Raven Ecology in the Mojave Desert at Edwards Air Force Base

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Edwards Air Force Base
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WESTERN ECOLOGICAL RESEARCH CENTER
Raven Ecology in the Mojave Desert at Edwards Air Force Base

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Executive Summary

Common ravens have experienced a tremendous population explosion in the California desert in recent years. As human communities have grown, ravens have followed, with population increases estimated at 1000% over a recent 25-year period. Ravens are a subsidized predator—one that makes use of resources inadvertently provided by human populations—whose population growth is a concern to natural resource managers because they prey on juvenile desert tortoises (*Gopherus agassizii*) and are a factor in tortoise population declines and listing as a Federally “Threatened” species. Predation by subsidized predators can drive rare native prey populations to endangerment and extinction because anthropogenic resources insulate the predator population from the effects of fluctuations in prey populations, allowing predator populations to stay high even as prey become more rare.

At Edwards Air Force Base (EAFB) and surrounding communities in the Western Mojave Desert, California, we performed a number of research projects that are described in this report. In Chapter 1, we present the results of surveys aimed to gain a better understanding of ravens’ use of anthropogenic habitat. We conducted raven counts for 3 years at six site types and determined raven locations using radio telemetry. Our results confirmed that ravens spend the majority of their time within 3 km of landfills. Some of the birds move away from the landfills either on foraging forays or to nest in native habitat where they have opportunities to prey on desert tortoises and other native prey. Many visited nearby dairy farms and dog kennels. Isolated anthropogenic structures may serve as stepping stones aiding the dispersal of ravens through and into desert tortoise habitat. Garbage containment practices implemented at EAFB
considerably reduced the numbers of ravens there and should be implemented on a broader basis in the region to help reduce conflicts between ravens and desert tortoises.

In Chapter 2, we examined raven diet by identifying prey items in pellets found at nests. While it has long been asserted that ravens benefit from human subsidies to increase their numbers, the mechanism by which they benefit had not been studied. Our research demonstrated that ravens gain a reproductive advantage by utilizing human-provided resources. Ravens whose diets included garbage and road-killed animals had increased fledging success over ravens whose diets did not contain these items, presumably because they could spend more time protecting their nests while taking advantage of this “free lunch.”

Chapters 3 and 4 examine whether two factors in ravens’ life history – reproductive success and juvenile survival – explain their population increase in the desert. In Chapter 3, we evaluate reproductive performance, nest site distribution, and their relation to anthropogenic developments. We found that ravens selected areas near point subsidies to build nests. In modeling the relationship between reproductive success and a number of natural and anthropogenic variables, we found that anthropogenic variables were much more predictive of reproductive performance than natural variables. We conclude that anthropogenic developments enhance raven reproductive success, and allow rapid raven population growth in the west Mojave. In Chapter 4, we asked whether juvenile survival from birth to the time of departure from the natal territory is related to nest proximity to human resources. We found that ravens nesting within 1.0 km of a point subsidy experienced survival rates to juvenile departure of nearly 60%, while those nesting farther than 1.5 km survived only 10-30% of the time. The benefit to those ravens using human subsidies did not end at fledging. Ravens reared in nests near subsidies had an increased survival benefit that lasted for 9 months after the young ravens
left their natal territories. These findings supported our hypothesis that anthropogenic resources increase raven recruitment.

Continuing our work with juvenile ravens, Chapter 5 presents our study on the movement of juvenile ravens in their first 2 years. Based on ecological theory on pre-breeding movement in other species, we expected that movement patterns would either be based on inbreeding avoidance or the distribution of resources. If movement patterns in ravens are based on inbreeding avoidance, we predicted that there would be a sex bias or evidence of heritability in movement behavior. If distribution of resources drives movement in ravens, we predicted that the movements would reflect resource availability within the landscape. After tracking 90 juvenile ravens over 2 years, we found that movement patterns had a low heritability factor and no difference between the sexes, but that they were influenced by the distribution of resources, all of which were anthropogenic in origin. Furthermore, movement was initially influenced by the location of flocks of conspecifics, perhaps suggesting that social development and mate finding are important driving factors in the ravens’ first 2 years.

In Chapter 6, we examine the spatial distribution of raven predation risk to desert tortoises. In the Mojave Desert, large numbers of non-breeding common ravens live in and around human communities, while breeding ravens are more evenly distributed across the landscape. Presumably, risk of predation on tortoises varies with raven distribution. To examine this, we used Styrofoam models which resembled juvenile tortoises about 2 inches long, placed at 100 sampling points on and around EAFB. Ravens attacked 29 of the tortoise models, as determined by the distinct marks left by their beaks. We used these data to develop mathematical models of predation risk relative to raven distribution. Our findings suggest that areas of elevated predation risk occur under two different circumstances. First, predation risk was close to 100 percent near
large groups of ravens that are distant from successful nests, usually near sources of anthropogenic subsidies such as roads and landfills. These raven groups may exert a higher predation pressure than if the same area was occupied by a territorial pair of ravens because they are densely concentrated and do not spend time and energy defending resources. Second, predation risk was great near successful nests that had few other ravens in the vicinity. In this case, the breeding ravens may not need to spend time defending their territory against intruders, allowing them to concentrate greater efforts on predation.

