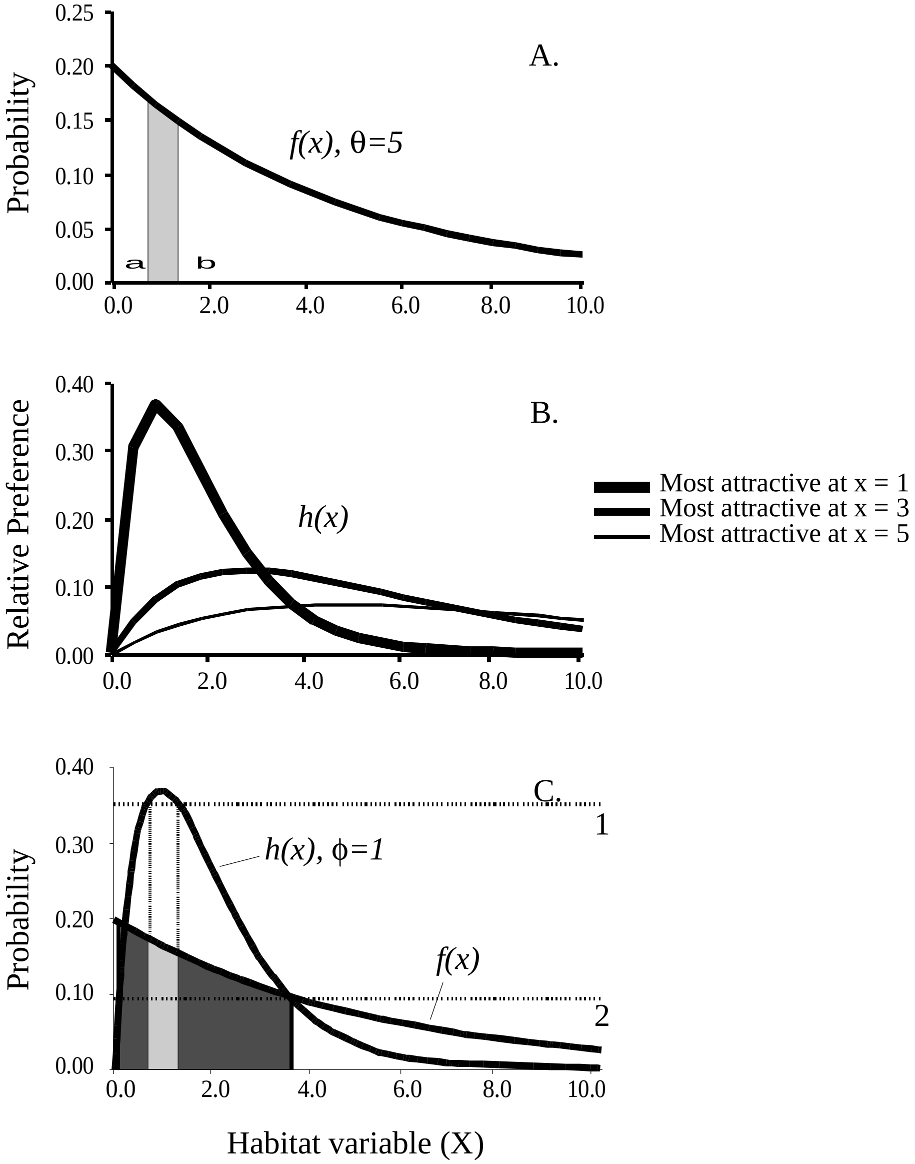

Figure 2.1. (A) The distribution of a habitat variable X in the environment, showing the relative number of territories with habitat at a particular value of X, f(x). Within this habitat distribution, the habitat that is used at a given population size is represented by the shaded area under f(x) between two endpoints a and b. (B) The relative attractiveness of x to an organism is represented by h(x), the most attractive habitat determined by the position of the mode. (C) The habitat that is actually occupied at a given population size is determined by its attractiveness. Horizontal lines intersect h(x) at points of equal attractiveness. When these points are projected to the x-axis, they define an area under f(x), representing the habitat occupied. Two example lines show how the endpoints of habitat used are found when 10% of the territories are occupied (line 1, lightly shaded area under f(x)), or 50% of territories are occupied (line 2, darkly shaded area under f(x)).

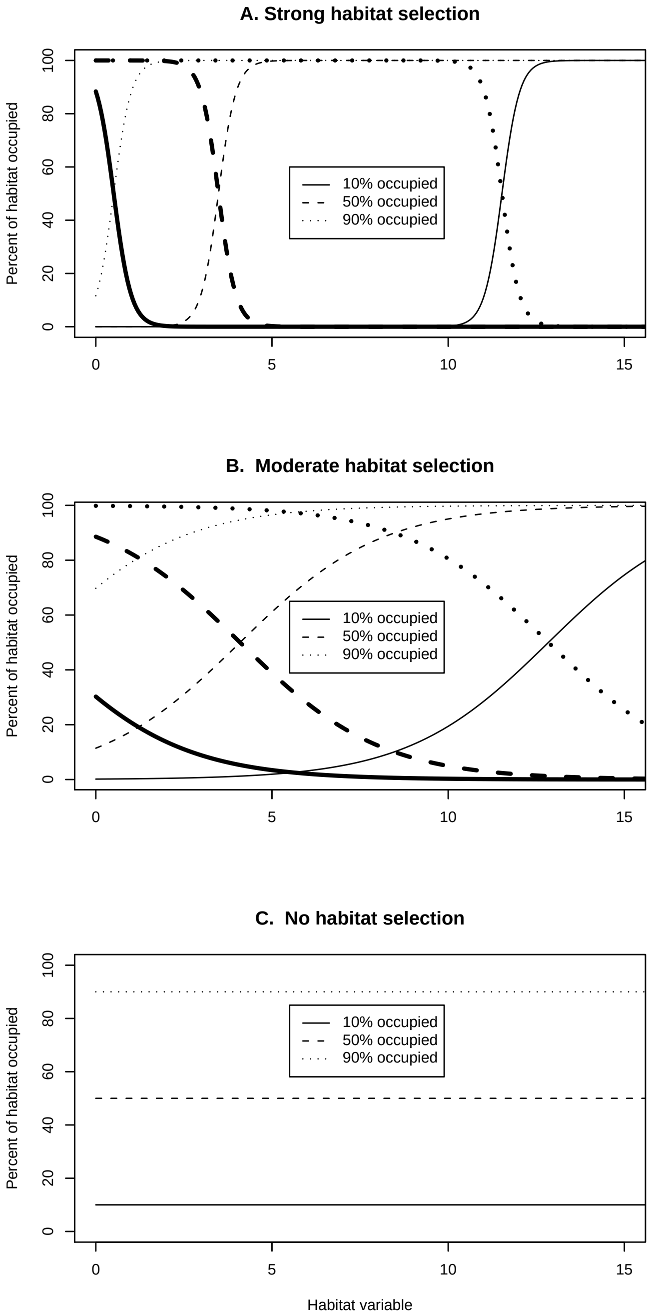

Figure 2.2. When a distribution of habitats are used at a given population size, the percent of territories occupied that had a given value of a habitat variable were represented with logistic curves. Organisms could exhibit strong, moderate, or no preference for habitat, and the habitat they preferred could either be common or uncommon (habitat is represented by an exponential, and habitat values of 0 are most common). By definition, attractive habitats are used disproportionately. As the more territories are occupied, progressively more of the less attractive habitat is used (from A to C).

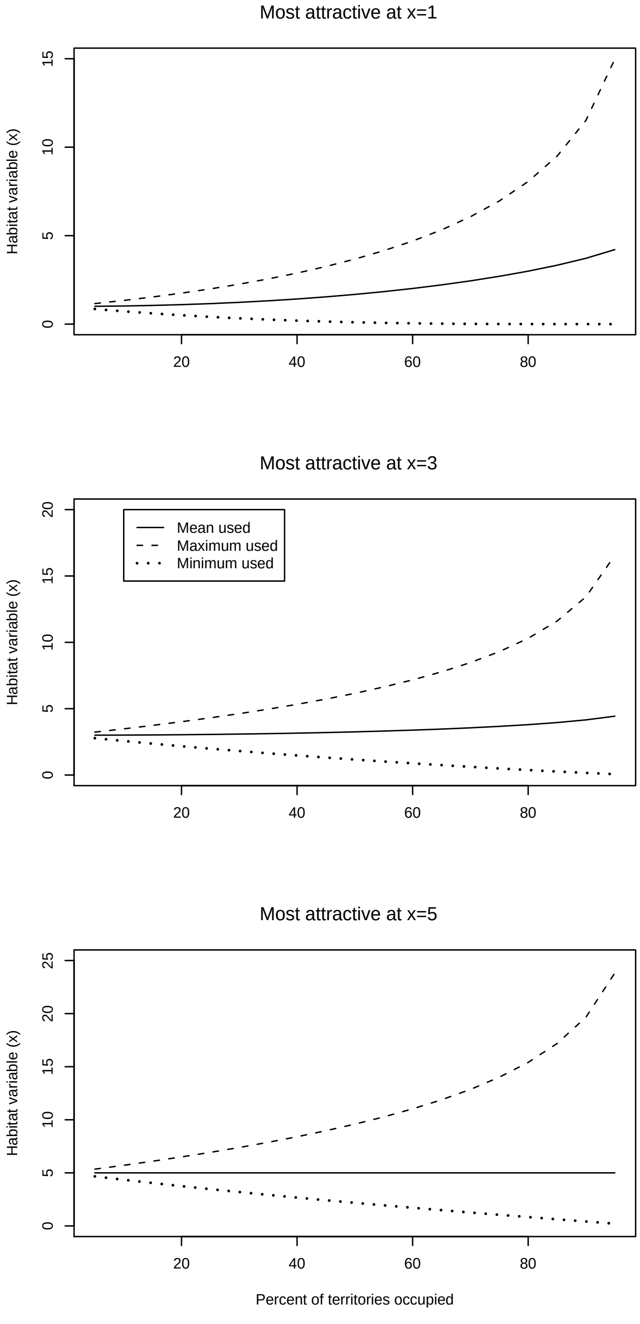

Figure 2.3. The range of habitats occupied (i.e. values of X) increases as population size increases. The mean of the habitat that is actually used moves away from the habitat preferred to the mean of the habitat distribution (θ=5) as population size increases (A and B), unless the mean of the habitat distribution is the most attractive (C).

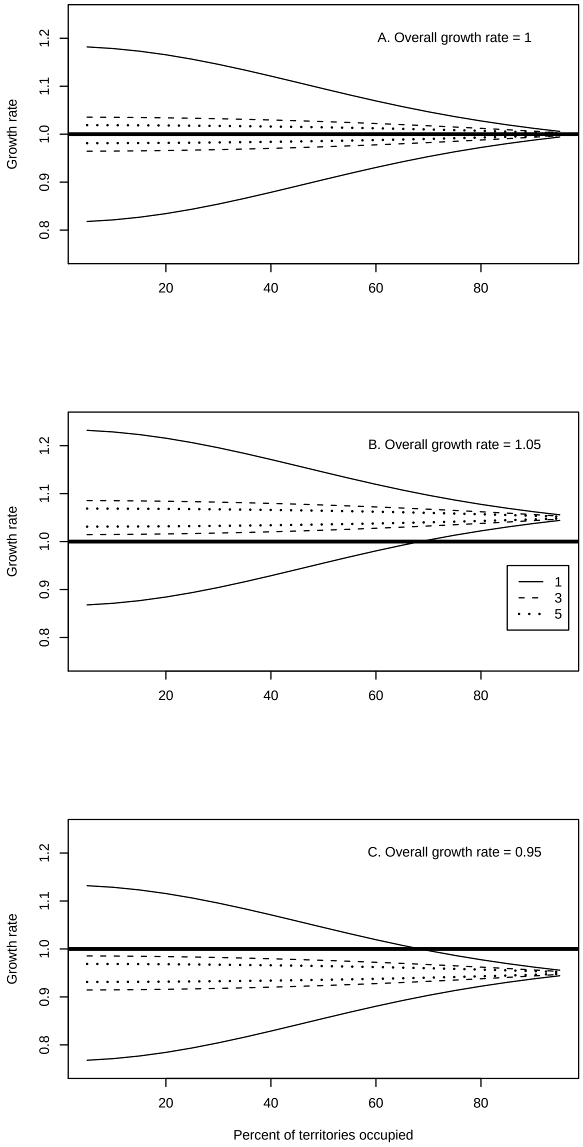

Figure 2.4. Habitat choice reduces population growth rate when ecological traps are present, but increases growth rates in source-sink systems. Growth rate curves for source-sinks and ecological traps converge on the same overall growth rate when all territories are filled, and curves above the point of convergence represent source-sink systems whereas curves below the point of convergence represent ecological traps. Each curve represents preference for a different habitat value from 1 to 5. Examples of overall growth rates of 1.00 (A), 1.05 (B), and 0.95 (C) are shown. Horizontal lines are drawn at growth rate = 1.0, and when the source-sink curves cross below this line the population as a whole becomes a pseudo-sink (C, most attractive at 1), whereas when the ecological trap curves cross above this line the population becomes a pseudo-source (B, most attractive at 1).

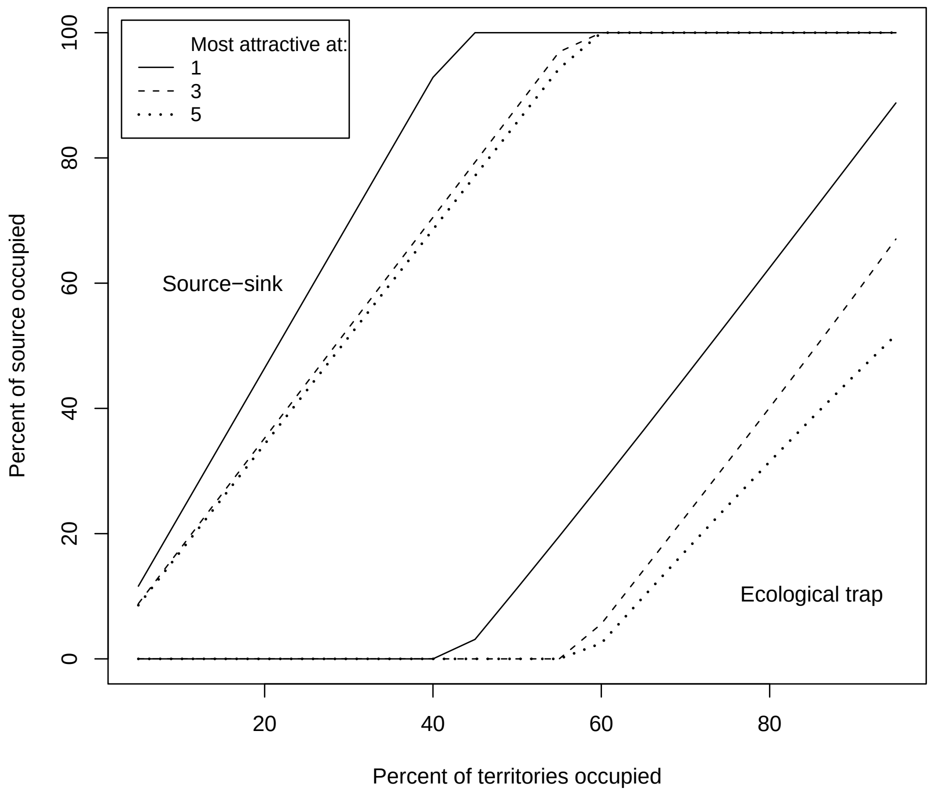

Figure 2.5. The percent of source habitat occupied increases with increasing population size when populations are small in source-sink systems, but only increase in ecological trap systems when populations are large.

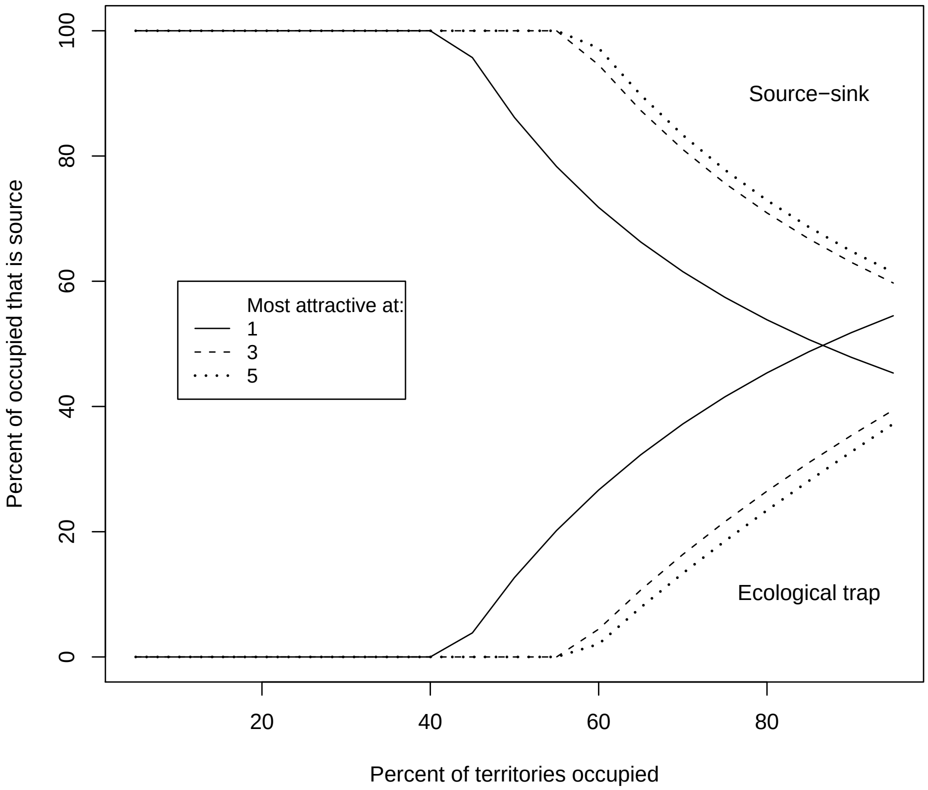

Figure 2.6. All occupied habitat is source habitat at small population sizes in source-sink systems but none of the habitat occupied is source at small population sizes in ecological traps.

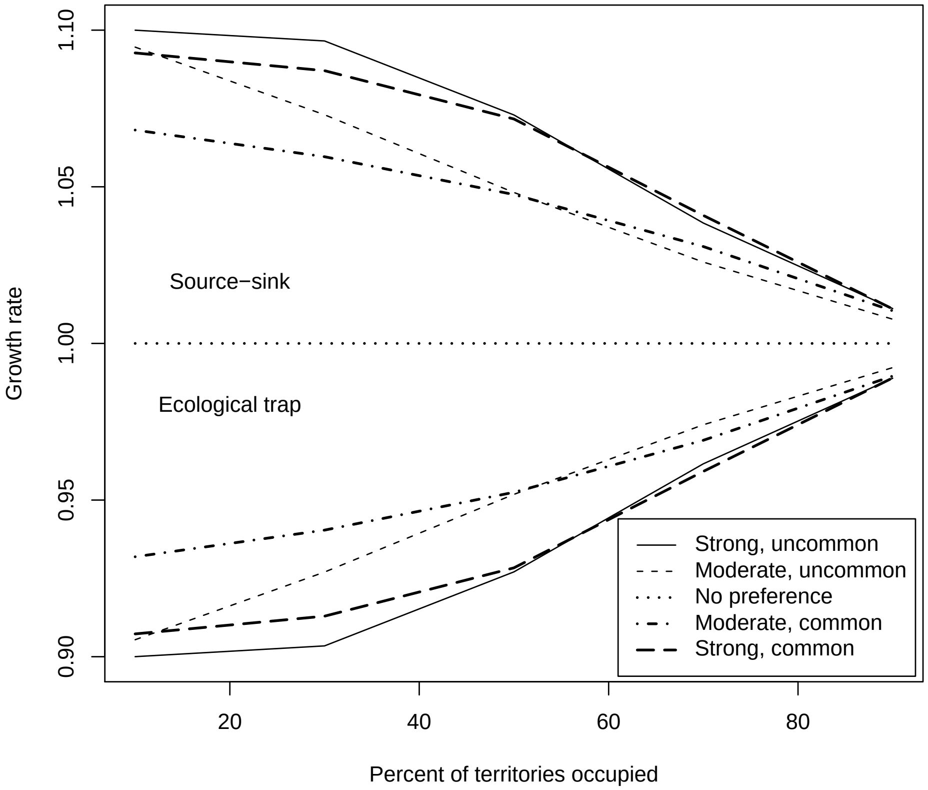

Figure 2.7. When habitat choice is probabilistic, habitat choice still enhances population growth rates in source-sink systems and decreases growth rates in ecological traps relative to random habitat use. The effect is greatest at small population sizes when habitat is rare and habitat choice selection is strong.

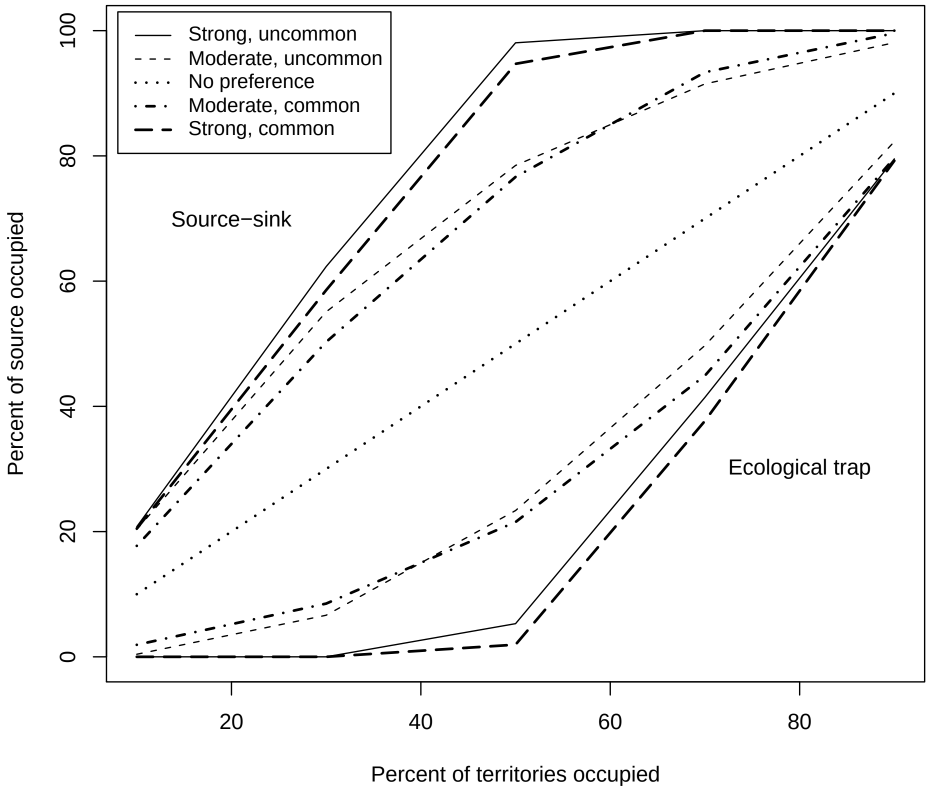

Figure 2.8. When habitat choice is probabilistic, the percent of source habitat occupied increases rapidly at low population sizes in source-sink systems compared with random habitat use. In ecological traps source habitat use is low at low population sizes, particularly when preference is strong.

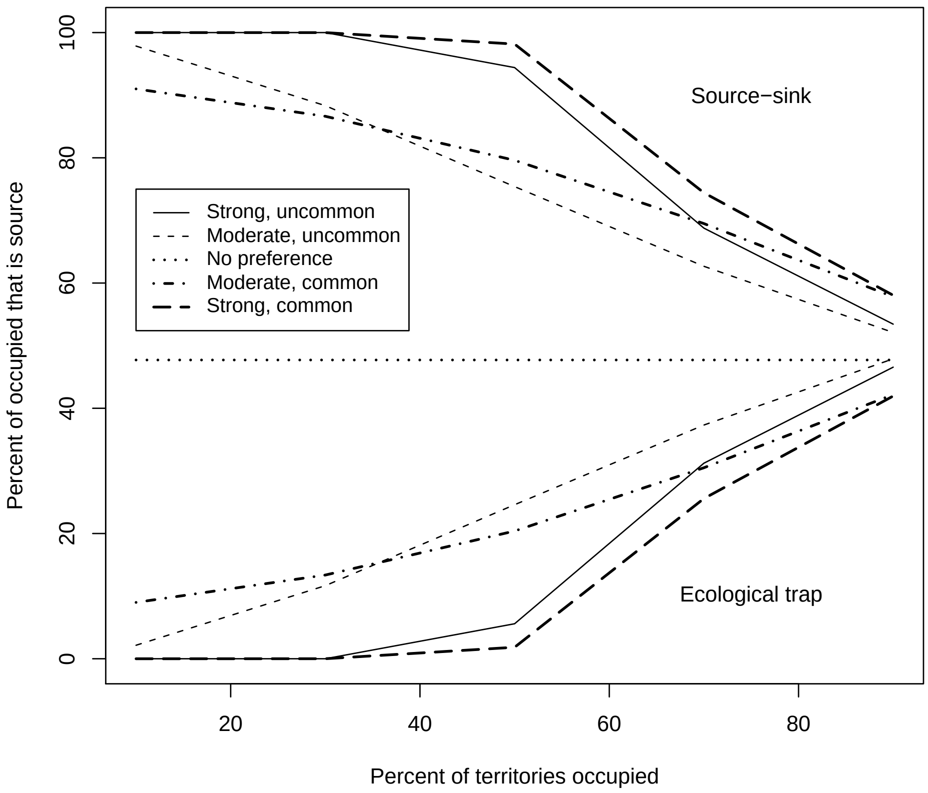

Figure 2.9. When habitat choice is probabilistic, a greater proportion of occupied habitat is source habitat at small population sizes in source-sink systems than in ecological traps or with random habitat use.

CHAPTER 3. Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub.

Abstract. Changes in the distribution and abundance of bird and small mammal species at urban-wildland edges can be caused by different factors. Edges can affect populations directly if animals respond behaviorally to the edge itself or if proximity to edge directly affects demographic vital rates. Alternatively, urban edges can indirectly affect populations if they alter aspects of adjacent wildland vegetation to which animals respond behaviorally or demographically. We studied edge effects of birds and small mammals in southern Californian coastal sage scrub, and assessed whether edge effects were due to direct behavioral responses to edges or to changes in vegetation at edges combined with habitat selection by the animal species. Vegetation species composition and structure varied with distance from edge, largely in site-specific ways. Because vegetation characteristics were confounded with distance from edge, the effects of habitat were explored by using independently-derived models of the species' habitat associations to calibrate vegetation measurements to the habitat affinities of each animal species. Of sixteen species examined, five bird and one small mammal species differed in occurrence among distances to edge, independent of the habitat, and thus habitat restoration at edges is expected to be an ineffective conservation measure for these species. Two additional species of birds and one small mammal responded to vegetation gradients that coincided with distance from edge, such that the effect of edge on these species was expressed via potentially reversible habitat degradation.

INTRODUCTION

Urban and agricultural development fragments wildland habitats, and creates sharp boundaries, or edges, between the natural and human-altered habitats. Edges can alter abiotic processes such as microclimate, light intensity, and hydrology (e.g., Janzen 1983, Camargo and Kapos 1995, Murcia 1995, Sisk et al. 1997), and biotic factors such as predator communities, habitat structure, and food availability (e.g., Soulé et al. 1988, Yahner 1988, Matlack 1994, Murcia 1995). Populations of birds and small mammals in turn can be changed at these edges, either by changes in their demographic rates (Paton 1994, Donovan 1997), or through behavioral avoidance of or attraction to the edge (Sisk et al. 1997). The consequences of edge effects can range from reduced effective area of suitable habitat within a reserve (Temple and Cary 1988) to increased probability of extinction (Woodroffe and Ginsberg 1998).

Rapid urbanization in southern California over the last 50-100 years has resulted in loss of large areas of native habitats, particularly in cis-montane coastal regions. One of the characteristic vegetation types in this region, coastal sage scrub (CSS), has been reduced to 10 to 30% of its former extent by conversion to human use, and supports approximately 100 animal and plant species considered by California or federal wildlife agencies to be rare, sensitive, threatened, or endangered (Atwood 1993, McCaull 1994, Dobson et al. 1997). Although the direct effects of habitat loss to urbanization are fairly obvious and irreversible, the indirect effects of urbanization on adjacent remaining patches of habitat can be more subtle, and are potentially subject to intervention and mitigation by land managers. Understanding how these remaining habitat patches are affected by surrounding lands through their shared edges is an important step towards protecting the populations of plants and animals that depend on them.

Although many studies of edge effects have been conducted (see Paton 1994 for a review of nesting bird studies), there is substantial disagreement among studies about the existence and intensity of edge effects and no clear, general patterns have emerged (Murcia 1995). In part this variety of results may be due to the variety of effects that edges can have on populations, only a subset of which may be expressed at a particular site (Donovan et al. 1997). For example, edge-abundance relationships are frequently interpreted as a behavioral response to the sharp transition found at edges between habitats with different structures (Sisk et al. 1997), a direct response to the edge itself. However, species may instead respond to changes induced in the vegetation at edges, and may be indifferent to the edge itself. Changes in vegetation will depend on a variety of factors that will differ in site-specific ways, and differences in edge-abundance relationships at different locations may therefore represent consistent responses by animals to effects of edge that are expressed inconsistently among locations. Few studies have attempted to distinguish between alternative mechanistic explanations for edge effects (Murcia 1995), making their population-level consequences difficult to predict. In this study we concentrate on distinguishing between direct responses to the edge and responses to the changes produced by urban edges in the structure or floristic composition of the adjacent coastal sage-scrub vegetation. Because these alternatives suggest different remediation strategies, our findings bear on the potential for success of restoration of edge habitats, and are therefore important considerations in reserve design.

METHODS

CSS VEGETATION

CSS is a drought-deciduous shrubland found in cis-montane southern California and Baja California that is dominated by shrubs of 0.5 to 2.0 m in height (Westman 1981). CSS is distinguished from other vegetation types in southern California by its distinct plant species composition and structure. The dominant shrubs include California sagebrush (*Artemisia californica*), black sage (*Salvia mellifera*), white sage (*Salvia apiana*), California encelia (*Encelia californica*), brittlebush (*Encelia farinosa*), and California buckwheat (*Eriogonum fasciculatum*; O'Leary et. al. 1992, Westman 1981, 1983). However, there is substantial geographic variation in plant species composition within this broadly defined vegetation type (Westman 1983, White and Padley 1997).

SAMPLING STRATEGY

Our sampling strategy used two independent studies, one that was designed to characterize general habitat associations of birds and small mammals in the absence of edge effects, and one that was designed to estimate the relative importance of distance to edge and habitat characteristics on animal distribution and abundance. Our measures of habitat association were based upon a regional assessment of bird and small mammal distributions in CSS throughout San Diego, Orange, and Riverside counties (the "regional study"). Assessments of edge-abundance relationships were based upon a smaller set of sites that contained developed edges (the "edge study"). We used this approach because, in the absence of an independent measure of habitat association, the correlation between distance from edge and characteristics of the vegetation (i.e., structure and plant species composition) made it impossible to determine whether species were responding to a vegetation gradient or to the edge itself. Once models of the habitat associations were obtained, they were used to calibrate vegetation measurements from the edge study to the habitat associations of the species, which could then be compared to the observed distributions of the species. Plant and animal sampling methods were the same for these two studies, except for the geographic extent and duration of sampling and the methods used to select sampling points, as noted below.

STUDY AREAS

Regional study

We sampled birds, small mammals and vegetation at 22 sites located throughout Orange, Riverside, and San Diego counties. All of the sites contained CSS vegetation, but varied geographically in floristic composition (Rotenberry et al. 1999). Sites in Riverside County contained greater amounts of brittlebush and buckwheat, whereas Orange County sites contained greater amounts of laurel sumac (*Malosma laurina*) and chamise (*Adenostoma fasciculatum*), the latter a dominant shrub in chaparral vegetation. Each site had been invaded to varying degrees by exotic grasses of the genera *Avena*, *Bromus*, and *Schismus*. The invasion consisted both of infusion of the CSS with exotic grasses in some areas and replacement of shrubs by grasslands in other areas. These are steps in a process of change from shrubland to grassland occurring throughout the region, driven by changes in fire frequency and intensity as exotic grasses invade (Minnich and Dezzani 1998).

Edge study

We studied edge effects at three areas that contained extensive, contiguous areas of CSS, and that were representative of the major gradient in CSS floristic composition found throughout the region. These sites were Lake Perris State Recreation Area in Riverside County (LAPE), Starr Ranch Audubon Sanctuary in Orange County (STRA), and Marine Corps Air Station Miramar in San Diego County (MIRA). In addition to the typical CSS plants, Miramar contained a fairly large amount of chamise. Each site was adjacent to suburban housing developments consisting of single-family homes. The edge at Lake Perris was actively developing, with houses completed and occupied at one end but under construction at the other. A golf course was situated between the houses and the CSS edge for part of its length, separating the CSS from the houses by a maximum of 75 m. At Starr Ranch a narrow belt of irrigated landscaping (less than 50 m wide) separated the CSS edge from the houses. Houses were immediately adjacent to CSS at Miramar.

Although land uses of the CSS at each site were nominally similar, there was some variation in the amount of recreational use. LAPE was open to the public and received the greatest degree of recreational use, primarily hiking. MIRA and STRA were not open to the public, but the edges were not patrolled and trespassing appeared to be fairly common.

LAPE had been most extensively invaded by exotic grasses, and contained large patches of exotic grasslands. Exotic grasses were common at both STRA and MIRA, but these sites also contained larger, contiguous patches of shrubs than LAPE.

SAMPLING DESIGN

Regional study

Sampling points were selected to fall within CSS habitat at least 250 m from developed edges, and were at least 250 m apart. Between five and 25 points were located within each of the 22 sites, depending on the area of CSS habitat. At each point we sampled birds, small mammals, and vegetation. Data were collected between 1995 and 1997, with sites surveyed one, two, or three years for birds, one or two years for small mammals, and once for vegetation.

Edge study

We established sampling points at three distances from the urban edge. "Edge" points were placed within undeveloped habitat as close as possible to the edge (typically less than 10 m). "Interior" points were placed a minimum of 1000 m from the edge, and "intermediate" points were placed 250 m from the edge. Sampling points were spaced at least 250 m apart, with the total number of points constrained by the length of the developed edge (five were used at each distance class at Lake Perris, ten at Miramar, and twelve at Starr Ranch). At each point we surveyed birds and small mammals, and measured vegetation composition and structure. Sampling was conducted in 1996 and 1997.

SURVEY METHODS

Survey methods within a sampling interval were identical between regional and edge studies, except where noted below.

Birds

Within a year, birds were sampled using two 5-minute unlimited-radius counts conducted at each point (Ralph et al. 1995). All birds detected from the point center were included, except for those not using the scrub or urban habitat types (such as birds flying over the point) or those species that are not well-sampled by point counts (such as raptors). Individual birds known to be recorded previously at another sampling point were not recorded again. First counts began in mid-March, and were concluded by late-April. Second counts began shortly after conclusion of the first counts (late-April to early May), and were completed by early June. Sites were visited in the same order for first and second samples. Samples at a point were therefore conducted 4-5 weeks apart, ensuring an opportunity to detect both early breeders and late arriving species (as suggested by Ralph et al. 1995). To avoid observer bias, each point was sampled by different observers on the first and second visit. Point counts took place between sunrise and 5 hours after sunrise on mornings with no rain or strong wind, and the order in which points were sampled within each site was reversed between the first and second visits to the site to avoid potential bias due to changes in detectability of species. Counts were conducted for 1-3 seasons (1995-1997) in the regional study, and once in 1997 for the edge study.

Small mammals

Small mammals were sampled over three consecutive days of trapping at each point in the regional study, and over five consecutive days in the edge study, using Sherman livetraps. A 4 x 4 array of 16 traps spaced 8 m apart centered on the sampling point was used in the regional study, and either a 1 x 5 or 2 x 5 array was used in the edge study. Small mammals were trapped on two occasions several months apart for the edge study, with fall samples conducted in October-December and spring samples conducted in May-June. Because small mammal activity can be affected by moonlight (Price et al. 1984), trapping was not done for two days before and after the full moon.

Traps were situated under the shelter of a shrub canopy and baited with a mixture of rolled oats, peanut butter, and corn syrup. Traps were opened at dusk, then cleared and closed between 0530 and 1100 the following day. If a sensitive species was detected at any census point, the protocol was immediately changed so that traps were opened at dusk, and then cleared immediately after dawn for the duration of sampling at all census points at the particular site. When nights were cold, traps were checked and closed at midnight. Mammals were identified to species using customized keys derived from Ingles (1965) and Jameson & Peeters (1988), and were aged, sexed, weighed, marked, and then released at the point of capture.

Vegetation

Vegetation structure and species composition were measured at sampling points using a modified version of the technique described by Wiens and Rotenberry (1981). All edge study vegetation measurements were taken in the spring of 1997. Regional study measurements were also taken in the spring, in 1996 for most sites, but in 1997 for sites that were not added until after spring 1996. Vegetation was sampled along two perpendicular 50-m transects connected at the end in an "L" shape. The vertex of the L was placed at the center of the sampling point, and at edge points the legs were constrained to fall within the CSS side of the edge. Vegetation data were gathered using both line intercept and pin drop methods. We also made visual assessments of the presence of cactus patches, rock outcrops, and trails. The variables measured consisted of species composition of perennial vegetation, and measures of horizontal and vertical structure (Appendix 3.1). Vegetation was sampled once at each point for both the regional and edge studies.

ANALYSES

Characterizing vegetation gradients

Gradients in vegetation structure and species composition were examined using ordination techniques. Ordinations of the regional study data were done on a reduced set of vegetation variables. Plant species composition was represented by 26 species that occurred in at least 5% of the plots sampled in the regional study. We then used detrended correspondence analysis (DCA; Gauch 1982, Pielou 1984) to reduce species composition to two quantitative, synthetic variables (i.e., the first two DCA axes, DCA1 and DCA2) which were used as proxies for species composition in further analyses. Similarly, regional study vegetation structure variables were reduced first by eliminating clearly redundant variables (those that were strongly correlated and that we considered to be alternative methods of measuring the same quantity), then by subjecting the remaining variables to a Principal Components Analysis (PCA). The scores for the first two axes (PC1 and PC2) were retained as proxies for vegetation structure for further analyses.

Vegetative differences among distances to edge

Once the DCA scores and PCA coefficients were obtained from the regional study, we scored the edge study vegetation into these ordinations, a process analogous to generating predicted values from a fitted linear regression model for new observations based upon the regression coefficients. The scores obtained represent the position of each edge study point relative to major gradients in species composition and vegetation structure of CSS throughout southern California. Once edge study points were scored, we confirmed that sites and distances from edge differed in vegetation structure and species composition by comparing scores on PCA1, PCA2, DCA1, and DCA2 using factorial MANOVA, with study site and distance to edge as the main effects. This analysis was followed by univariate ANOVA's for each of the dependent variables to determine which had the greatest effect upon the multivariate result.

Calibrating vegetation data to animal habitat affinity

The inter-correlation between distance to edge and vegetation composition and structure was the motivation for our analysis, but it also posed difficulties in interpretation of results. For example, it was possible for large proportions of the variance in animal abundance to be explained by the combination of distance to edge and vegetation but not be uniquely attributable to either effect. Additionally, it would not be possible on statistical grounds alone to tell whether a species was avoiding edges in spite of the presence of good habitat there unless vegetation characteristics could be calibrated to the habitat affinities of the species. We used the regional data to accomplish this calibration.

Habitat associations were derived from the regional data set with logistic regression, relating the presence of species to the vegetation sampled at a point (Hosmer and Lemshow 1989). The vegetation variables used consisted of the scores on the two DCA axes and two PCA axes, plus additional raw variables that were poorly represented by the PCA or DCA axes (i.e., those with low correlations with PCA or DCA axes). Details of the modeling strategy are presented in Rotenberry et al. (1999). Points were sampled for different numbers of years at different sites in the regional study, so the number of years of sampling was used as a covariate in all models.

Once logistic regression coefficients were derived for each independent variable, predicted values were calculated for each edge point based on the vegetation measured there, using a number of years sampled of one. Assuming that species' responses to habitat were consistent between the regional and edge studies, predicted values were interpretable as the predicted probability that a species would be detected at a point given the vegetation there. These predicted probabilities could then be used in place of the vegetation variables themselves in assessing the relative effects of habitat and distance to edge on a species' distribution, and we will refer to these predicted values simply as "habitat suitability" hereafter.

The relative effects of habitat suitability and distance to edge

The final analysis of the effects of habitat suitability and distance to edge was a logistic regression of the presence/absence of a species on habitat suitability, distance to edge, and site (included as a nuisance parameter to control for differences in overall population sizes and vegetation characteristics among study sites). We followed these analyses with ANOVA's of habitat suitabilities among sites and distances to edge. Species whose edge effects were due to response to habitat changes had significant differences in habitat scores among distances that paralleled their observed distribution patterns. This approach had the further advantage that it could detect inverse relationships between habitat suitability and abundance, such that species that were less abundant at edges in spite of the presence of preferred habitat could be accurately identified.