Overall, the research presented in this report confirms that ravens utilize anthropogenic resources during many life history stages, improving their rates of reproduction, recruitment, and survival. These benefits are most notable near landfills and other point subsidies in human developments. Controlling raven access to these types of resources will be critical in the long-term conservation of the desert tortoise. As discussed in Chapter 7, we recommend that managers at EAFB make it a priority to restrict raven access to such resources, which will presumably help restore the balance between ravens and tortoises. Other human subsidies are less easily controlled. For example, benefits associated with roads (road-killed animals available for scavenging) are widespread throughout the anthropogenic landscape. Similarly, artificial nesting substrate such as billboards and power towers is ubiquitous in the Mojave Desert. Still, these items have been shown to provide significant benefits to ravens; therefore, we recommend that efforts such as removing road-killed animals and destroying nests built on anthropogenic structures are important in the management of ravens. A comprehensive, long-term management plan for ravens should be put in place by managers at EAFB to reduce raven numbers and their predation on desert tortoises. This long term plan should include a strong component of research and monitoring, as they are important components of successful management. New research will
provide needed information about raven predation on tortoises, while monitoring of raven populations will provide feedback on the effectiveness of current management efforts. Taken together, research and monitoring will yield information necessary to develop and modify future phases of a comprehensive raven management program.
Chapter 1: Anthropogenic Habitat Use by a Subsidized Predator: Common Ravens in the West Mojave Desert*

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EXECUTIVE SUMMARY OF CHAPTER

Subsidized predators are those that benefit from resources inadvertently provided by human populations. Subsidies such as food, water, nesting substrate, and refugia from predators and inclement weather may enhance survival and reproduction, resulting in population stability, increase, or range expansion. The concept of subsidized predation was introduced by Soulé et al. in 1988. Since then, there have been several references in the literature to subsidized predation, but little empirical or conceptual development of the idea. Because the population dynamics of a subsidized predator are decoupled from their effects on prey populations, subsidized predators can sometimes have disastrous effects on native populations. Therefore, management of the predator population may be necessary.

In the Mojave Desert of California, common ravens (*Corvus corax*) and desert tortoises (*Gopherus agassizii*) are examples of a subsidized predator and a declining species of prey. Common raven populations in the desert have increased dramatically in recent years as they are adept at using human-provided resources. Ravens are known to prey on juvenile desert tortoises, and their increase has been implicated as one of the many causes of the decline in the Federally threatened desert tortoise. An understanding of how resource subsidies aid raven predation on desert tortoises is essential for developing management actions to reduce their effects.

We conducted research at Edwards Air Force Base to determine the role anthropogenic resources play in facilitating the increase in raven populations, to understand the temporal and spatial dynamics of the relationship, and to help develop methods to reduce raven impacts on tortoise populations. We hypothesized that ravens would use anthropogenic resources most heavily during times when natural resources were less abundant (e.g., summer for water and
winter for food).

Raven counts were conducted for 3 years at six site types (landfills, sewage ponds, city streets, golf courses, and desert reference sites located >1 km and >2 km from resource sites) surveyed in three towns (Mojave, Boron, and EAFB Housing) for a total of 18 sites. In addition, rocket nets were used to capture a total of 210 birds, all of which received wing tags while 80 were fitted with backpack radio transmitters. Locations of sightings of radio- and wing-tagged birds were categorized by site-type (same categories as used for counts, with the addition of agricultural areas), and were used to calculate home range sizes. Because of the obvious regional importance of the EAFB landfill, we generated probability maps of raven occurrences, which showed the zone of influence of the landfill, and we compared patterns of presence among seasons.

We further explored the regional patterns of inter-connection among attraction sites by testing the relative influence of site-type and distance in explaining which sets of sites individual ravens visited. To test the relative influence of distance and attraction site-type on the likelihood that ravens would be found at any pair of sites, we divided this analysis into two separate datasets. One dataset represented all ravens seen at both the EAFB landfill and one other site (one-legged trips). The other dataset represented all ravens seen at pairs of sites other than the EAFB landfill (two-legged trips). One-legged trips could be represented with a single distance (the distance between the EAFB landfill and the other site) and a single site-type (the site-type of the other site). The number of marked ravens observed were then related to attraction type and distance from the landfill, using an ANOD. For two-legged trips, we represented the effect of distance in an ANOD analysis with two variables: the straight-line distance between the EAFB landfill and the nearest of the two sites, and the straight-line distance between the two sites.
Additionally, since attraction site-types could differ between the pair, we included a variable for each attraction site-type.