RESULTS

DIFFERENCES IN VEGETATION AMONG SITES AND DISTANCES TO DDGE

The first DCA axis of regional study vegetation species composition data revealed a transition from large amounts of chamise and black sage at small values of DCA1 to large amounts of California sagebrush and white sage at large values of DCA1. The second DCA axis represents a gradient from large amounts of shrub cover (particularly laurel sumac and California sagebrush) at small values of DCA2 to large amounts of exotic grass cover at large values of DCA2. The first gradient in vegetation structure consisted of a change from shrubless areas covered with herbaceous plants, exotic grass and bare ground at small values of PCA1 to large, diverse patches of tall shrubs underlain by deep litter at large values of PCA1. The second gradient in vegetation structure was associated with a change from herbaceous plants, cryptogammic soil, exotic grass, and woody debris at small values of PCA2 to short shrubs and cactus at large values of PCA2.

Vegetation found at the edge sites fell largely within the range of variation found at the regional level (Figure 3.1A and 3.1B). The sites were floristically distinct from one another (Figure 3.1A). LAPE was typical of Riverside County sites, containing greater amounts of brittlebush than STRA or MIRA. STRA sites had greater amount of laurel sumac, typical of Orange County sites. MIRA was somewhat atypical from other San Diego County sites, falling at the edge of the regional gradients rather than the middle, primarily because MIRA had relatively high amounts of chamise for CSS vegetation. Structurally, LAPE had sparser, smaller shrubs than either of the other sites, but STRA and MIRA had similar vegetative structures (Figure 3.1B). All three sites were typical of the regional patterns of vegetation structure.

Vegetation differed among sites and among distances (Table 3.1). All four vegetation variables differed among sites. Distances also differed from one another, primarily due to higher PCA2 scores at the edge. The differences among distances in PCA1 and DCA1 were only evident in the interaction term, indicating that these variables differed among distances, but the differences were not consistent among sites (Figure 3.1). DCA2 did not differ among distances and had no interaction with site, indicating that although the study sites differed in the amount of shrubs and exotic grasses, the relative amounts did not differ among distances at any of the sites.

Species Responses to Site, Distance to Edge, and Habitat Suitability

A significant proportion of the variation in the observed presence of 12 of 16 species was accounted for by an overall model that included site, distance to edge, and habitat suitability (Table 3.2). Model R^2 for significant models ranged from 0.12 for western harvest mouse to 0.64 for Cactus Wren (scientific names of all animal species are in

Appendix 3.2). California Gnatcatcher, California Towhee, San Diego pocket mouse, and cactus mouse did not have significant overall models (Table 3.2), although the models for California Towhee and cactus mouse had $p < 0.1$.

For every species, habitat suitabilities differed among sites (Table 3.3). Habitat suitability also differed among distances to edge for several species (Table 3.3). As expected, species without unique contributions of vegetation or edge in Table 3.2 (e.g., Cactus Wren and California mouse) differed in habitat suitability among distances, indicating that these species responded to vegetation gradients that coincided with distance to edge. In contrast, independent contributions of distance to edge were detected for California Towhee (Table 3.2), even though habitat suitability differed among distances to edge (Table 3.3). This was due to a large number of towhees at interior points, where the habitat suitability predicted smaller numbers, and an intermediate number of towhees at intermediate points where the habitat suitability predicted larger numbers (Figure 3.2). Edges provided equivalent habitat to interiors (Table 3.3) for several species that exhibited edge abundance relationships (e.g., Sage Sparrow, California Thrasher, deermouse, which were less abundant at edges, and Northern Mockingbird, European Starling, which were more abundant at edges; Figure 3.2 and 3.3). California Gnatcatcher and San Diego pocket mouse did not respond to distance or habitat (Table 3.2), in spite of significant differences in habitat among distances (Table 3.3).

DISCUSSION

DIFFERENCES IN VEGETATION AMONG SITES AND DISTANCES TO EDGE

Urban edge affected the structure and species composition of adjacent vegetation. However, only PCA2, the gradient in structure from short shrubs to grasses and forbs, differed in a consistent, linear manner with increasing distance from edge. Differences in PCA2 scores showed that edge points contained less cactus and bunch grass and more forb cover than intermediate or interior points. That PCA1 (diverse patches of large shrubs to bare ground and herbaceous vegetation) and DCA1 (chamise and black sage to white sage and California sagebrush) displayed site-specific patterns of change with increasing distance from edge is confirmation that not all urban edges are alike. At STRA, for example, a wide buffer of irrigated landscaping abutted the edge, and this may have enhanced the growth of the native vegetation there. In contrast, at LAPE the edge had greater amounts of exotic grass cover, and no evidence of water subsidies from the adjacent land. Exotic grasses have become common throughout each of these sites, but are patchily distributed across our three distance classes. The vegetation was relatively undifferentiated among distances at MIRA. These differences among sites illustrate the problems with interpreting results from edge studies conducted at single study sites, as well as the need to account for habitat heterogeneity when studying edge effects.

HABITAT MODEL PERFORMANCE

Our analyses rely heavily on habitat suitability scores obtained from independently-derived habitat models whose predictive accuracy is not known. The problem we needed to address was that vegetation characteristics varied with distance to edge. This effect was a source of uncertainty in ascertaining how species responded to the edge based on the data collected in the edge study. Our use of independent assessments of habitat associations would reduce uncertainty in several circumstances:

1. Significant association with a vegetation gradient that did not differ with distance to edge. These species exhibited a habitat association, but were unresponsive to the vegetation gradient that differed with distance to edge, and their habitat suitability scores would be uncorrelated with distance to edge. In this case the confounding between distance to edge and vegetation would be eliminated by converting vegetation to predicted habitat suitability, making it easier to detect the direct responses to edge.

2. Significant association with the vegetation gradient that differed with distance to edge. For these species habitat suitability was correlated with distance from edge, as were the raw vegetation variables. However, since the vegetation was calibrated to the habitat associations of the species it was possible to detect cases in which edge-abundance relationships were due to positive response to habitat suitability gradients, and to see that the effect of edge was expressed through a change in the species' habitat. It was also possible to detect cases in which the species responded to the edge in opposition to its habitat associations.

3. Non-significant habitat associations. For species that had no significant association with vegetation, the variation in vegetation that we observed would be expected to have no effect on the species' distribution. This reduced uncertainty by both flattening (through regression coefficients near zero) and randomizing (through coefficients whose magnitude and sign were statistically arbitrary) the vegetation relative to distance to edge. Non-significant habitat models provided a way to essentially ignore the correlation

between distance to edge and vegetation, which improved our ability to detect direct edge responses. In this sense even very poor habitat models (i.e., regional study models that failed to explain species distribution and abundance from local vegetation) provided useful information for this analysis.

In all of the cases described above, we preferred to use the independently-derived habitat models instead of deriving habitat associations from the edge study data directly. The habitat models were based on more extensive and intensive sampling in the absence of urban edge effects, and we expected them to be more reliable estimates of the responses of species to variation in vegetation. We also expected the usual difficulties in using habitat models to predict distribution and abundance to be reduced in our case because we sampled both the regional and edge studies at the same time and within the same geographical area (at the same study sites for LAPE and STRA). This meant that our predicted habitat suitabilities were spatially and temporally interpolated rather than extrapolated, and were more likely to accurately represent the responses of the species to vegetation at our edge study areas.

SPECIES RESPONSES TO SITE, EDGE, AND VEGETATION

Habitat suitability varied among distances for several species (Cactus Wren, California Gnatcatcher, California Towhee, San Diego pocket mouse, and California mouse; Table 3.3). This illustrates how habitat and distance can be statistically confounded, and in the case of Cactus Wren it prevented either variable from making a unique contribution to the species' occurrence (Table 3.2, Figure 3.2). The habitat adjacent to urban edges in our areas contained less cactus than interior areas, and the effects of urban edge on Cactus

Wren therefore appear to be due to habitat degradation at the edge rather than due to a direct behavioral response by the birds to the edge. This conclusion cannot be based purely on statistical grounds, because it is also possible that the birds responded to the edge, and differences in the habitat were coincidental. However, because habitat associations are evolved responses, whereas urban edge is a relatively recent feature in the environment, when habitat suitability and distance to edge coincided we considered it more parsimonious to attribute the pattern to a species' habitat preference.

Although California Gnatcatcher and San Diego pocket mouse habitat differed among distances, their occurrences did not differ significantly among distances. This result may be due to low power, since both of these species were somewhat less common at edges than interiors (Figure 3.2 and 3.3). California Gnatcatcher occurrence roughly paralleled their predicted occurrence, suggesting that edges change the suitability of their habitat. More extensive study would be required to determine whether these patterns are spurious for California Gnatcatcher.

This analysis also clearly demonstrated that the decreased occurrence of Sage Sparrows, California Thrasher, and deermice at edges could not be explained by habitat degradation since habitat suitability was equivalent among distances to edge (Figure 3.2 and 3.3). Consequently, edge-abundance relationships for these species appear to be direct responses to the edge. California mice were found in equal numbers at each distance to edge, in spite of significantly poorer habitat at the edge, which could be interpreted as weak evidence of a positive edge response. We also detected two possible cases of inverse relationships between occurrence and habitat suitability, Scrub Jay and cactus mouse (Figure 3.2 and 3.3, respectively). These species may have responded to the edges in opposition to their habitat preferences, a pattern that could not have been detected without independent calibration of the vegetation. However, since cactus mice did not have a significant overall model (Table 3.2) and Western Scrub-Jay habitat suitability was not significantly different among distances, these patterns should be considered weak, and the results tentative.

Our results suggest different strategies for reducing the effects of edges on different species. Both Sage Sparrows and California Thrashers showed strong evidence of direct, negative responses to edges. These species are also known to be fragmentation sensitive (Bolger et al. 1997), and our results suggest that this may be due in part to their edge sensitivity. Other species, such as Cactus Wren, California Gnatcatcher, San Diego pocket mouse, and California mouse, may also be fragmentation sensitive because of edges, but for these species the mechanism is likely to be habitat degradation rather than aversion to the edge per se. This distinction is important, because the reduced effective area of habitat caused by the developed edge would not be reversed by restoring the habitat at edges for Sage Sparrows or California Thrashers, but may be reversed for Cactus Wrens, California Gnatcatchers, San Diego pocket mice or California mice.

Edges differed substantially among study areas. Habitat differences among distances to edge were largely site-specific, making it possible in some cases to detect independent effects of habitat suitability and distance to edge. In other cases habitat suitabilities differed among distance to edge consistently among sites. These different patterns were obtained from the same vegetation data, calibrated to the habitat preferences of different species. In light of this, it is not surprising that counts of individuals at different distances from edge would yield inconsistent results among studies. Our results suggest that consistent edge-abundance relationships would only be expected for species that respond directly to the edge, or that respond to effects of edge that are consistently expressed among sites. Species that are indifferent to the edge itself will only exhibit an edge-abundance relationship when an edge changes its habitat, which may occur at some sites but not others. These species will appear to have inconsistent responses to edge, when in fact they are responding consistently to changes in vegetation that are expressed inconsistently.

The different responses to edge that we observed suggest different consequences of edge on populations. We have found greater numbers of mammalian predators at edges at these sites (Appendix 3.3). Species that avoid the edge itself will suffer a reduction in effective area of habitat, but may benefit by avoiding depredation. Others, such as Cactus Wrens and possibly California Gnatcatchers, apparently use preferred habitat where they find it. Although lost habitat area could be recovered for these species it may be inadvisable if attracting animals to edges exposes them to predators (Gates and Gysel 1978). Habitat mitigation measures should be done with caution to avoid creating ecological traps for species that are not intrinsically edge-averse.

ACKNOWLEDGMENTS

I thank P. Addison, P. Aigner, M. Chase, E. Clarke, S. Dodd, K. Ellison, C. Koehler, D. Kristan, M. Lulow, M. Misenhelter, L. Pagni, M. Patten, S. Remington, J. Ruvinsky, M. Spiegelberg, and P. Wellburn for field assistance. We especially thank the reserve managers of our study sites and their institutions for their interest in this project and for facilitating our access to their reserves: E. Almanza, B. Carlson, J. Chew, L. Cohen, P. DeSimone, G. Hund, E. Konno, K. Lovelady, D. Lydy, S. McKelvey, T. Miller, L. Munoz, J. Opdycke, R. Perales, S. Shapiro, T. Smith, M. Sanderson, S. Weber, M. Wells, J. King, and A. Yuen. The manuscript benefited from review by D. Kristan and W. Boarman. This paper includes work funded through Cooperative Agreement No. 14-45-0009-94-1064 between the University of California, Riverside, and the National Biological Service (now Biological Resources Division, U.S. Geological Survey). We thank S. Viers and P. Stine for administrative assistance.

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Appendix 3.1. Vegetation variable codes and descriptions

Variable	Description
GC_Bare	Percent of ground cover that is bare ground.
GC_BG	Percent of ground cover that is bunch grass.
GC_Cac	Percent of ground cover that is cactus.
GC_Crypt	Percent of ground cover that is cryptogammic soil.
GC_Forb	Percent of ground cover that is forb.
GC_Grass	Percent of ground cover that is exotic grass.
GC_Litter	Percent of ground cover that is litter (small, disaggregated debris).
GC_Rock	Percent of ground cover that is rock.
GC_Wood	Percent of ground cover that is woody debris.
Hits_1_3	Number of times plants touched the pin between 1 and 3 dm.
Hits_3_5	Number of times plants touched the pin between 3 and 5 dm.
Hits_>5	Number of times plants touched the pin over 5 dm.
Litter_Depth	Average depth of litter.
Max_ht	Average height of the tallest plant at each pin drop.
Mean size	Mean horizontal patch size.
Num_sp	Mean number of species that touched each pin drop.

Appendix 3.2. Codes, common names, and scientific names of all species mentioned in tables or text.

Code	Common Name	Scientific Name
Plants		
ADFA	Chamise	*Adenostoma fasciculatum*
AMME	Fiddlenecks	*Amsinckia menziesii*
ARCA	California sagebrush	*Artemesia californica*
BG	Bunch grasses	
BRAS	Mustard	*Brassica* spp.
BRSP	Thistle	*Brickellia* spp.
CAC	Prickly pear and cholla	*Opuntia* spp.
CETO	California-lilac	*Ceonothus tomentosus*
CNDU	Bushrue	*Cneoridium dumosum*
ENFA	Brittle bush	*Encelia farinosa*
ERCR	Yerba santa	*Eriodictyon crassifolium*
ERFA	California buckwheat	*Eriogonum fasciculatum*
FORB	Herbaceous dicots	
GASP	Bedstraw	*Galium* spp.
GRASS	Exotic grasses	
HEAR	Toyon	*Heteromeles arbutifolia*
LEFI	Cham	*Lessingia filaginifolia*
LOSP	Deerweed	*Lotus scoparius*
MALA	Laurel sumac	*Malosma laurina*
MAMA	Wild cucumber	*Marah macrocarpus*
MISP	Monkey flower	*Mimulus* spp.
QUSP	Oak	*Quercus* spp.
RUSP	Lemonadeberry	*Rhus* spp.
SAAP	White sage	*Salvia apiana*
SAME	Black sage	*Salvia mellifera*
SN	Standing dead woody	
XYBI		*Xylococcus bicolor*

Appendix 3.2 (cont.)

Code	Common Name	Scientific Name
Birds		
CACW	Cactus Wren	*Campylorhynchus brunneicapillus*
CAGN	California Gnatcatcher	*Polioptila californica*
CALT	California Towhee	*Pipilo crissalis*
CATH	California Thrasher	*Toxostoma redivivum*
CORA	Common Raven	*Corvus corax*
EUST	European Starling	*Sturnus vulgaris*
NOMO	Northern Mockingbird	*Mimus polyglottos*
SAGS	Sage Sparrow	*Amphispiza belli*
SCJA	Scrub Jay	*Aphelocoma coerulescens*
Small mammals		
CHCA	Dulzura pocket mouse	
CHFA	San Diego pocket mouse	
DIAG	Pacific kangaroo rat	
NEFU	Dusky-footed woodrat	
NELE	San Diego woodrat	
PECA	California mouse	
PEER	Cactus mouse	
PEMA	Deermouse	
REME	Western harvest mouse	

Appendix 3.3. Mean number of days carnivore species were detected out of ten sampling days among the edge transects.

	Transect		
Species	Edge	Intermediate	Interior
Domestic cat	0.19	0.00	0.00
Bobcat	0.37	0.85	0.52
Coyote	6.81	5.26	5.00
Domestic dog	2.30	0.81	0.30
Grey fox	0.37	0.78	1.44
Oppossum	0.78	0.56	0.00
Raccoon	0.63	0.37	0.00
Skunk	0.56	0.48	0.22

Table 3.1. Univariate (ANOVA) and multivariate (MANOVA) differences in vegetation structure (PC1 and PC2) and floristics (DCA1 and DCA2) among sites (Lake Perris, Starr Ranch, Miramar) and among distance classes (edge, intermediate, interior).

Effect	Variables	Test	F	df	Statistical Significance
Whole Model	All	Multivariate	19.46 [a]	24, 201	<0.001
	PC1	Univariate	17.02	8, 71	<0.001
	PC2		7.08	8, 71	<0.001
	DCA1		117.30	8, 71	<0.001
	DCA2		12.93	8, 71	<0.001
Site	All	Multivariate	88.42 [a]	6, 138	<0.001
	PC1	Univariate	59.16	2, 71	<0.001
	PC2		10.88	2, 71	<0.001
	DCA1		453.60	2, 71	<0.001
	DCA2		49.42	2, 71	<0.001
Distance	All	Multivariate	1.78 [a]	6, 138	0.107
	PC1	Univariate	1.94	2, 71	0.152
	PC2		4.51	2, 71	0.014
	DCA1		1.12	2, 71	0.332
	DCA2		0.25	2, 71	0.777
Site*Distance	All	Multivariate	3.37 [a]	12, 183	<0.001
	PC1	Univariate	1.79	4, 71	0.139
	PC2		5.42	4, 71	<0.001
	DCA1		4.58	4, 71	0.002
	DCA2		1.10	4, 71	0.361

[a] Approximate F-statistic from Wilks' lambda

Table 3.2. Effects of site, distance from edge, and independent measures of habitat affinity upon the distribution of birds and small mammals. Bold denotes $P < 0.05$. See Appendix 2 for interpretation of species codes.

	Overall			Site		Habitat		Edge		
Species	R^2	χ^2	P	χ^2	P	χ^2	P	χ^2	P	Response
Birds										
CACW	0.64	65.6	<0.001	36.2	<0.001	0.0	0.920	3.6	0.160	
CAGN	0.14	6.0	0.300	4.9	0.090	0.0	1.000	1.2	0.550	
CALT	0.13	10.1	0.070	0.6	0.730	0.5	0.460	9.4	0.010	-
SCJA	0.17	18.7	0.000	5.4	0.070	0.2	0.670	1.0	0.610	
SAGS	0.50	39.8	<0.001	22.5	<0.001	4.2	0.040	10.0	0.010	-
NOMO	0.30	32.8	<0.001	2.9	0.230	2.4	0.120	27.6	<0.001	+
EUST	0.33	30.7	<0.001	0.0	0.980	5.3	0.020	29.6	<0.001	+
CATH	0.16	17.3	<0.001	6.8	0.030	0.1	0.790	10.6	0.010	-
Small Mammals										
CHFA	0.10	8.5	0.130	1.7	0.430	1.4	0.250	2.3	0.320	
DIAG	0.32	24.0	<0.001	0.5	0.760	7.3	0.010	0.5	0.770	
NEFU	0.30	32.9	<0.001	20.7	<0.001	2.1	0.140	3.3	0.190	
NELE	0.57	60.9	<0.001	35.6	<0.001	0.1	0.750	1.0	0.610	
PECA	0.57	51.1	<0.001	22.8	<0.001	0.2	0.670	0.0	0.990	
PEER	0.11	10.3	0.070	8.4	0.020	2.0	0.160	2.2	0.340	
PEMA	0.36	40.0	<0.001	1.1	0.580	6.2	0.010	6.2	0.050	-
REME	0.12	13.3	0.020	11.8	<0.001	0.4	0.540	0.4	0.820	

Table 3.3. Differences in the expected probability of occurrence for each species, predicted by each species' NCCP habitat models, among sites and distances to edge. Bold denotes statistical significance.

	Site and Distance			Site		Distance	
Species	R^2	F	p	F	p	F	p
Birds							
CACW	0.54	22.35	**<0.001**	41.11	**<0.001**	3.99	**0.022**
CAGN	0.36	10.53	**<0.001**	17.54	**<0.001**	3.26	**0.044**
CALT	0.28	7.20	**<0.001**	9.65	**<0.001**	4.66	**0.012**
SCJA	0.67	37.80	**<0.001**	75.50	**<0.001**	0.44	0.647
SAGS	0.71	46.62	**<0.001**	93.23	**<0.001**	0.09	0.910
NOMO	0.82	87.46	**<0.001**	174.85	**<0.001**	0.14	0.867
EUST	0.20	4.73	**0.002**	7.02	**0.002**	2.41	0.100
CATH	0.71	45.49	**<0.001**	90.39	**<0.001**	1.14	0.324
Small mammals							
CHFA	0.65	34.33	**<0.001**	64.32	**<0.001**	3.35	**0.041**
DIAG	0.55	45.79	**<0.001**	45.79	**<0.001**	0.54	0.585
NEFU	0.56	24.11	**<0.001**	47.41	**<0.001**	0.87	0.420
NELE	0.45	15.61	**<0.001**	30.58	**<0.001**	0.60	0.552
PECA	0.66	36.70	**<0.001**	67.5	**<0.001**	7.11	**0.001**
PEER	0.70	43.47	**<0.001**	85.56	**<0.001**	2.09	0.130
PEMA	0.90	180.38	**<0.001**	360.61	**<0.001**	1.02	0.366
REME	0.36	10.83	**<0.001**	21.54	**<0.001**	0.08	0.923

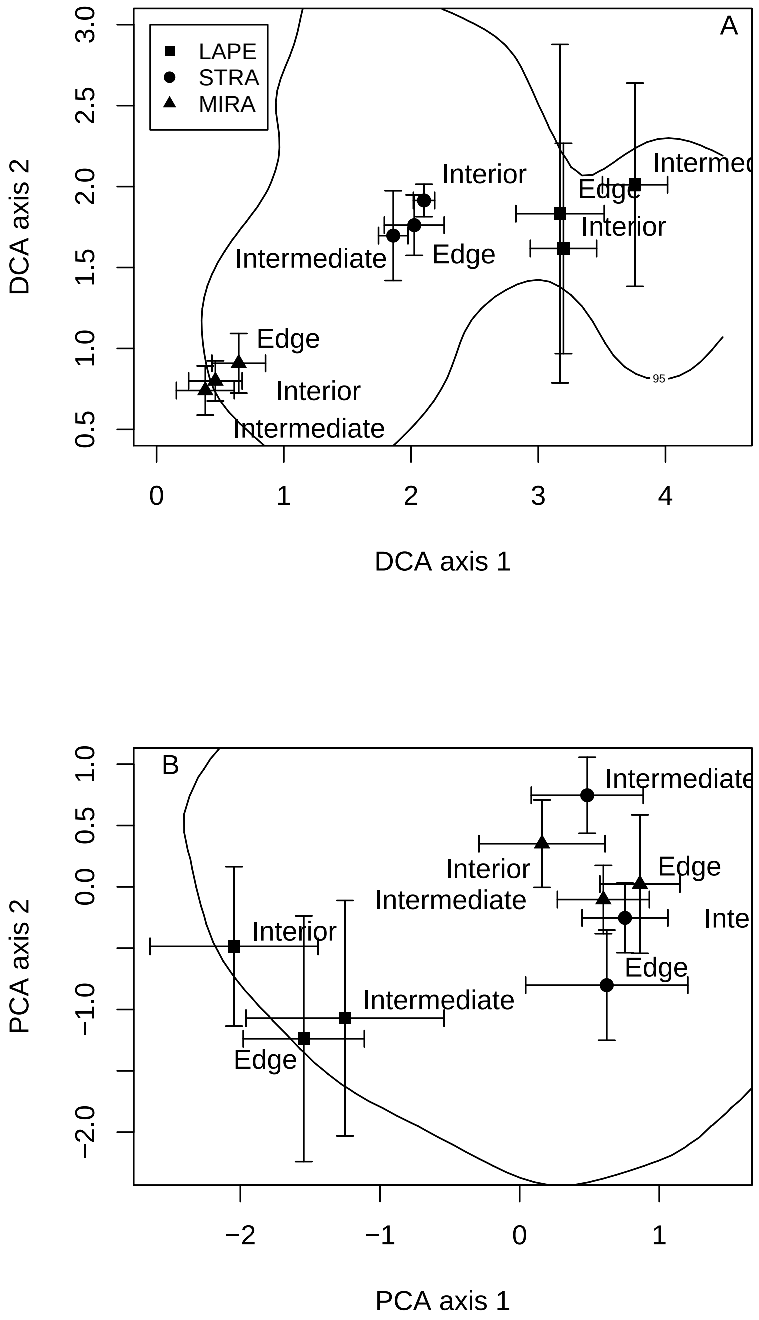

Figure 3.1. Variation in vegetation among edge sites (symbols, ± 2 std. dev.), superimposed on regional patterns of variation in vegetation (contour lines). Vegetative species composition (Figure 3.1A) and structure (Figure 3.1B) varied among edge study sites, but overlapped the regional range of variation. Contour lines enclose 95% of the regional study points.

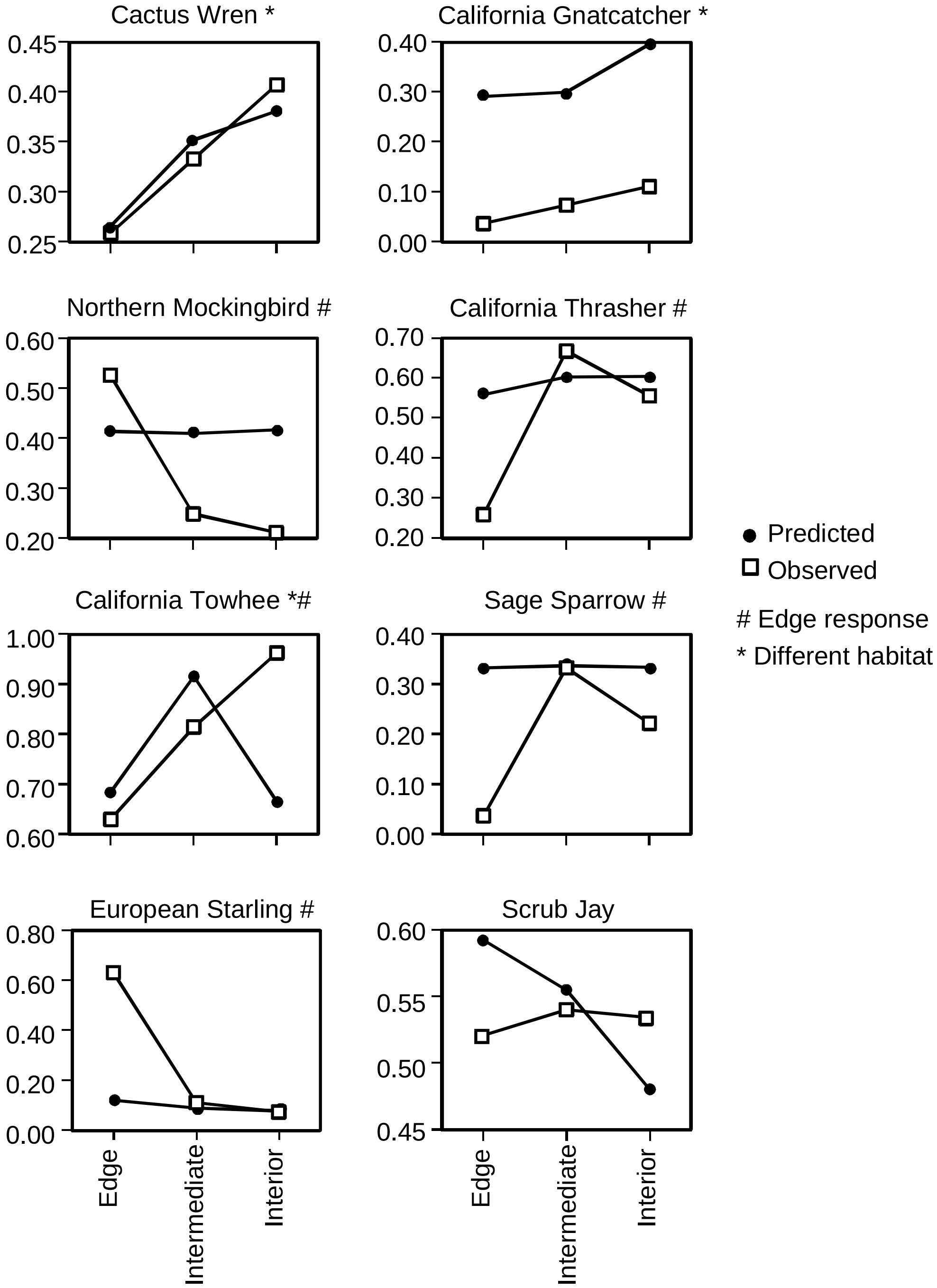

Figure 3.2. Observed (open squares) and predicted (black circles) occurrence of birds among distances from edge. Significant differences in preferred habitat among distances to edge (Table 3.3) are denoted with *, and significant effects of edge on occurrence (Table 3.2) are denoted with #.

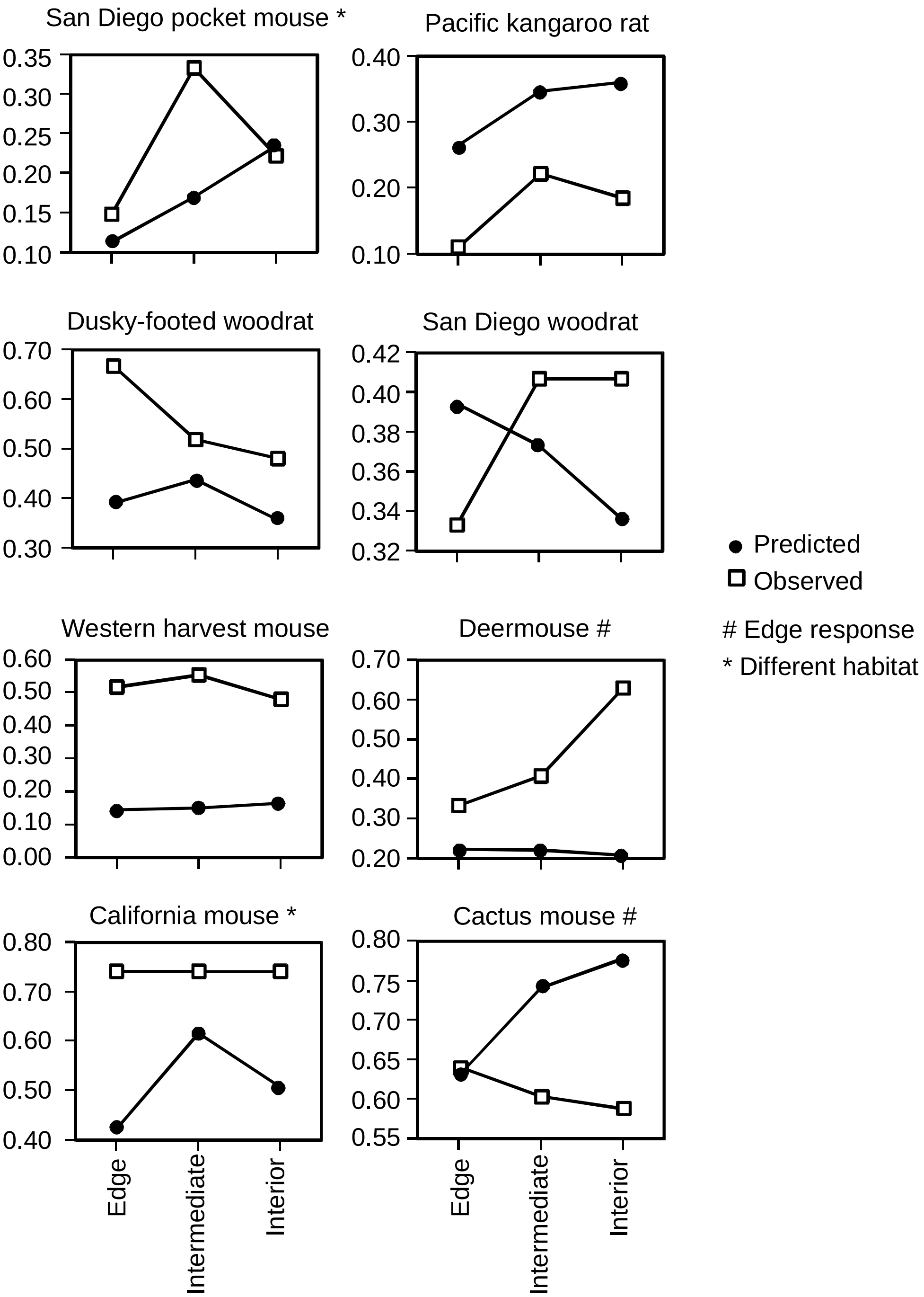

Figure 3.3. Observed (open squares) and predicted (black circles) occurrence of small mammals among distances from edge. Significant differences in preferred habitat among distances to edge (Table 3.3) are denoted with *, and significant effects of edge on occurrence (Table 3.2) are denoted with #.

CHAPTER 4. Effects of anthropogenic developments on raven nesting biology in the west mojave desert

Abstract. Common Ravens (*Corvus corax*) have increased in number in the Mojave Desert over the last 3-4 decades, and are considered human commensals there. Anthropogenic subsidies to raven population growth may indirectly impact other vertebrate species in the Mojave on which ravens prey. Over a five year period from 1996-2000, we examined whether anthropogenic features (i.e., roads, food and water subsidies from urban areas) augmented raven reproductive success, whether anthropogenic factors or natural environmental cues had a greater influence over raven reproductive investment decisions, and whether ravens were able to adjust investment in their reproductive effort in response to predictable effects of anthropogenic factors on reproductive success. We found that ravens only nested preferentially near point subsidies even though roads and urban areas also increased fledging success. Initiation of breeding was affected by biological factors (particularly the presence of previous years' nests at the beginning of the breeding season), but not by anthropogenic factors. Anthropogenic factors affected raven nesting habitat, but the effects did not explain anthropogenic effects on raven reproductive success, indicating that anthropogenic factors acted through direct resource subsidies (such as supplemental food and water) rather than through an increase in the availability of suitable raven nesting habitat. Ravens were broadly distributed throughout the study area, and most ravens bred in habitat they did not prefer, such that the concentration of high-quality, anthropogenically subsidized habitat near the small towns and major roads in the study area did not prevent

ravens from using poor habitat far from these sites, where they would be expected to depredate the local fauna to feed themselves and their chicks. By subsidizing ravens, anthropogenic sites can therefore potentially have effects on sensitive vertebrates that extend far from roads and beyond city limits.

INTRODUCTION

Common Ravens (*Corvus corax*) have increased in number throughout southern California over the last several decades (Boarman and Berry 1995, Sauer et. al. 2000). Increases in raven numbers have been concommittant with expanding human development in the region, and this pattern has implicated human subsidies as contributors to raven population increases (Boarman 1993). In addition to these population trends there is a great deal of indirect evidence supporting human contributions to raven population growth, including observations of large numbers of ravens breeding in urban areas and feeding on human refuse (Boarman and Heinrich 1999).

Although it appears obvious that anthropogenic developments would subsidize raven populations, thereby contributing to the growth and expansion of raven populations, the way that this effect is expressed can have large impacts on the rate and extent of the population expansion. For example, breeding populations in the Mojave Desert are largest in the west Mojave, where urban development is most extensive, and ravens are found in association with anthropogenic features, such as roads (Austin 1971, Knight and Kawashimi 1993) and urban areas (Knight et al. 1993) throughout the region. Whether this is a stable condition or a temporary state prior to expansion into undeveloped lands will depend on the extent to which the Mojave Desert environment is capable of supporting raven populations without subsidy from human activities. Human developments bring both food and water to the desert, either of which could promote raven population growth. If human subsidies are increasing raven population growth, the spatial distribution of subsidies may influence population dynamics by establishing productive source areas that support large regional populations, including those in marginal, sink habitats that are far from subsidies (Pulliam 1988). Furthermore, raven populations will have the greatest potential to increase if they are able to capitalize on predictable human subsidies by preferentially using areas where human subsidies are available (Kristan 2001).

In this paper we address these questions by evaluating variation in reproductive performance (fledging success) relative to proximity to anthropogenic subsidies (urbanization, food and water sources, roads), and by evaluating whether investment choices (facultative factors such as positions of breeding territories, occupancy of territories, initiation of breeding, and timing of initiation) reflect reproductive performance (fledging success). We further distinguished between “natural” cues that are potentially relevant to ravens selecting territories, and “anthropogenic” cues that are present only because of human activities. This distinction allowed us to evaluate whether individuals are recognizing the effects of anthropogenic subsidies directly, or are responding to "natural" habitat cues that are in turn affected by anthropogenic activities.

We concentrate on breeding because the nesting period is the time when ravens are least mobile (Boarman and Heinrich 1999) and are most likely to be affected by the sort of spatial variation in habitat quality produced by placing urbanizing areas adjacent to undeveloped lands. Because adult ravens spend most of their time, and do most of their foraging, within sight of their nests during breeding (Sherman 1992, Boarman and Heinrich 1999) chick survival should be sensitive to nest site characteristics.

METHODS

STUDY AREA

The primary study area was within the western half of Edward Air Force Base (EAFB), and in lands immediately surrounding the base, in the west Mojave Desert (Figure 4.1). Vegetation on the study area was composed of creosotebush (*Larrea tridentata*) and saltbush (*Atriplex* spp.) scrub, often in association with Joshua tree (*Yucca brevifolia*). Creosotebush is a large shrub, standing 1.5-3 m in height, and individual plants were generally widely spaced. Saltbushes were short, standing one meter or less, and individuals were more densely spaced than creosotebush.

Several permanent water bodies were present on the study area, which contributed water, food, and riparian vegetation types to the study population. Piute Ponds, an artificial wetland within EAFB, contained well-developed riparian vegetation, including willows (*Salix* spp.), cattails (*Typha* spp.), and rushes (*Juncus* spp.). The ponds supported breeding populations of waterfowl, waders, and shorebirds as well as amphibians, such as the African clawed frog (*Xenopus laevis*), which were potential raven prey. Open sewage treatment facilities were also present near two towns in the study area, Mojave (pop. 3,763) and Rosamond (pop. 7,430).

Lands within the EAFB boundary that were included in the study area were used primarily for recreation rather than military exercises. Consequently, the vegetation was not heavily disturbed in the portion of the study area within EAFB bounds. Undeveloped lands outside of the EAFB boundary were used for a variety of purposes, including sheep grazing and recreation. The housing area within EAFB (pop. 7423) had similar characteristics to Rosamond and Mojave, with all three consisting of single-family homes, apartment complexes, and commercial developments (e.g. restaurants, grocery stores, etc.). Solid waste disposal sited (landfills) were present near EAFB housing and near the town of Mojave.

RESEARCH QUESTIONS

To address the interacting effects of natural and anthropogenic effects on reproductive investments and performance we posed several specific questions.

Investment:

1. Do ravens nest preferentially near anthropogenic resources?
2. Do ravens initiate breeding more often, or invest more in individual breeding efforts, near anthropogenic resources?

Performance:

3. Is reproductive success affected by distance to anthropogenic resources?

Relationship between investment and performance:

4. Are investments more strongly affected by natural environmental cues, or by anthropogenic resources?
5. Are the distributions of "natural" environmental cues affected by anthropogenic

developments?

6. Do individual ravens choose territories in which they are most likely to breed successfully?

Ravens are expected to preferentially select territories and initiate breeding where they are most likely to breed successfully. If anthropogenic resources increase raven reproductive output, nests should be spatially clustered near them, and ravens with territories nearest these resources should be most likely to initiate breeding. Anthropogenic resources could effect reproduction directly, via food and water subsidy, or indirectly, by altering natural variables that ravens use when choosing territories.

DATA COLLECTION

Nest searching and breeding measures

Ravens built large (approximately 0.5-1m in diameter) open cup stick nests, usually on elevated platforms, such as telephone or electrical poles, Joshua trees, buildings, or cliffs. The nests are conspicuous, and most nests were visible from several hundred meters. We attempted to find all raven nests in the study area by scanning all visible, suitable platforms for nests while driving throughout the area. Most of the area had extensive networks of roads and trails, and it was possible to travel within 0.5 – 1 km of all points in the core area in which potential raven nest platforms were present. When nests were found they were assigned unique identifiers and their positions were recorded to within 10 m using global positioning system (GPS) units. Many nests were used repeatedly by ravens over the five years of the study, and consequently the number of nests under observation increased with time. In 1999 and 2000 we increased our search effort in areas that were far from our typical travel routes, and by 2000 we had found sufficient numbers of nests to be confident that we had found a majority of the nests on the study area (we believe 90% or more), and that we had not under-sampled any portion of the study area.

Once nests were found, we returned to record breeding activity weekly. We made several reproductive measures from each nest, representing different aspects of breeding biology: nest site occupancy, initiation of breeding, clutch size, clutch initiation date, and number of chicks fledged. Not all nests were equally accessible, and not all variables could be recorded for each nest. Occupancy, initiation (including any breeding activity from laying on), and fledging success could be observed from the ground without access to the nests themselves, as could the number of chicks fledged in most cases. Clutch size was only recorded from nests that could be observed using a telescoping pole with a mirror attached to observe clutch size, or from those nests that could be climbed.

We recorded fledging date for all successful nests, as well as clutch initiation date. When nests were found before clutch completion we estimated initiation date by subtracting the number of eggs added after a nest was discovered from the date of discovery, assuming one egg was laid each day (Boarman and Heinrich 1999). When clutches were found after completion, we calculated initiation day based on the timing of other events, such as hatching or fledging (Boarman and Heinrich 1999).