Overall, raven counts were highest at landfills, followed by sewage ponds, then city streets, while desert reference sites and the golf course had very low numbers. Telemetry data showed that ravens captured at the landfill tended to stay close to it, but that many of them moved off the Base as far as 150+ km into the Central Valley, and often visited dairy farms and dog kennels south and west of the Base. Temporal use of resources varied at multiple scales. Diurnally, raven presence at the EAFB landfill was at its lowest in the morning and peaked in late afternoon. Seasonally, raven numbers at desert reference sites were lower than expected in the summer, numbers at landfills were lower than expected in the fall, and numbers at resource sites other than landfills were greater than expected in the fall and lower than expected in the spring.

This study demonstrated that large numbers of ravens are attracted to landfills and spend the majority of their time within 3 km of landfills. Some of those birds move away from the landfills either on foraging forays or to nest in native habitat where they have opportunities to prey on desert tortoises and other native prey. This supports the hypothesis that spillover predation occurs around anthropogenic resources. Raven life history may also help the population to prosper from human-provided resources. Their generalist diet and ability to readily switch foods allows them to adapt to seasonal changes and exploit seasonally variable food sources. Prior to human subsidies, edaphic characteristics of the harsh arid environment constrained raven populations, particularly through drought in the summer and starvation in the winter.
Management Implications

This study suggests that some individual ravens are reliant on human subsidies, especially those provided by landfills. With this in mind, EAFB managers should attempt to make waste at their landfill even less available to ravens throughout the year, thus lowering the overall raven population and presumably the rate of predation on desert tortoises. Raven access needs to be reduced at other sources of organic waste, such as residential waste left out for weekly garbage pickup and dumpsters at commercial establishments. Ravens at EAFB are part of a population inhabiting a much broader area than the base. Similar garbage containment practices should be implemented at other landfills in the vicinity if ravens numbers are to be reduced. The availability of free-standing water, particularly in and around the EAFB housing and operations area, should be reduced. Regional impacts of human resources are affected by the spatial distribution of attraction sites, with isolated anthropogenic structures serving as stepping stones for movements and dispersal. One way of limiting the penetration of ravens into undeveloped areas may be to avoid providing “stepping stones” that facilitate their spread. Because of ravens wide-ranging movements, it is essential that raven management occur at a regional level; changes implanted at EAFB are not likely to have a lasting effect if they are not also implemented beyond the base’s boundaries. Thus, EAFB should attempt to work with agencies responsible for managing neighboring lands to reduce their facilitation of raven populations.
ABSTRACT

Common Ravens (*Corvus corax*) in the west Mojave Desert are quintessential subsidized predators. Supported by anthropogenic resource subsidies, their large populations exert heavy predation pressure on desert animals, including the declining desert tortoise (*Gopherus agassizii*). We studied the spatial and temporal association between ravens and anthropogenic “attraction sites” from 1994 to 2000 and found that ravens exhibited patterns of variation in abundance at attraction sites a) throughout the day, b) between seasons, and c) between localities (i.e. different towns). Undeveloped desert reference sites had the fewest ravens, and landfills and sewage ponds had the most. Golf courses, putative sources of water and shade but not food, did not have large numbers of ravens. Radio-marked ravens also extensively used agricultural areas, and moved between the landfills and sewage ponds of nearby localities, but were less likely to move to localities that were further away or that were a less-attractive attraction site-type. Overlapping home range boundaries of ravens trapped at the Edwards Air Force Base landfill showed that the area of influence of the landfill via ravens was asymmetrical, weighted toward more developed areas, and that it varied seasonally, with a larger area of influence in the spring and a smaller one in the winter. Garbage containment practices implemented at Edwards Air Force Base considerably reduced the numbers of ravens there and should be implemented on a broader basis in the region to help reduce conflicts between ravens and desert tortoises. Other management recommendations are made.
INTRODUCTION

Soulé (1988) introduced the concept of a subsidized predator population being one that survives and prospers partially as a result of resources provided by myriad human activities. Since then, there have been several references in the literature to subsidized predation (e.g., Boarman 2003; DeLap & Knight 2004; Holt & Lawton 1994; Kristan & Boarman 2003; Polis & Hurd 1996; Schneider 2001), but little empirical or conceptual development of the idea. Food is the most often cited resource subsidy. However, we suggest that a subsidy is any limiting resource augmented by humans, so long as it enhances survival and reproduction, which may result in population stability, increases, and range expansions (Steenhof et al. 1993). Resource subsidies may include water, nesting substrate, and refugia from predators and inclement weather. By supporting an expanded predatory population, the subsidies can facilitate density-independent predation of native prey populations through hyperpredation (Courchamp et al. 2000) and spillover predation (Holt 1984; Schneider 2001). Because the population dynamics of a subsidized predator are decoupled from their effects on prey populations, subsidized predators can drive native prey populations, even rare ones, to endangerment and extinction (Sinclair et al. 1998). Because subsidized predators can sometimes have disastrous effects on native populations, management of the predator population may be necessary. To do so, managers need to understand the temporal and spatial nature of resource use and the relative importance of various resources to the predator population.