Nests in which no breeding activity was observed were checked weekly until it became too late for a pair to initiate a successful brood (mid-May), then were checked once more in early June to confirm that no late attempts were made. Nests with pairs that initiated breeding were checked weekly until the fate of the breeding attempt was known.

Nest site characteristics

We recorded characteristics of the nest site that might represent environmental cues to which ravens would respond in the absence of anthropogenic effects, i.e. "natural" variables. We recorded the nesting substrate and species of the dominant shrub (creosotebush, saltbush, both species, or neither), which were persistent features of the nest site, for all nests. In 1999 and 2000 we began visiting known nest sites and searching for new sites early enough to record whether the previous year's nest was present at the beginning of the breeding season. In 2000 we additionally recorded the presence of drinkable water within sight of the nest at the time when breeding was initiated.

Anthropogenic resources

Anthropogenic effects on ravens were divided into three classes: point subsidies, roads, and local levels of urbanization (just “urbanization” from now on). Point subsidies were large, permanent sources of food or water that could be represented by a single point (such as a landfill or pond) or polygon (such as housing areas) on a map. Roads were expected to affect ravens by contributing edible refuse or roadkill (Austin 1971, Knight and Kawashima 1993) and associated powerlines contributed nest sites (White and Tanner-White 1988, Knight and Kawashima 1993). We confined our analysis to highways and high-speed, high traffic volume paved roads, such as the roads ringing the core study area, but not the lightly-used dirt roads covering much of the study area. Urbanization resulted in developed areas adjacent to undeveloped areas, and we defined an urbanization gradient based on the relative amount of a raven breeding territory (defined as a circle with a 400 m radius surrounding the nest) that contained developed areas. For the anthropogenic variable "urbanization," breeding territories could be located completely within human developments (urban), could contain both human development and natural vegetation (mixed), or could be located completely within undeveloped habitat (natural).

STATISTICAL ANALYSES

Spatial distribution of nests

We compared the spatial distribution of raven nests with randomly located points placed in raven nesting habitat within the study area. We generated 5000 random points within the study area, then omitted areas that had no nesting substrate, such as dry lake beds. This procedure resulted in 4345 points with a random distribution relative to the anthropogenic sites in the study area (i.e. point resource subsidies or roads). Distances to anthropogenic sites from raven nests and random points were calculated from GIS maps.

We assessed two attributes of nest distribution: the numerical abundance of nests as a function of distance from anthropogenic sites, and preference for nesting near anthropogenic sites (disproportionate use of particular distances, Manley et al. 1993). We measured preference by calculating a modified form of a selection ratio (log(proportion used/proportion available)), using kernel density estimates (Bowman and Azzalini 1997) to measure proportional use and proportional availability as a function of distance from roads and point subsidies. The log of the ratio of these density estimates is symmetrical around zero (i.e. zero indicates use in proportion to availability, and no preference).

Relationship between reproductive measures, natural factors, and anthropogenic factors.

We wished to examine the extent to which ravens responded to natural factors and anthropogenic factors, as well as the potential for indirect effects of anthropogenic factors on raven reproduction via their effects on natural factors. In each case we wanted to evaluate both the independent contribution of each single variable on a measure of raven reproductive activity as well as the relative contribution of groups of variables, either natural or anthropogenic. Although the details of the statistical models used for different reproductive measure varied (each is described below) the overall approach was consistent. In each case we first evaluated whether a significant relationship existed between a reproductive variable and the full set of environmental variables, both natural and anthropogenic, using general linear models (e.g. logistic regression for occupancy and initiation, and poisson regression for clutch size, number of chicks fledged, number of years occupied, and numbers of years successful). For significant overall models we then assessed the relative importance of the groups of natural and anthropogenic variables by comparing the fit of models that included all of the variables to ones that omitted one of the groups of variables. Significant decreases in model fit when a group of variables was omitted was determined using likelihood ratio tests. A group of variables that had significant effects on the reproductive variable were further analyzed with a model including only that group, so that the relative importance of each of the variables within the group could be determined.

We related natural and anthropogenic factors to occupancy patterns, both within a year and over time. Occupancy over time was measured by the number of years that nests were occupied. Because new nests were discovered each year we used the number of years that the nest was observed as a covariate in this analysis, and determined significance by comparing the fit of a model that included all of the independent variables, including the number of years observed, against one that included only the number of years observed. We analyzed occupancy within a year beginning with 1997, since most nests in 1996 were found occupied.

We related natural and anthropogenic factors to initiation of breeding within each year using logistic regression. We related natural and anthropogenic factors to clutch size using poisson regression. The number of chicks fledged and years that a territory was successful were analyzed using poisson regression.

We related fledging success to initiation date, then related initiation date to anthropogenic factors to explore whether anthropogenic effects on reproduction were expressed by affecting the timing of breeding.

The relationship between anthropogenic and natural variables

Anthropogenic factors can affect raven reproductive activity directly by contributing sources of food or water. Alternatively, anthropogenic factors can affect raven reproduction indirectly by altering natural factors, such as availability of suitable nesting substrates. We analyzed the effects of anthropogenic factors on natural factors to explore whether anthropogenic factors affected raven reproduction by altering their nesting habitat.

RESULTS

INVESTMENT

Raven nests were most common near point subsidies (Figure 4.2a) and near roads (Figure 4.2b), and declined in abundance with increasing distance from either. Ravens selected nest sites within 2 km of point subsidies, and avoided areas that were over 2 km from point subsidies (Figure 4.3). In contrast, ravens selected nests that were over 2 km from roads and avoided areas that were within 2 km of roads (Figure 4.3).

Nest site occupancy models were significant in all years except 1999 (Table 4.1). Natural variables had greater affects on occupancy in 1998 and 2000, and anthropogenic variables had a greater affect in 1997. Years of nest site occupancy was not significantly affected by either set of variables.

Although natural variables affected occupancy in both 1998 and 2000, different variables accounted for the relationship. In 1998 both shrub cover and substrate affected occupancy, but in 2000 only nest presence affected occupancy (Table 4.2). This variable was not recorded in 1998. The overall occupancy model became non-significant for 2000 when nest presence was omitted (deviance = 17.33, df = 11, p = 0.098). In 1997, roads and subsidies had similar effects on occupancy, and both had greater effects than urbanization, but none had significant effects independent of the others (Table 4.3).

Initiation of breeding in occupied territories was significantly associated with natural variables in both 1999 and 2000, but not with anthropogenic variables (Table 4.4). In both years the presence of a nest at the beginning of the breeding season significantly increased the probability of initiation (Table 4.5), with initiation increasing from 1.4% to

62.2% in 1999 and from 28.9% to 71.0% in 2000 when nests were present. Nest substrate was also significantly associated with initiation in 1999, with initiation in occupied territories occurring in 75% of buildings (n=4), all of cliffs (n=4), 56.8% of Joshua trees (n=125), 57.5% of poles (n=80) and 57.6% of trees (n=33). The effect of substrate in 1999 was thus primarily due to high initiation rates in the two smallest classes (buildings and cliffs).

Clutch size was unaffected by natural and anthropogenic factors in all years (Table 4.6).

PERFORMANCE

Number of chicks fledged from territories in which breeding was initiated was significantly affected by anthropogenic factors every year from 1996-2000, as was the number of years a nest was successful (Table 4.7). Natural factors were also significant in 1997 and 2000.

Numbers of chicks fledged declined as distance from roads increased in every year but 1998, as did the number of years successful (Table 4.8). Numbers of chicks fledged declined as distance from point subsidies increased in 1998, as did the number of years successful. Degree of urbanization was significantly associated with number of chicks fledged only in 2000, with 1.92 chicks per nest fledged from urban territories, 1.67 chicks per nest fledged from territories with a mix of urban and natural habitat, and 0.81 chicks per nest fledged from territories in natural habitat.

Numbers of chicks fledged was affected by shrub cover in both 1997 and 2000, and by substrate in 1997 (Table 4.9). In 1997 the mean number of chicks fledged was 1.00 (n= 2) for building nests, 0.00 for cliff nests (n = 2), 1.35 for Joshua tree nests (n = 45), 0.67 for pole nests (n = 45), and 1.13 (n = 15) for tree nests. In 1997 the mean number of chicks fledged was 0.57 (n = 28) for nests in creosotebush, 1.17 (n = 48) for nests in saltbush, 1.35 (n = 14) for nests with both dominant shrub species, and 1.00 (19) for nests with neither shrub species. In 2000 the mean number of chicks fledged was 0.42 (n = 24) in creosotebush, 1.12 (n = 81) in saltbush, 0.37 (n = 24) for nests with both dominant shrub species, and 1.80 (n=15) for nests with neither shrub species.

Fledging success decreased with increasing laying date in both 1999 (deviance = 26.45, df = 1, p < 0.0001) and 2000 (deviance = 31.42, df = 1, p < 0.0001). Anthropogenic variables affected initiation date in both 1999 and 2000. In 1999 nests that were near roads initiated earlier (Table 4.10). In 2000 the relationship between day of initiation and distance from subsidies was positive, such that nests near subsidies initiated earlier. Additionally in 2000 nests in urbanized areas nested earlier than nests in mixed or natural habitats.

ANTHROPOGENIC EFFECTS ON NATURAL VARIABLES

Anthropogenic factors did not affect the probability of nests being present in territories at the beginning of the breeding season in either 1999 or 2000 (1999: deviance = 5.93, df =4, p = 0.2. 2000: deviance = 7.56, df = 4, p = 0.11). Distance to roads differed among nests with different shrub cover types (F = 2.70, df = 3, 350, p = 0.045), as did distance to subsidies (F = 9.80, df = 3, 350, p < 0.0001). Nests without either dominant shrub species were in urban areas (n = 35), and were closer on average to roads and subsidies than were nests with either dominant shrub type.

Shrub cover varied with degree of urbanization, with all shrub classes (saltbush, creosote, and both) most common in natural habitat, and nest sites with neither dominant shrub all within urban areas (Table 4.11). Urbanization also affected substrate use (Table 4.12). Urban nests were in trees (n = 23), poles (n = 6) or buildings (n = 3), whereas nests in natural areas were primarily in Joshua trees (n = 191), and in poles (n = 74), trees (n = 18), and cliffs (n = 3). In mixed habitat nests were found in all of these substrates (building = 1, cliff = 1, Joshua tree = 5, pole = 13, and tree = 5).

DISCUSSION

Common Ravens are not new to the Mojave Desert, but have increased in number in the last 30-40 years (Sauer et al. 2000). They are common in urban areas, such as Lancaster and Palmdale (populations 119,186 and 103,423 respectively), near our study area. Ravens living in these cities could subsist entirely on anthropogenic features and resources, including nest substrates (e.g. buildings, poles, ornamental trees), food (e.g. refuse, roadkill), and water (e.g. artificial water bodies, runoff from irrigated landscaping). In contrast, ravens on our study area were exposed to a mix of habitats, and breeding territories could include exclusively urban habitat or exclusively natural habitat, roads or roadless areas. The arrangement of human dominated and natural areas allowed us to evaluate whether raven reproduction was enhanced by anthropogenic factors, whether the effects were likely to be due to direct resource subsidies to breeding adults or by manipulating natural habitat characteristics, and whether ravens adjusted their reproductive investments to reflect predictable effects of anthropogenic factors on the likelihood of successfully breeding.

Although ravens are capable of travelling long distances, breeding ravens are strongly associated with nest sites (Boarman and Heinrich 1999), and as nests are placed further from anthropogenic features it becomes increasingly unlikely that individuals are exploiting the resources provided by people, resulting in spatial variation in the likelihood of breeding successfully. The effects of human activities on raven population dynamics will depend on whether ravens are able to recognize the benefits of selecting nests where human subsidies are available and preferentially exploit the best habitat (Kristan 2001).

To understand the relationship between investment choices and performance consequences, it is important to distinguish between aspects of the nesting cycle that are under facultative control by individual birds and aspects that are consequences of those decisions, and beyond the control of the individual. Settling and occupancy patterns are clearly under facultative control, and are considered investment decisions. Clutch size varied substantially in this population, is a direct investment of energy in a breeding attempt, and therefore lacking evidence to the contrary we treated clutch size as facultative in this species. Clutch size was not affected by either natural or anthropogenic variables, and we have no evidence that clutch size was varied with variation in habitat quality. Events occurring after laying would be strongly constrained by the position and local characteristics of the territory, in the sense that the consequences to a pair of misjudging factors such as resource levels or predator risk will be inescapable for chicks stranded in the nest, such that laying marks the beginning of a decrease in a pair's control over the fate of their offspring. We therefore considered fledging success to be the performance consequences of the investment decisions.

INVESTMENT

We examined several different aspects of investment choices made by ravens. The primary distinction is between the choice of the location for a breeding territory, and the choice of whether to breed once a territory is established. Because ravens don't breed every year (Boarman and Heinrich 1999), both the spatial distribution of nests and initiation of breeding can be considered under facultative control.

Ravens in the Mojave have typically been found more commonly in urban areas (Knight and Kawashima 1993) and near roads (Knight et al. 1993). We found that raven nests were most common near point subsidies, including urban areas, and near roads (Figure 4.2a and 4.2b), with 59% of nests falling within 2 km of a road and 38% falling within 2 km of a point subsidy. We also found that ravens preferred to nest within 2 km of point subsidies (Figure 4.3). However, there were disproportionately more nests over 2 km from roads and disproportionately fewer nests within 2 km from roads compared to the available habitat (Figure 4.3), indicating that ravens prefer to nest far from roads. In both cases this means that the majority of individuals are nesting in habitat that they don't prefer, because most of the nests were found closer than 2 km from roads and further than 2 km from point subsidies. Urban areas in our study area were relatively small and raven populations were dense, such that available territories may have been limited, forcing individuals to nest in non-preferred habitats. Ravens did not prefer to nest near roads in our study, in contrast to ravens in Idaho, Nevada, and the eastern Mojave who overwhelmingly used artificial platforms along roads and power lines (White and Tanner-

White 1988, Steenhof et al. 1993, Knight et al. 1995). Most of the roads on our study area had powerlines, telephone lines, or billboards nearby, which in these other studies have concentrated raven nests near roads. We believe the difference is due to the large proportion of nests in our study that were found in Joshua trees, which were common on the study area. Natural nest sites were therefore abundant, and the artificial platforms associated with roads were less important to the ravens than was proximity to anthropogenic point subsidies.

Occupancy, the presence of ravens in a breeding territory during the breeding season, had inconsistent relationships with both anthropogenic and natural variables. Occupancy was unrelated to both sets of variables in one year (1997), and the number of years a territory was occupied was also unrelated to both sets of variables (Table 4.1). The set of natural variables were significant in 1998 and 2000, but different variables were significant in each year. The presence of the previous year's nest at the beginning of the breeding season was significant in 2000, but this variable was only recorded in 1999 and 2000, and when it was omitted from the analysis natural variables were no longer significant in 2000. We believe that some of the inconsistency in results among years may be due to the complex nature of the variable "occupancy" as we measured it. Since most breeding individuals were not marked we could not tell whether birds observed in a territory were the breeding individuals rather than vagrants, or if the territory holder had changed from previous years. Lack of occupancy could also be due either to a decision by the breeding pair to forego breeding or to mortality. Additionally, in spite of the fact that we visited unoccupied nests repeatedly it was possible for a pair to occupy a territory without being observed.

Initiation of breeding was determined only for territories that were known to be occupied in a year, and were less subject to the measurement uncertainty that we encountered with unoccupied nests. Initiation was affected by natural variables in both years analyzed (1999 and 2000) but was not affected by anthropogenic factors in either year. The best predictor of initiation in both years was the presence of the previous year's nest at the beginning of the breeding season. Similar patterns of re-use of nests has been observed elsewhere (Steenhof et al. 1993), but has not been related to breeding success. We hypothesize that the nest may either act as a cue that stimulates breeding behavior, or the presence of a nest may reduce the amount of energy required for a pair to prepare for egg laying.

Clutch size was not affected by either anthropogenic or natural factors in any year. Although a clutch is clearly an investment by a breeding pair in a reproductive effort, it is not known whether clutch size is under facultative control in this species. Other aspects of investment in a clutch, such as egg mass, are sensitive to the mother's nutritional state in passerines, but we were unable to measure this variable.

PERFORMANCE

As expected, anthropogenic features had positive effects on raven breeding performance. The number of chicks fledged per nest was affected by anthropogenic factors every year of the study, as was the number of years that a territory was successful. Somewhat surprisingly, distance from major roads had a greater effect than either distance from point subsidies or the degree of urbanization in several years. Urbanization was assessed in the field, based on the observed presence of an anthropogenic source of food or water, and point subsidies were features such as towns, landfills, and artificial water bodies that were known to provide food or water resources. Roads probably increase raven reproductive success by providing road-killed carrion, particularly roads through otherwise natural habitat (Austin 1971, Camp et al. 1993). Roads allow ravens to scavenge food that they would otherwise need to hunt, and make available prey that would otherwise be too big for them to kill and open (Boarman and Heinrich 1999). Because roads are spatially more dispersed than a point source of food, such as a landfill, the birds may be able to take advantage of this subsidy without incurring negative effects of crowding.

The effects of natural factors on numbers of chicks fledged were not as consistent as were anthropogenic effects. However, in both years that natural factors were significant shrub cover was an important effect, with nest substrate also contributing to number of chicks fledged in 1997. In both 1997 and 2000 nests in creosotebush scrub areas did poorly, fledging 0.57 and 0.42 chicks, respectively, and nests in saltbush scrub did better, fledging 1.17 and 1.12 chicks, respectively. This consistent difference between habitats cannot be explained by differences in distance from roads or point subsidies. Urban nests were on average closest to roads and point subsidies, and had no native shrub cover, but urban nests did not consistently outperform nests in saltbush (nests with neither type of shrub fledged 1.0 chicks in 1997, and 1.8 chicks in 2000). We hypothesize that the differences between creosotebush and saltbush nests are due to differences in prey availablility, but data on prey abundance and habitat-specific raven foraging behavior would be needed to confirm this.

THE RELATIONSHIP BETWEEN ANTHROPOGENIC AND NATURAL FACTORS

The strongest, most consistent effects on fledging success were direct effects of anthropogenic factors. Several natural factors were also affected by anthropogenic factors, such as reduced shrub cover and increased use of trees as nest substrates in urban areas. However, the only natural factor that had consistent direct effects on fledging success was shrub cover, and the reduced cover of creosotebush and saltbush in urban areas was only associated with increased fledging success in one year. The more consistent difference due to shrub cover was due to differences between creosotebush scrub and saltbush scrub, which were not associated with urbanization. Our analysis suggests that the effects of anthropogenic factors on raven reproductive success are direct, and are therefore probably related to the resources provided by anthropogenic features to the ravens rather than to augmentation (including substitution of natural features with artificial ones) or degradation of natural habitat characteristics.

One way that anthropogenic factors affected raven reproduction was through affects on initiation date. Nests near roads or subsidies or in urban areas initiated earliest (Table 4.10). Intercorrelations between the anthropogenic factors mask this effect somewhat, but overall ravens nesting in urban areas laid eggs 13 days earlier on average than nests in natural habitats in 2000 and 9 days earlier in 1999. Pairs that laid eggs earlier had greater fledging success in both years. This has been observed in ravens breeding in undeveloped habitats in Grand Teton National Park, Wyoming (Dunk et al. 1997), which was attributed to the positive effects of mild winters on the breeding condition of the ravens or on food availability. Similarly, in our study population resource subsidies available at anthropogenic sites may bring individuals into breeding condition sooner, allowing them to initiate sooner and increasing the likelihood that they will succeed.

Early breeding could have large benefits to ravens nesting in the Mojave Desert. The earliest clutches in both years were laid in the first or second week of March, and the latest were in the last week of May. For ravens the interval from laying to fledging is approximately eight weeks, which results in the earliest chicks fledging before the latest eggs are laid, and the fledging dates for the latest clutches would be late July. Average high temperature at EAFB in May is 26.6 °C and in July is 36.1 °C, and chicks hatched later in the season would have to endure much warmer temperatures than those hatched earlier. Adult ravens move to shade during the heat of the day, and since they are also able to use surface water sources they can pant to cool themselves without risking dessication. Nestlings in poorly shaded nests may overheat, and even in shaded nests they may become dehydrated if their parents are not able to provide them with enough prey to meet the water demands of evaporative cooling. High temperatures would exacerbate these problems for late breeders. A similar effect has been suggested for ravens in Idaho (Steenhof et al. 1993), but in that case power transmission lines were expected to provide cooler micro-climates than exposed cliff nests.

All of the anthropogenic factors that affected reproductive success in our population are persistent environmental features. In spite of this, anthropogenic factors had inconsistent effects on measures of reproductive investment. Raven nests were more numerous near roads and near point subsidies, and ravens preferentially placed territories near point subsidies, but did not preferentially use areas near roads. Anthropogenic factors only affected occupancy in one year out of four, and did not affect initiation of breeding at occupied nests in either year analyzed. Occupancy was more often affected by natural factors (two years out of four), and initiation was affected by a natural factor, the presence of the previous year's nest, in both years. Even though the presence of a nest influenced initiation, it was a poor predictor of fledging success, and was not related to anthropogenic factors (i.e., nests near roads and in urban areas were not more likely to be present the next year than other nests). Overall this suggests that some of the information that ravens use to guide their investment decisions do not predict their reproductive success, and ravens do not use some of the information available. Thus, ravens are using territories in which they have a low probability of successfully breeding when habitat is available that would increase their probability of success.

Use of poor-quality habitat will influence the population growth and distribution of ravens in the region. The fact that ravens do not capitalize fully on anthropogenic resources means that population growth will not be as fast as it could be (Kristan 2001), because ravens using poor habitat far from resources will contribute little to population growth. Consequently, the fact that high-quality territories are spatially clustered near roads and human developments does not restrict the raven populations to these high-quality sites, and we found many occupied, active raven nests far from roads and human developments. The birds that attempted to breed in these territories would primarily forage in the habitat surrounding the nest (Sherman 1993), and would thereby affect prey populations near these nests. Ravens are effective predators as well as opportunistic scavengers, and may impact sensitive vertebrate species within their breeding territories, notably the desert tortoise. To the extent that human developments in the region are promoting the persistence of a large number of ravens in areas that are marginal breeding habitat, human activities can have effects on these sensitive species far from the actual developments.

ACKNOWLEDGMENTS

Field work between 1996 and 1998 was conducted by G.C. Goodlett, T. Goodlett, K. Anderson, and P. Frank. J. Spickler participated in the 1999 field season. W.C. Webb contributed nest locations and nestling data in 1999 and 2000. Funding was provided by Edwards Air Force Base and the USGS Biological Resources Division. This manuscript benefitted from comments from J.T. Rotenberry and M.V. Price.

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Table 4.1. Effects of all anthropogenic and natural variables on nest site occupancy.

Effect	DF	Deviance	P	Variables Included in the Model
1997				
All	11	24.46	0.010	
Anthropogenic	4	16.15	<0.001	Roads, subsidies, urbanization
Natural	7	10.24	0.180	Shrub cover, substrate
1998				
All	11	46.33	<0.000	
Anthropogenic	4	8.2	0.080	Roads, subsidies, urbanization
Natural	7	23.8	<0.001	Shrub cover, substrate
1999				
All	12	17.33	0.140	Roads, subsidies, urbanization, shrub cover, substrate, nest
2000				
All	12	66.26	<0.001	
Anthropogenic	4	5.48	0.240	Roads, subsidies, urbanization
Natural	8	62.03	<0.001	Shrub cover, substrate, nest, water at initiation
Years occupied				
All	11	7.22	0.781	Roads, subsidies, urbanization, shrub cover, substrate

Table 4.2. Effects of natural factors on occupancy of a nest site by one or more adult ravens.

Year	Effect	DF	Deviance	P
1998	Shrub cover	3	15.64	<0.000
	Substrate	4	24.26	0.000
2000	Shrub cover	3	6.24	0.100
	Substrate	4	6.41	0.170
	Nest	1	51.97	<0.000

Table 4.3. Effects of anthropogenic factors on occupancy of nest sites by one or more adult ravens.

Year	Effect	Coefficient	DF	Deviance	P
1997	Roads	-0.000257	1	3.63	0.057
	Subsidies	-0.000239	1	3.17	0.075
	Urbanization	0.035496	2	0.07	0.965

Table 4.4. Effects of all anthropogenic and natural variables on initiation of breeding.

Effect	DF	Deviance	P	Variables Included in Model
1999				
All	12	51.9	<0.001	
Anthropogenic	4	5.8	0.210	Roads, subsidies, urbanization
Natural	8	49.5	<0.001	Nest substrate, shrub cover, nest
2000				
All	13	124.4	<0.001	
Anthropogenic	4	6.0	0.200	Roads, subsidies, urbanization
Natural	9	119.4	<0.001	Nest substrate, shrub cover, nest, water at initiation

Table 4.5. Effects of natural variables on initiation of breeding.

Year	Effect	DF	Deviance	P
1999	Substrate	4	12.1	0.020
	Shrub cover	3	7.56	0.060
	Nest	1	35.32	<0.000
2000	Substrate	4	8.26	0.080
	Shrub cover	3	1.4	0.710
	Nest	1	56.49	<0.000
	Water at initiation	1	2.05	0.150

Table 4.6. Effects of all anthropogenic and natural variables on clutch size.

Year	Deviance	DF	P	Variables Included in the Model
1996	3.23	7	0.86	Roads, subsidies, urbanization, shrub cover, substrate
1997	10.34	11	0.50	Roads, subsidies, urbanization, shrub cover, substrate
1998	15.18	10	0.13	Roads, subsidies, urbanization, shrub cover, substrate
1999	6.82	11	0.81	Roads, subsidies, urbanization, shrub cover, substrate, nest, initiation date
2000	6.65	10	0.76	Roads, subsidies, urbanization, shrub cover, substrate, nest, initiation date, water at initiation

Table 4.7. Effects of anthropogenic and natural factors on numbers of chicks fledged within a year and on numbers of succussful years.

Effect	Deviance	DF	P	Variables Included in the Model
1996				
All	38.46	10	<0.001	
Anthropogenic	22.21	3	<0.001	Roads, subsidies, urbanization
Natural	11.62	6	0.070	Substrate, shrub cover
1997				
All	39.60	11	<0.001	
Anthropogenic	13.56	4	0.010	Roads, subsidies, urbanization
Natural	27.60	7	<0.001	Substrate, shrub cover
1998				
All	22.65	10	0.010	
Anthropogenic	12.78	3	0.010	Roads, subsidies, urbanization
Natural	2.92	6	0.820	Substrate, shrub cover
1999				
All	27.69	11	<0.001	
Anthropogenic	15.64	3	<0.001	Roads, subsidies, urbanization
Natural	4.35	7	0.740	Substrate, shrub cover, nest
2000				
All	52.84	12	<0.001	
Anthropogenic	17.79	4	0.001	Roads, subsidies, urbanization
Natural	34.01	8	<0.001	Substrate, shrub cover, nest, water at fledging
Years successful				
All	53.10	11	<0.001	
Anthropogenic	34.84	4	<0.001	Roads, subsidies, urbanization
Natural	12.72	7	0.080	Substrate, shrub cover

Table 4.8. Effects of anthropogenic factors on number of chicks fledged within a year and numbers of successful years.

Year	Effect	Coefficient	DF	Deviance	P
1996	Roads	-0.00108	1	7.36	0.007
	Subsidies	-0.00024	1	1.22	0.270
	Urbanization [a]	1.62904	2	3.67	0.160
1997	Roads	-0.00015	1	5.21	0.022
	Subsidies	-0.00011	1	2.75	0.097
	Urbanization	0.09549	2	2.41	0.300
1998	Roads	0.00000	1	0.00	0.970
	Subsidies	-0.00343	1	17.41	<0.001
	Urbanization	-0.57590	2	0.77	0.680
1999	Roads	-0.00023	1	13.39	<0.001
	Subsidies	-0.00009	1	2.80	0.094
	Urbanization	0.13870	2	0.65	0.723
2000	Roads	-0.00012	1	4.46	0.035
	Subsidies	-0.00001	1	0.07	0.798
	Urbanization	0.15740	2	8.03	0.018
Years successful	Roads	-0.00014	1	10.10	0.001
	Subsidies	-0.00016	1	15.19	<0.001
	Urbanization	-0.37900	2	2.21	0.332

[a] The coefficient for this categorical variable is for the "urban" class.

Table 4.9. Effects of natural variables on number of chicks fledged.

Year	Effect	Df	Deviance	P
1997	Substrate	4	15.08	<0.001
	Shrub cover	3	9.00	<0.001
2000	Substrate	3	0.62	0.891
	Shrub cover	3	28.37	<0.001
	Nest	1	1.95	0.162
	Water at initiation	1	0.53	0.467

Table 4.10. Effects of anthropogenic variables on dates of initiation of egg laying.

Year	Effect	Coefficient	SS	DF	F	P
1999	All		1644.0	4, 118	2.8	0.031
	Roads	0.0012	683.5	1	4.6	0.034
	Subsidies	0.0001	88.6	1	0.6	0.441
	Urbanization [a]	-0.1144	436.0	2	2.9	0.057
2000	All		2605.0	4, 141	4.1	0.004
	Roads	0.0002	278.0	1	1.7	0.189
	Subsidies	0.0009	1018.0	1	6.4	0.013
	Urbanization	-8.0710	1309.1	2	4.1	0.019

[a] The coefficient reported for this categorical variable is for "urban."

Table 4.11. Numbers of nests with each species of dominant shrub among urbanization classes.

	Urbanization		
Shrub cover	Natural	Mixed	Urban
Both	41	4	0
Saltbush	174	16	0
Creosote	69	4	0
Neither	4	1	35

Table 4.12. Effects of anthropogenic factors on substrate use, using loglinear analysis. Distances to roads and distances to substrates are broken into one km intervals, and counts were made of nests within combinations of distance form roads, distance from point subsidies, and urbanization class.

Effect	DF	Deviance	P
Roads*subsidies, roads*urbanization, subsidies*urbanization	54	59.02	0.300
Roads	11	14.1	0.230
Subsidies	14	14.89	0.390
Urbanization	5	19.05	<0.001

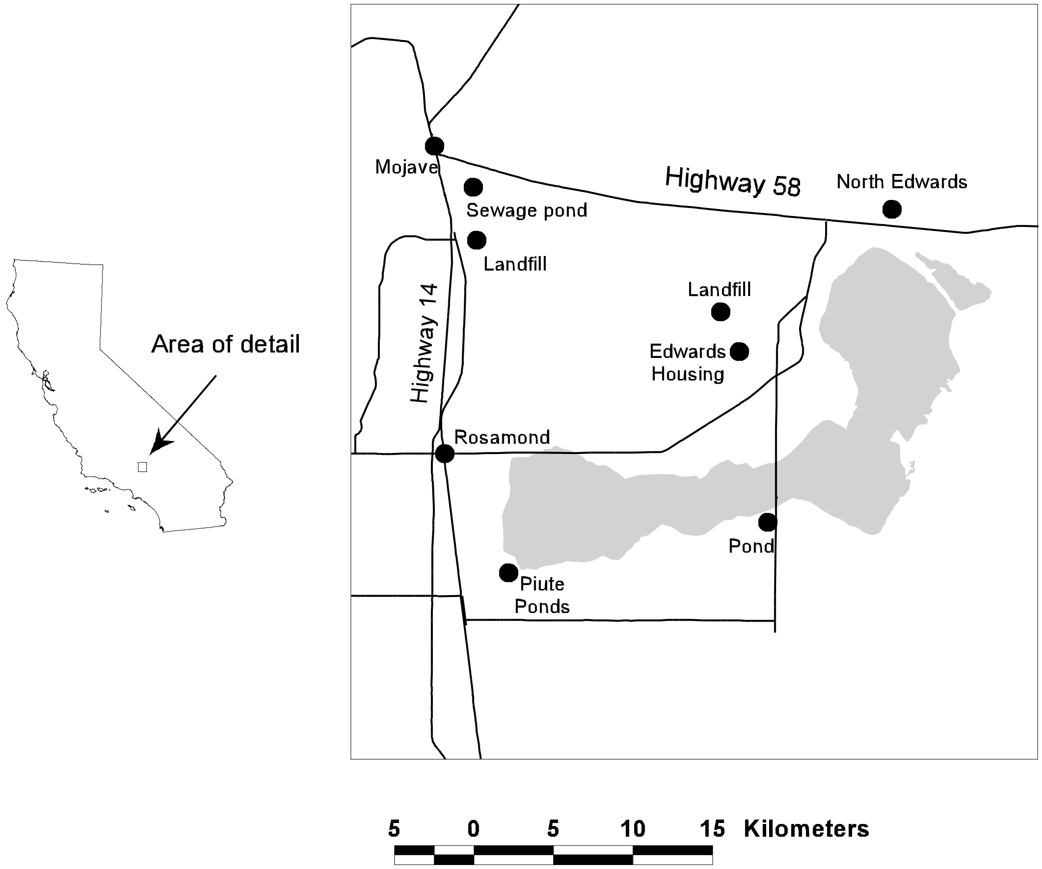

Figure 4.1. A map of the study area. The grey polygon is dry lake bed, considered non-habitat to ravens.

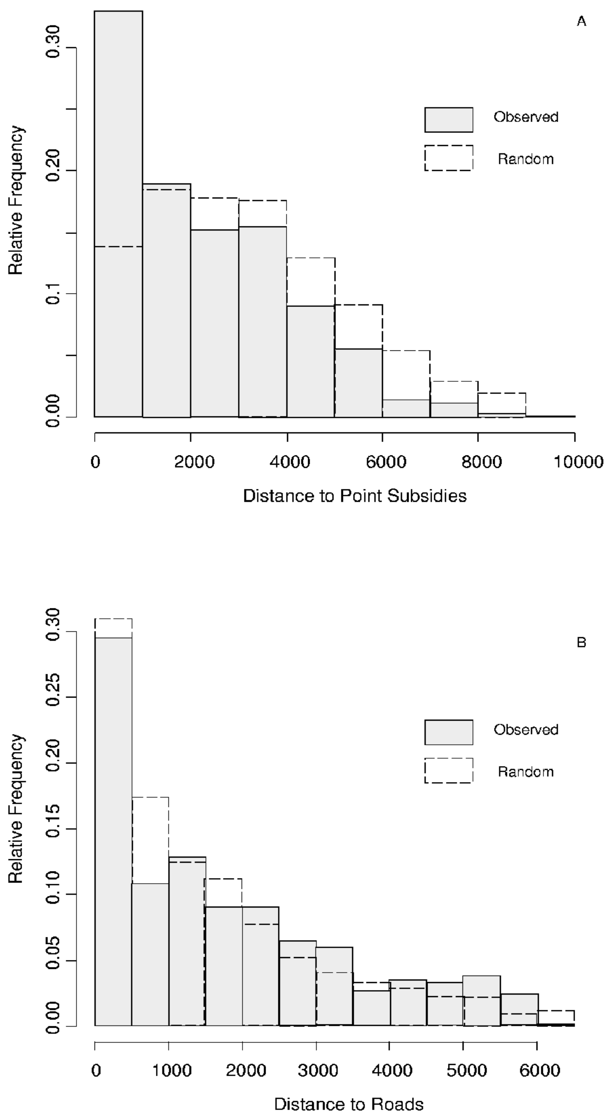

Figure 4.2. The relative frequency of occurrence of nest sites and randomly placed points relative to distance from anthropogenic point subsidies (A) and from roads (B).

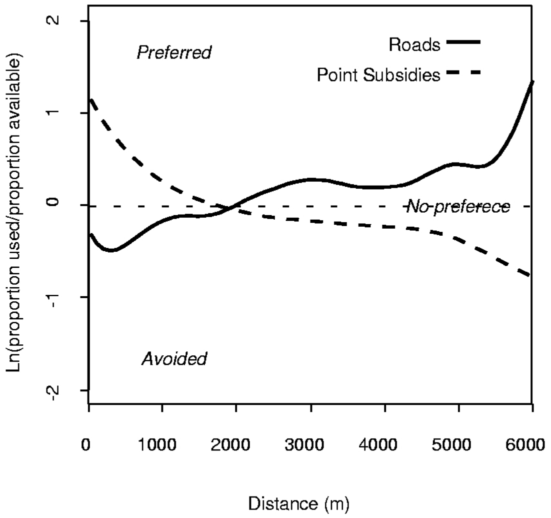

Figure 4.3. Selection ratios of raven preference for nesting relative to distance from anthropogenic point subsidies and distance from roads. The selection ratio is the natural log of the ratio of the proportion of nests found at a particular distance divided by the proportion of random points (i.e. the availability) at that distance. The ratio is symmetrical around proportional use equal to proportional availability, at which the selection ratio equals zero. An index value of 1.0 indicates that a distance was used approximately 2.1 times more than expected, and an index value of -1.0 indicates that 2.1 times more habitat was available than was used.

CHAPTER 5. The spatial distribution of Common Ravens (*Corvus corax*) and raven depredation risk

Abstract. Common Raven (*Corvus corax*) populations in the Mojave Desert are subsidized by resources obtained from human developments such as housing, landfills, and artificial ponds and wetlands. As generalist predators and scavengers, ravens prey on a variety of desert animals, including the threatened desert tortoise (*Gopherus agassizii*). Human developments that attract large numbers of ravens in the region are spatially restricted, and are surrounded by undeveloped land. We investigated whether depredation risk for raven prey was detemined by the spatial structure in human developments, or alternatively was distributed equally throughout developed and undeveloped areas. Raven numbers were greater near anthropogenic point subsidies (e.g. landfills, ponds) but were unaffected by roads and weakly affected by distributions of active nests. Depredation risk, measured using styrofoam models of juvenile desert tortoises, increased near successful raven nests in spite of the small numbers of ravens within defended breeding territories, and increased far from successful nests when large numbers of non-breeding individuals were present. Proximity to anthropogenic point subsidies quantitatively modified the joint effects of raven numbers and proximity to successful nests, but the qualitative pattern was consistent across a wide range of distances from subsidies. Depredation risk was clustered near places such as housing developments that attracted both large numbers of individuals and high nesting densities, but the dispersed distribution of successful nests throughout most of the study area produced scattered pockets of increased depredation risk. Our results suggest that the most effective means of managing depredation risk from ravens will be to manage the

distribution and abundance of both breeding and non-breeding ravens.

INTRODUCTION

Common Ravens (*Corvus corax*) in the west Mojave Desert of California are found in association with human developments (Kristan 2001, Boarman unpub. data), and the association is sufficiently strong that ravens are considered by some to be human commensals in the Mojave (Knight et al. 1993). In spite of their apparent reliance on food and water subsidies from anthropogenic sources, ravens are also capable hunters that prey on small vertebrates and invertebrates (Boarman and Heinrich 1999). Because ravens eat the threatened desert tortoise (*Gopherus agassizii*) in the west Mojave, they have been implicated as a contributor to declines in tortoise populations (Boarman 1993).

The risk posed to a prey population by a subsidized generalist scavenger and predator like the Common Raven is potentially great, since the predator population does not depend solely on the prey and could drive the prey species to extinction (Andrén et al. 1985, Andrén 1992, Namba et al. 1999). Two aspects of raven ecology in the Mojave complicate predictions about their impacts on prey. The first complication is that although ravens are in greater abundance near anthropogenic sites (e.g. landfills, artificial water bodies, roads), it is unknown whether the spatially restricted distribution of anthropogenic sites leave refugia for the prey beyond the reach of urban-associated birds. The second complication is that breeding ravens are territorial, whereas subadult and non-breeding adult ravens are gregarious (Boarman and Heinrich 1999), and these birds compose the majority of the large, conspicuous groups found at landfills. This difference in behavior may be reflected in differences in foraging ecology, such that the ravens that nest far from anthropogenic areas may be less inclined to scavenge and more inclined to hunt, making breeding birds a greater risk for prey than non-breeding birds. Alternatively, the much greater density of non-breeding birds may make the localized areas around anthropogenic developments particularly hazardous to prey, whereas areas far from anthropogenic developments with lower densities of raven individuals may be relatively safe.

We investigated the effects of major roads and sources of food or water (i.e., anthropogenic point subsidies) on the distribution of ravens. We then related proximity to roads, anthropogenic point subsidies, and breeding and non-breeding ravens to the probability of raven depredation.

METHODS

STUDY AREA

The primary study area was within the western half of Edward Air Force Base (EAFB), and in lands immediately surrounding the base, in the west Mojave Desert of California (Figure 5.1). The small number of human developments, such as towns, artificial water bodies, and landfills, were distributed throughout the area, surrounded be undeveloped shrublands. Shrubland vegetation was composed of creosotebush (*Larrea tridentata*) and saltbush (*Atriplex* spp.) scrub, often forming a woodland in association with Joshua tree (*Yucca brevifolia*).

Artificial, permanent water bodies contributed water, food and riparian vegetation types to the study population. Piute Ponds, an artificial wetland within EAFB, contained well-developed riparian vegetation, including willows (*Salix* spp.), cattails (*Typha* spp.) and rushes (*Juncus* spp.). The ponds supported breeding populations of waterfowl, waders, and shorebirds as well as amphibians, such as the African clawed frog (*Xenopus laevis*), which were potential raven prey. A small park with a permanent pond was located in the southeast corner of the study area. Open sewage treatment facilities were also present near two towns in the study area, Mojave (pop. 3,763) and Rosamond (pop. 7,430).

Lands within the EAFB boundary that were included in the study area were used by the air force primarily for recreation rather than military exercises. Consequently, the vegetation was not heavily disturbed in the portion of the study area within EAFB bounds. Undeveloped lands outside of the EAFB boundary were used for a variety of purposes, including sheep grazing and recreation. The housing area within EAFB (pop. 7423) had similar characteristics to Rosamond and Mojave, with all three consisting of single-family homes, apartment complexes, and commercial developments (e.g. restaurants, grocery stores, etc.). Solid waste disposal sited (landfills) were present near EAFB housing and southeast of Mojave.

RAVEN POPULATIONS

The raven population consisted of breeding birds distributed throughout the area and non-breeding birds that aggregated in conspicuous flocks near anthropogenic resources. Nest sites were most common near roads and point subsidies. Most of the known nests were in Joshua trees (Kristan 2001), but were also found in telephone and electrical utility poles, buildings, and cliffs.

EXPERIMENTAL PROTOCOL

Selection of sampling points

To investigate the relationship between anthropogenic sites, the distribution of individual ravens, and the distribution of raven depredation risk, we established sampling points (n = 100) in March of 2000 throughout the portion of the study area within which the distribution of raven nests was known, an area covering 769 km^2 (Kristan 2001). Points were selected to provide even coverage of the region, but with a minimum of 500 m between them. No points were placed in the dry lake bed, because we considered it not to be suitable habitat for either ravens or desert tortoises. Points were placed within the area that raven nests were searched to avoid introducing edge effects into our distance measures. At each point we collected data on the number of ravens present, distance to anthropogeic sites and raven nests, and raven depredation.

Raven distributions

The distribution of raven nests was known from five years (1996-2000) of intensive nest searching and reproductive monitoring of the population in the area (Kristan 2001). Raven reproductive monitoring was ongoing during this investigation, so that the breeding status of the nests was known. We characterized the distribution of raven individuals using ten-minute unlimited-radius point counts. Counts were conducted within four hours of dawn. Both the total number of ravens observed and the number within 200 m of the sampling point were recorded. Counts were conducted on either the first or last day of depredation risk trials to ensure that they accurately represented the distribution of raven individuals at the time of the trial. All counts were conducted between 30 March 00 and 25 May 00.

Depredation risk trials

To evaluate the relative risk of raven depredation we used styrofoam models of juvenile desert tortoises placed at each sampling points. The models were originally used by the USDI Bureau of Land Management to study trampling by livestock, which involved placing known numbers of models in areas of desert scrub. Ravens were observed attacking the models (G. Goolett and P. Frank, pers. comm.), leading us to believe they would be effective gauges of raven depredation. Ravens are only known to attack juvenile desert tortoises with carapace lengths < 100 mm, usually by piercing the carapace with their bills or biting at the head or limbs (Boarman and Heinrich 1999). Both modes of attack leave distinctive marks in the styrofoam models, either punctures in the top of the model, or long cuts around the sides. Other abundant potential avian predators of tortoises in the area included Red-tailed Hawks (*Buteo jamaicensis*), but raptors have sufficiently different bill morphology that mis-identification was unlikely. None of the models used in this study showed signs of attack from other species, avian or mammalian.

Styrofoam tortoises were anchored with ten inch spikes in the ground, attached using pieces of adhesive-backed industrial velcro. Single tortoise models were placed at sampling points and left for four nights. The points were not visited during this interval to avoid attracting or repelling ravens. At the end of the interval the models were retrieved and scored by whether they had raven bill impressions.

Anthropogenic sites

Point sources of anthropogenic resources were taken from USGS Geographical Names Information System data, augmented by sites we identified in the field. Locations of paved, high traffic volume roads on the study area were taken from USGS digital maps. Roads used for this analysis were the major travel corridors between towns and through EAFB which subsidize raven reproduction (Kristan 2001).

Distance measurements

Distances from sampling points to anthropogenic sites and nests were measured using a geographic information system. Distances to raven nests were stratified by breeding status, either occupied, breeding initiated (presence of eggs, incubation, etc.), or successful. The mean distance to the five nearest occupied nests or nests with breeding initiated were calculated for further analyses, but the distance to the nearest successful nest was used instead of a five-nest mean because of the smaller number of successful nests.

STATISTICAL ANALYSIS

Distribution of raven individuals.

The association between counts of individual ravens and proximity to anthropogenic sites and raven nests was evaluated using multiple regression. We modeled both the total number of ravens observed at a point and the subset that were within 200 m of the point. Raven counts were log-transformed. We evaluated the relative effects of the breeding status of the nearest nests (occupied, breeding initiated, successful) on raven counts by comparing models that included distances to nests of each breeding status, as well as the number of chicks fledged from the nearest successful nest. Mean distance to the five nearest occupied nests was used to model the effects of occupied nests, and the five nearest nests with breeding initiated were used to model the effects of initiated nests, whereas distance to the nearest successful nest was used because of the relatively small number of successful nests compared to the other two groups. Distance to anthropogenic point subsidies and roads were used in all models, including one model with no distances to nests. Model fit was compared using Akaike's Information Criterion values (AIC; Burnham and Anderson 1998). The degree to which a single model was better-supported than the others considered was evaluated using Akaike weights (w_i; Burnham and Anderson 1998). Akaike weights estimate the relative frequency with which a model would be best-supported out of a set of alternatives if the experiment were repeated a large number of times (Burnham and Anderson 1998). A model that has a substantially larger w than the set of alternatives under consideration inspires more confidence than would the best model from a set of alternative models with roughly equivalent weights.

Determinants of raven depredation risk.

We modeled attacks on styrofoam tortoises using logistic regression. We compared the AIC's of models including different combinations of distances to anthropogenic sites, raven nests of different breeding status, counts of raven individuals, and the number of chicks fledged from the nearest successful nest. The last variable was used to evaluate whether the risk of depredation from breeding ravens was related to the energetic requirements of their brood. We included the number of ravens observed within 200 m of the sampling point with a measure of human development (either distance to roads or point subsidies) and a measure of raven breeding activity (occupied, initiated, successful, number of chicks fledged). The variables in the best-supported of these initial models were further examined by omitting interaction terms and variables to see whether simpler models were better supported.

Spatial distribution of raven depredation risk.

The previous statistical analysis was useful for identifying depredation risk factors, which could then be applied to maps of the study area to examine the spatial distribution of depredation risk. We mapped the probability of attack predicted from the best-supported depredation risk model, and visually assessed the extent to which the spatial structure in anthropogenic sites and association of ravens near those sites resulted in areas of low depredation risk within the study area. Values for each independent variable were derived using GIS. Number of ravens was estimated by interpolating expected numbers from the point count data using inverse distance weighting.

RESULTS

DISTRIBUTION OF RAVEN INDIVIDUALS

The average number of ravens in unlimited radius counts was 2.49 (sd = 3.55) and the average within 200 m of the point was 0.55 (sd = 1.17). For unlimited radius counts raven number declined most strongly with increasing distance from point subsidies, and no other variable made significant, unique contributions to raven number in any model (Table 5.1). Roads did not affect raven counts in any model. The best supported model (i.e. the model with the lowest AIC) included the number of chicks fledged from the nearest successful nest, but the AIC's were similar among the models, including model 4 which did not include any nest variable, and the three models had similar Akaike weights (w_i).

Whereas model R^2's ranged from 0.24 for model 4 to 0.28 for model 1 for unlimited-radius counts, model R^2's ranged from 0.07 for model 4 to 0.09 for model 1 for counts of ravens within 200 m. The best supported model of ravens within 200 m included mean distance to the five nearest occupied nests, but AIC values were similar and no one model was substantially better supported than the alternatives (Table 5.2). Ravens declined in number with increasing distance from point subsidies in each model. Roads did not affect raven counts in any model.

DETERMINANTS OF RAVEN DEPREDATION RISK

Depredation risk was most strongly related to the number of ravens counted within 200 m of the point, the distance from the nearest successful nest, and the interaction between these variables (Table 5.3). The next best-supported model also included distance to anthropogenic point subsidies, with similar support to the first model. All other models evaluated were substantially less well-supported than these first two, with much smaller Akaike weights (w). The non-linear relationship between depredation risk, distance from successful nests, and numbers of ravens observed was well-supported, because when the interaction term was omitted the AIC increased substantially, and the model became non-significant. Univariate models were also poor predictors of depredation risk. Models including nest success had better support than models including breeding initiation or nest site occupancy.

The non-linear relationship between depredation risk and the number of ravens observed and distance from successful nests is best displayed graphically (Figure 5.2). Near successful nests (i.e. within 1 km) depredation risk decreases as the number of ravens observed increases. Far from successful nests (i.e. over 2-3 km) depredation risk increases with increasing number of ravens. Between these distances depredation risk becomes insensitive to variation in raven numbers. Within the range of variation observed, predicted probability of attack changed from less than 0.1 to over 0.9. The model that also included distance from anthropogenic point subsidies exhibited qualitatively similar behavior (Figure 5.3). The overall effect of point subsidies was to increase the probability of attack near successful nests that were near point subsidies (distance to subsidies = 0 km) when few ravens were observed, and to increase the probability of attack far from successful raven nests that were far from point subsidies (distance to subsidies = 8 km) when few ravens were observed.

SPATIAL DISTRIBUTION OF RAVEN DEPREDATION

The estimated number of ravens was greatest near the Edwards housing area and landfill, with pockets of elevated numbers near other point subsidies, such as the ponds in the southeast and soutwest (Figure 5.4). Large numbers also occurred near the Mojave landfill. Successful nests were clustered near these point subsidies.

Predicted depredation risk was highest in areas that were both close to large numbers of ravens at point subsidies and successful nests (Figure 5.5). Areas of elevated risk were associated with each successful nest.

DISCUSSION

RAVEN NUMBERS

The result from this study, in which sampling was not specifically targeted at different land-use types, agreed with studies that were stratified by land-use type (Knight et al. 1993, Boarman unpubl. data) in that raven numbers were greatest at sources of food and water, such as landfills and artificial water bodies. Additionally, the social structure of raven populations exerts strong effects on both the distribution of individuals and on the risk to their prey. Breeding ravens maintain large (5.1 km in coastal southern California, Linz et al. 1992) exclusive territories, but their territorial defense can be overcome when the number of intruders is large (Boarman and Heinrich 1999). The distribution of breeding individuals had relatively little influence on observed numbers of ravens, since the distance from sampling points to active and successful nests had little effect on distributions of raven individuals. In areas far from concentrations of non-breeding individuals most of the ravens present should be territorial breeders, which are at low densities. Observing individual ravens is much more opportunistic than at anthropogenic features such as landfills, and counts should be both low and highly variable in breeding areas, resulting in weak relationships between numbers of individuals and distances to known, active nests.

DETERMINANTS OF RAVEN DEPREDATION RISK

Styrofoam tortoise models, being non-living, cannot be depredated. Our models were placed in one position, and left there unmoving for four nights. If the ravens believed these objects to be food they were attempting to scavenge rather than hunt when they attacked the models. However, even if ravens did not approach the models expecting them to be edible, we assumed that the varied diet and opportunistic foraging habits of the species (Engel and Young 1989, Stiehl and Trautwein 1991, Sherman 1993, Camp et al. 1993, Nogales and Hernandez 1997) would render the distribution of attacks to our models a reasonable index of relative depredation risk to raven prey. The relationship between the rate of attack on the models and the actual probability of depredation risk to any particular vertebrate species is not known, and would have to be determined empirically, including for the desert tortoises which the models resembled. Clearly a juvenile desert tortoise that is above ground during daylight hours would be vulnerable to attack by a raven, and the spatial distribution of raven attacks on models should provide a reasonable depiction of the relative risk to a tortoise behaving in this way.

The effects of raven abundance on depredation risk depended on distance from the nearest successful nest (Figure 5.2). Depredation risk increased with increasing raven numbers far from successful nests, but decreased with increasing raven numbers close to successful nests. The effect of proximity to anthropogenic point subsidies was to quantitatively modify the joint effects of raven abundance and distance to successful nests (Figure 5.3). Proximity to anthropogenic sites increased depredation risk near successful nests, whereas points that were distant from subsidies had decreased depredation risk near nests and increased risk far from nests when few ravens were observed.

We believe these results can be understood in the context of the social structure of raven populations. Breeding ravens are territorial, but territorial defenses can be overwhelmed by large numbers of non-breeding individuals. Counts of raven individuals within a successfully defended territory would be low, including at most only the territory occupants, if they were observed at the time of the survey. Depredation risk would be from the breeding adults, with risk increasing closer to the nest. When a large count was made near a successful nest, it would most likely be due to inclusion of intruding birds that were relatively far away, at the periphery of the sampled area, where they would pose a small depredation risk. Under these circumstances depredation risk would be relatively insensitive to the number of ravens observed, as was seen at intermediate distances from nests. Successful nests that were near anthropogenic sites would more frequently experience intrusions by non-breeding ravens, and the territory occupants may be less able to defend against them, thereby increasing the risk of depredation near nests that were at anthropogenic sites.

Several models that were statistically significant had substantially less support than the best-supported model. Information-theoretic approaches to model selection focus on finding the model in a set of alternative models with the best balance between fit to the data and the number of parameters that must be estimated. Use of the p-value from a null hypothesis test to evaluate competing models works poorly, since over-fitted models (i.e., those with many parameters) can achieve low p-values but are extremely sensitive to the peculiarities of the data from which they were estimated. The w illustrate the problem with over-fitting for the model close ravens*subsidies*fledged from Table 5.3, which has both a small w and low p-value. This model would not be expected to be well-supported if it was applied to new data. In short, although it is not appropriate to conclude from the AIC that a set of independent variables has no relationship with the dependent variable, high AIC's and low w indicate low confidence in a model, and that the effects of the independent variables are subtle if they exist at all.

SPATIAL DISTRIBUTION OF RAVEN DEPREDATION RISK

When depredation risk is predicted across the study area, the spatial variation in depredation risk can be observed. The model including only distance from successful nests and number of ravens observed yielded a similar map as the model that also included distance from anthropogenic sites, and so only the former is presented here. Spatial distribution of individual ravens was interpolated from the point count data (Figure 5.4). Depredation risk was particularly high near the housing area at EAFB, where both the density of successful nests and numbers of individual ravens was high (Figure 5.5). Some areas that had low predicted depredation risk also did not contain raven nesting habitat, such as the dry lake bed in the middle of the study area. These areas are also poor habitat for most vertebrates. An artificial wetland in the southwest of the study area was also an area of high depredation risk, since it attracted both breeding and non-breeding ravens, as to a lesser extent did a small pond in the southeast. Landfills attracted large numbers of raven individuals, but did not have large numbers of successful nests associated with them, resulting in small, localized areas of high risk (such as at the

Mojave landfill).

Ravens nesting far from roads and anthropogenic point subsidies reproduce poorly (Kristan 2001). However, many raven nests in this part of the west Mojave were far from anthropogenic sites, where they consistently attempt to breed. Breeding ravens forage primarily within the area immediately surrounding their nests, spending 75% of their time within 400 m of their nests while breeding (Sherman 1993). Ravens that are far from anthropogenic subsidies and lack a source of carrion or refuse would need to hunt. The distribution of successful nests therefore reduced the association of depredation risk with anthropogenic sites, and resulted in pockets of relatively high risk throughout the study area. The predictability of depredation risk would be further reduced over time, because the location of successful raven nests changes over time. As the location of successful nests changes areas of high depredation would also move, and some of the areas that are predicted to have low risk in one year may have high risk at other times.

CONSERVATION IMPLICATIONS

Anthropogenic point subsidies and roads affect raven breeding success but had much smaller effects on depredation risk than did the distribution and abundance of breeding and non-breeding ravens. The effects of roads were negligible, and the effects of point subsidies modified the relationship between breeding and non-breeding birds, but otherwise were not intrinsic risk factors. Because the observable distribution of ravens predict depredation risk well, the indirect effects of human activities on sensitive animal species via subsidized ravens can be reduced by managing the distribution and abundance of ravens.

ACKNOWLEDGMENTS

Funding was provided by Edwards Air Force Base and the USGS Biological Resources Division. This manuscript benefitted from comments from J.T. Rotenberry and M.V. Price.

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Table 5.1. The effects of point subsidies, roads, and distances to nests of ravens of different breeding status on log-transformed numbers of ravens observed in unlimited radius point counts.

Effect	Coefficient	Std. Error	t	P	AIC [a]	ΔAIC [b]	w [c]
Model 1				<0.001	180.1	2.42	0.11
Occupied nests	-1.1E-04	9.0E-05	-1.20	0.234			
Point subsidies	-1.5E-04	3.7E-05	-4.04	<0.001			
Roads	3.7E-05	3.4E-05	1.10	0.274			
Model 2				<0.001	181.4	3.72	0.06
Initiated nests	3.1E-05	7.4E-05	0.42	0.680			
Point subsidies	-1.7E-04	3.2E-05	-5.22	<0.001			
Roads	3.8E-05	3.4E-05	1.11	0.270			
Model 3				<0.001	178.2	0.52	0.30
Successful nests	-1.1E-04	6.3E-05	-1.82	0.070			
Point subsidies	-1.6E-04	3.3E-05	-4.81	<0.001			
Roads	5.6E-05	3.5E-05	1.61	0.110			
Model 4				<0.001	179.6	1.90	0.15
Point subsidies	-1.7E-04	3.2E-05	-5.26	<0.001			
Roads	3.6E-05	3.4E-05	1.08	0.280			
Model 5					177.7	0.00	0.38
Number fledged	-1.3E-01	6.7E-02	-1.96	0.054			
Point subsidies	-1.8E-04	3.2E-05	-5.55	<0.001			
Roads	2.3E-05	3.4E-05	0.69	0.490			

[a] Akaike's Information Criterion

[b] The difference between the model AIC and the smalles AIC in the set under consideration

[c] Akaike weights

Table 5.2. The effects of point subsidies, roads, and distances to nests of ravens of different breeding status on log-transformed numbers of ravens observed within 200 m of the sampling point.

Effect	Coefficient	Std. Error	t	P	AIC [a]	ΔAIC [b]	w [c]
Model 1				0.030	143.8	0.44	0.24
Occupied nests	-9.2E-05	7.5E-05	-1.22	0.220			
Point subsidies	-4.3E-05	3.1E-05	-1.41	0.160			
Roads	-8.5E-06	2.8E-05	-0.30	0.760			
Model 2				0.079	144.8	1.44	0.15
Initiated nests	4.3E-05	6.2E-05	0.70	0.480			
Point subsidies	-6.1E-05	2.7E-05	-2.24	0.030			
Roads	-6.9E-06	2.8E-05	-0.24	0.810			
Model 3				0.038	144.4	1.04	0.18
Successful nests	-5.1E-05	5.3E-05	-0.97	0.340			
Point subsidies	-5.6E-05	2.8E-05	-2.02	0.050			
Roads	-5.4E-08	3.0E-05	0.00	1.000			
Model 4				0.020	143.4	0.00	0.30
Point subsidies	-6.1E-05	2.7E-05	-2.28	0.020			
Roads	-9.1E-06	2.8E-05	-0.32	0.750			
Model 5					145.1	1.77	0.13
Number fledged	2.7E-02	5.7E-02	0.47	0.640			
Point subsidies	-6.0E-05	2.7E-05	-2.19	0.030			
Roads	-6.4E-06	5.7E-02	0.47	0.640			

[a] Akaike's Information Criterion

[b] The difference between the model AIC and the smalles AIC in the set under consideration

[c] Akaike weights

Table 5.3. Comparison of models of the effects of roads, point subsidies, nests with different levels of breeding activity, and numbers of ravens observed on the probability of attack on artificial tortoises.

Model	DF	P	AIC [a]	ΔAIC [b]	w [c]
Close ravens*successful nest	3	0.010	118.1	0.00	0.42
Close ravens*subsidies + close ravens*successful nest + subsidies*successful nest	6	0.020	119.9	1.78	0.17
Close ravens*subsidies*successful nest	7	0.030	121.6	3.49	0.07
Close ravens*subsidies*fledged	7	0.030	122.0	3.93	0.06
Subsidies	1	0.080	122.0	3.96	0.06
Subsidies*successful nest	3	0.100	122.9	4.80	0.04
Close ravens*roads + close ravens*successful nest + roads*successful nest	6	0.070	123.3	5.25	0.03
Close ravens*subsidies	3	0.150	123.9	5.78	0.02
Close ravens*roads*successful nest	7	0.069	124.0	5.91	0.02
Close ravens	1	0.850	124.3	6.22	0.02
Close ravens*roads* initiated nests	7	0.079	124.4	6.29	0.02
Close ravens*roads* initiated nests	7	0.082	124.5	6.42	0.02
Successful nest	1	0.480	124.6	6.53	0.02
Close ravens*subsidies*initiated nests	7	0.090	124.8	6.71	0.01
Close ravens+successful nest	2	0.590	126.1	7.97	0.01
Close ravens*subsidies*occupied nests	7	0.176	126.9	8.80	0.01
Close ravens*roads*occupied nests	7	0.212	127.5	9.43	0.00

[a] Akaike's Information Criterion

[b] The difference between the model AIC and the smalles AIC in the set under consideration

[c] Akaike weights

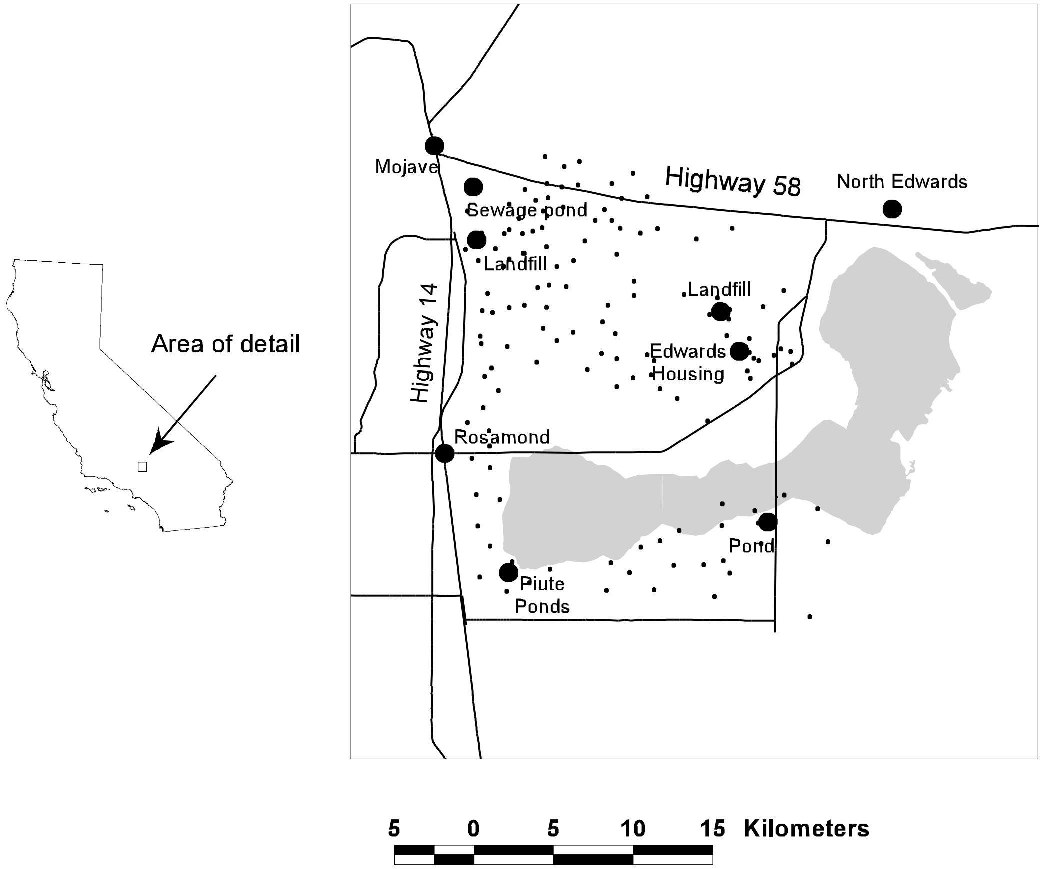

Figure 5.1. Study area map. The grey polygon is a dry lake bed, which is non-habitat for both ravens and desert tortoises. The small filled circles are the locations of sampling points.

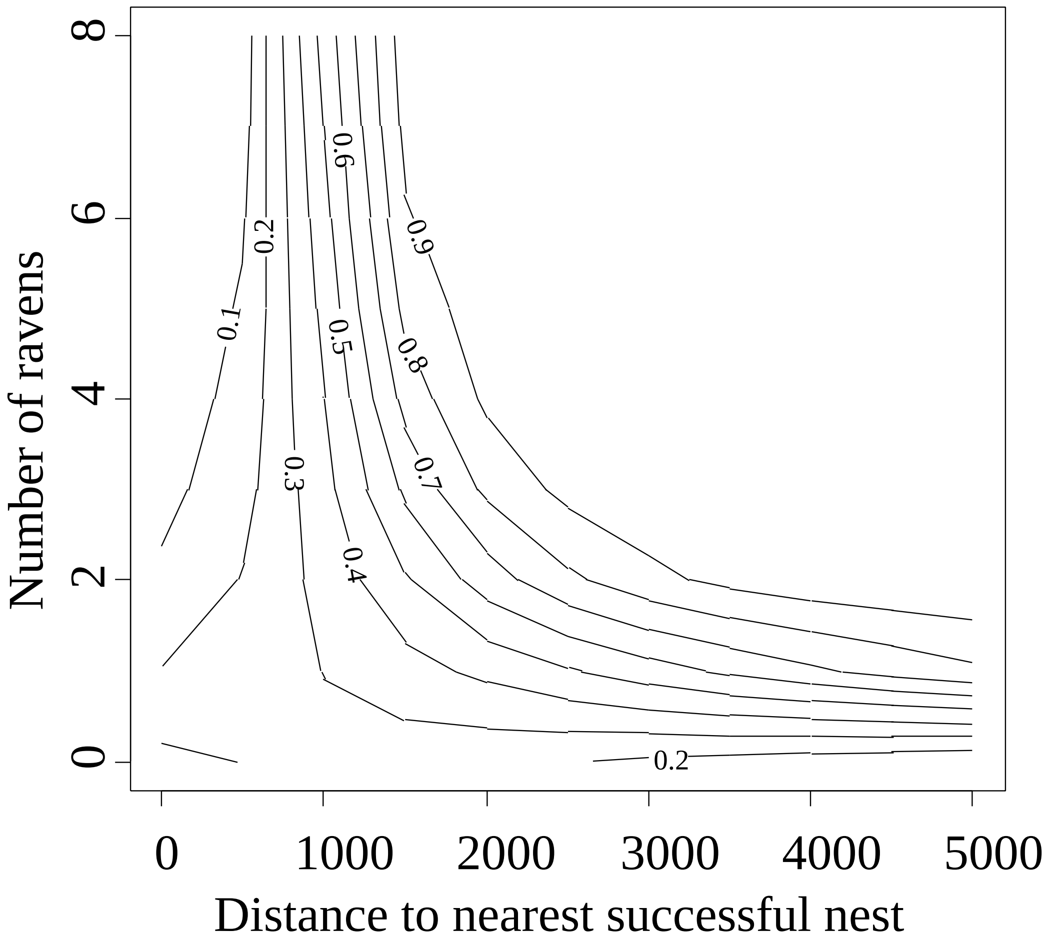

Figure 5.2. The effects of distance to the nearest successful raven nest and number of ravens observed within 200 m of the sampling point on risk of depredation (i.e. attack by a raven on a styrofoam tortoise model).

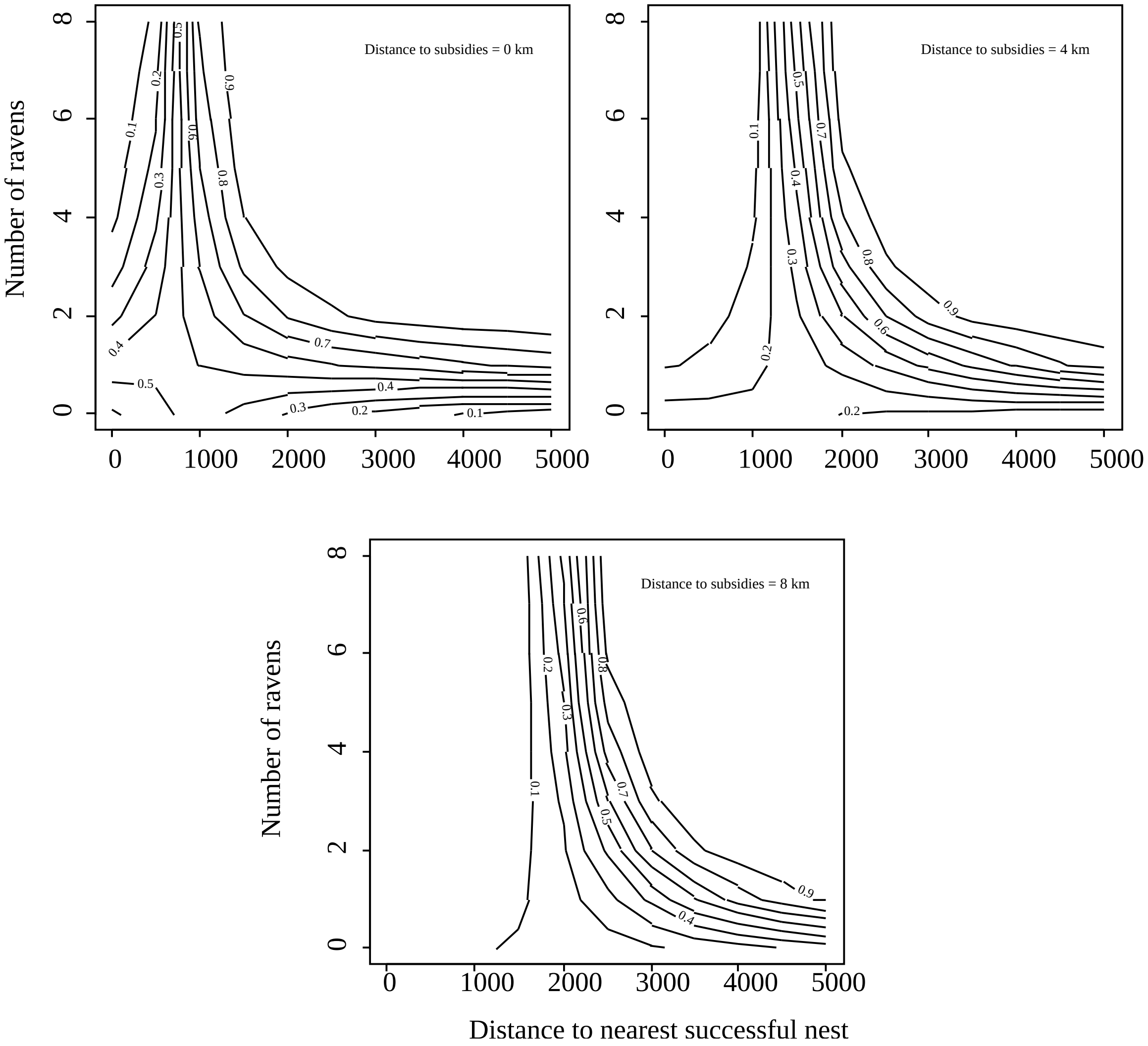

Figure 5.3. The effects of distance to the nearest successful raven nest, number of ravens observed within 200 m of the sampling point, and distance from anthropogenic point subsidies (e.g. landfills, artificial wetlands) on risk of depredation (i.e. attack by a raven on a styrofoam tortoise model).

Figure 5.4. Successful nests (marked with an X) and estimated number of ravens within the area that depredation risk trials were conducted. The contour interval is one.

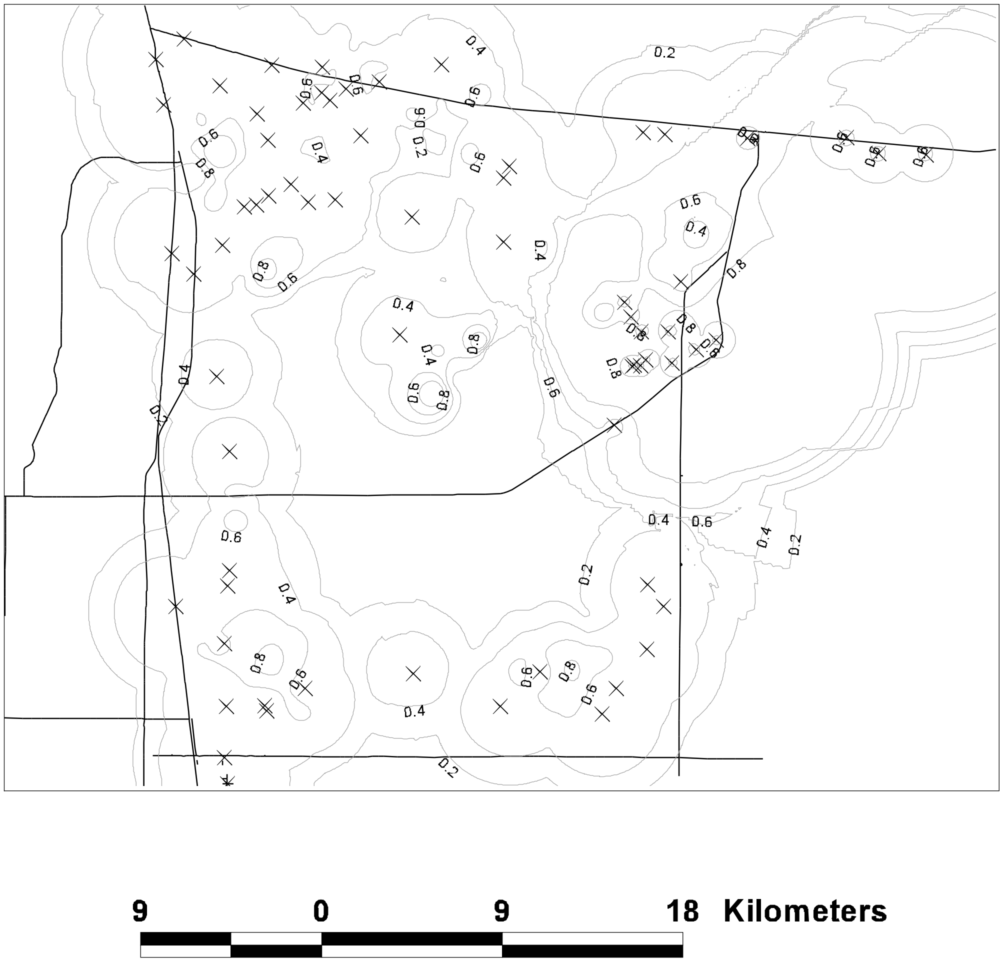

Figure 5.5. Risk of depredation predicted from the distance to the nearest successful nest and the estimated number of ravens at a point, with a contour interval of 0.2. Successful raven nests are marked with an X.

CHAPTER 6. General Conclusion

BEHAVIORAL ECOLOGY OF LANDSCAPES

Habitat selection behavior affects space use, and has to be considered to understand large-scale patterns of distribution and abundance (Lima and Zollner 1996). Perhaps less obviously, habitat choice also has to be considered when interpreting spatial patterns in population demography (Lomnicki 1988, Sutherland 1996). The ability of mobile species to selectively experience a subset of the environmental conditions in a landscape makes individual habitat selection behavior an important mechanism determining the distribution, abundance, and dynamics of populations over complex landscapes (Wiens et al. 1993, Lima and Zollner 1996). This dissertation explored the effects of one component of individual decision making, choice of breeding habitat, on the distribution, abundance, demography and dynamics of populations.

Choice of a breeding territory is a complex forecasting exercise. The consequences of choosing poorly can be severe because, as I showed in Chapter 1, preferential use of poor habitat decreases individual fitness and increases a population's vulnerability to extinction. In both Chapter 2 and Chapter 3 I found that species did not always use information that was present in the environment when choosing habitat. Many species of small mammals in CSS vegetation did not avoid edges in spite of the increased number of predators there. Although birds were more generally edge responsive, California Gnatcatcher and Cactus Wrens avoided edge because of edge-associated changes in the habitat, but did not respond to the edge itself. Ravens in the Mojave did not preferentially nest near roads in spite of their positive effects on reproductive success. Although ravens did preferentially nest near anthropogenic point subsidies where reproductive success was high, they did not adjust their reproductive investment in these areas. Spatial consistency in habitat quality, such as introduced by anthropogenic developments, is important to animals because it allows them to exploit resources more efficiently than would be possible if they needed to learn the locations of resources each time a patch was exploited (Valone and Brown 1989, Valone 1991). Although any environmental cue with predictable statistical relationships with habitat quality are potentially usable to species choosing habitats, urban developments should be particularly good cues because their locations are constant throughout the life of the animals, and it is surprising that some animals do not respond to them.

There are at least two reasons that animals may not use urban developments as environmental cues. The first is that urban developments in the American west are relatively novel, and species may not have had time to develop proper responses to them. The second reason that species might not use anthropogenic developments as cues is that, in spite of their spatial constancy, they may vary temporally. The value of information to foraging animals is reduced when rewards become highly variable, and they begin to use simple decision rules (Bateson and Kacelnik 1998). Ravens benefitted from both point subsidies and roads directly, presumably because of the food and water subsidies they received. The subsidy ravens receive from roads is road-killed carrion, whose availability varies stochastically, and may also vary seasonally due to changes in movement patterns of animals (such as periods of juvenile dispersal, torpor, or migration) throughout the year. This may limit the ability of individual ravens to associate the presence of a road with increased food availability. A similar argument can be applied to the risk posed by predator associations with developed edges, an association that may be difficult for prey to learn when predators that move over large areas only periodically travel along the edge. In contrast, subsidies from point sources in our study included refuse at landfills, and water and an increased prey base at artificial water bodies, both of which were fairly constant, abundant resources.

Depredation risk is expected to affect the distribution of individuals, as well as the amount of time spent in anti-predator activities such as vigilance behavior (Lima and Dill 1990, Ydenberg 1998). However, predator distributions may not be predictable at the scale of individual home ranges at the time when individuals are choosing habitat. The unpredictability of depredation risk can be seen in Chapter 4. Anthropogenic sites that attract large numbers of both breeding and non-breeding individuals represent fixed locations that consistently increase depredation risk, but risk also increased near successful nests whose distribution would change as different nests experience successes and failures over time. Møller's (1988) argument that the distribution of a predator's nests was a less reliable predictor of depredation risk for prey than the predator's habitat associations may apply to ravens and desert tortoises in the Mojave. However, whether tortoises or other raven prey are able to recognize and appropriately respond to the risk posed by anthropogenic areas that attract ravens is not known.

FUTURE DIRECTIONS FOR THIS WORK

The results of these investigations suggest several avenues for additional study. In general I am interested in continuing to investigate the ways that individual habitat decisions affect population dynamics, but several issues require clarification before a complete understanding is possible.

1. What is the nature of predictability in ecological landscapes?

Much effort could be wasted arguing whether a particular quantity is predictable or not. Before progress can be made it will be necessary to establish the ways in which environmental variables can be predicted by organisms. For example, over any time period of interest variables can be constant, can change deterministically, can exhibit a trend with some stochastic variation, or can be completely unpredictable. Constant conditions, such as topography, distribution of rock outcrops, etc., are by definition highly predictable over ecological time frames. Other variables, such as day length or tidal cycles, change over ecological time frames, but in highly predictable ways. The last two categories, statistical trends and stochastic variation, apply to many variables that affect animals, such as food resources and predator distributions. Most of these variables are predictable at some spatial and temporal scales but are stochastic at others (Orians and Wittenberger 1991). The location of a particular individual predator at some time in the future may be impossible to predict, but areas of high or low predator density may be predictable. Under these circumstances prey would avoid areas of high predator density but then select nest sites without reference to distributions of predators within the area. Animals that are prey for many predator species may face the additional task of avoiding depredation by a suite of predators with different home range sizes, habitat associations, foraging ecologies, etc., that collectively render depredation risk unpredictable even if the risk by each single predator is predictable.

2. How much information about habitat quality is present in the environment?

It is usually assumed that factors that have large effects on individual fitness must drive habitat selection. In passerine birds, nest predation is responsible for most reproductive failures, and nest-site selection is explained in terms of predator avoidance (Martin 1988). However, for this to be true there must be reliable cues to depredation risk present at the time when habitat choices are made. I am interested in identifying the factors that affect individual fitness (both mortality factors in adults and independent offspring as well as causes of nest failures), and then evaluating the predictability of these factors based on the information available in the environment at the time that nest sites are chosen. This approach requires separating the quality of the habitat (in terms of predictable relationships between habitats and the probability of successful reproduction or survival based on levels of different known risk factors) from the performance of individuals in those habitats (based on occupancy patterns and observed survival and reproductive success).

3. What determines habitat quality in complex environments?

Individual habitat variables can affect one or more component of individual fitness, and species are expected to prefer the habitat in which they experience the greatest fitness. A single habitat variable that has opposing effects on different components of fitness will complicate assessment of habitat quality, because no single measure of individual performance would be a reliable proxy for fitness. This is a known problem with a relatively simple solution (conceptually, if not practically), to study multiple components of fitness, at least including both reproduction and survival. Using a better measure of fitness, it would be possible to better evaluate whether individuals are making good habitat choices. Studies of population dynamics would benefit from this approach as well, since covariation between components of fitness will affect the accuracy of population models.

However, in complex, multi-dimensional environments it is possible for one habitat variable to affect one component of fitness (e.g. survival) while another affects another component of fitness (e.g. fecundity). When this is true the spatial distribution of the habitat variables becomes important because individuals will only be able to maximize both survival and fecundity if habitat exists that has favorable conditions for both. If the habitat variables are correlated in their distribution the best habitat will be some compromise between survival and fecundity. A population-level correlation in survival and fecundity will occur, and will affect population models. Whereas the joint effects of a single habitat variable on more than one fitness component can also cause a correlation in survival and fecundity the spatial distribution of the habitat variable is not intrinsically important. In contrast, in complex habitats the distribution of habitat variables relative to one another becomes important, and is intrinsically a spatial effect. Recognizing this distinction will be important both in understanding the decisions made by individuals, and in scaling from individual behavior to population dynamics.

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