Although they are commonly thought of as generalist scavengers, Common Ravens (*Corvus corax*) regularly hunt small prey, and, particularly when they are abundant, can affect prey populations (Boarman 1993, 2003). In recent years, raven numbers have increased throughout the Mojave Desert (Boarman & Berry 1995), where they are locally abundant in association with human developments.
There is growing evidence that, in the absence of human developments, the Mojave Desert is poor habitat for ravens (Camp et al. 1993; Kristan & Boarman, unpublished data; Kristan et al. 2004), and that the raven population increases in this region may be driven by their use of anthropogenic resource subsidies (Boarman 1993; Kristan & Boarman, unpublished data; Knight & Kawashima 1993; Kristan et al. 2004; Webb et al. 2004). As such, ravens are subsidized predators, and their predatory effects can be considered an indirect anthropogenic impact on raven prey (Kristan & Boarman 2003). Because they are relatively well known and easy to study, ravens make an excellent candidate for further exploring the use of anthropogenic resources by subsidized predator populations.

Raven depredation has been implicated as one of the causes for the decline of several threatened and endangered species, including the desert tortoise (*Gopherus agassizii*; Boarman 2003; United States Fish and Wildlife Service 1994), marbled murrelet (*Brachyramphus marmoratus*; Marzluff & Neatherlin, unpublished data), snowy plover (*Charadrius alexandrinus*; Page et al. 1995), California least tern (*Sterna abtillarum*; Knittle 1992), and California condor (*Gymnogyps californianus*; Snyder et al. 1986). To illustrate the dynamics of a subsidized predator’s reliance on resource subsidies, we report on a 6-year study exploring the likely role anthropogenic resources play in facilitating increases in the Mojave raven population and its potential impact on desert tortoise populations. In this study, we determined which anthropogenic sites were most heavily used by ravens, then investigated the temporal variation in raven use of those sites. To evaluate the spatial influence one landfill, a particularly important resource site, has on the raven population, we estimated the area of influence of the anthropogenic resource site that supported the largest number of ravens during our sampling. Finally, we test the relative influence distance and resource site-type have on the probability that ravens will utilize a given site. The results of the study have previously been used to propose methods to reduce raven impacts on tortoise populations (Boarman 2003), but here we take a landscape-scale approach to
examine the relationship between raven populations and the subsidies that sustain them.

METHODS

The study site comprised approximately 4000 km² of Edwards Air Force Base, and surrounding communities in the western Mojave Desert, Kern, Los Angeles, and San Bernardino counties, California, (Fig. 1), which lie within the Mojave Desert Floristic Province (Hickman 1993). The habitat consists of a mixture of natural and anthropogenic types (California Natural Diversity Database 1999). Mean annual precipitation is 112 mm, and falls mainly in the form of rain between November and March (MacMahon 2000). Mean annual temperature is 18.1 °C, with hot summers (mean monthly temperature 25-30 °C, June, July, and August), and cool winters (mean monthly temperatures 10–15 °C, December, January, February) (MacMahon 2000). The most common natural community types are Mojave Creosote Bush (*Larrea tridentata*) Scrub and Desert Saltbush (*Atriplex spp.*) Scrub. The most common anthropogenic land uses include residential areas and various kinds of military flight-support operations, irrigated agriculture, dairy farms, and recreation.

Data Collection

From 1994 through 2000, we counted ravens at up to six resource site-types (landfills, sewage ponds, towns, golf courses, and two undeveloped desert reference sites) in each of three towns (18 survey sites total): Mojave (human population = 3,760), Boron (human population = 2,100), and EAFB Housing area (human population = 7,420), Kern Co., California. The six desert reference sites were located greater than 1 km (Desert Reference Site 1; DC1) and 2 km (Desert Reference Site 2; DC2) from the nearest resource site, city, or residential structure. The golf course at California City (human population = 5,955), approximately 35 km away, served as the Boron associated resource site since no
golf course existed in Boron. Except for city streets, all surveys were conducted as point counts for 5
minutes. Because the structure of the habitat at each of the resource site-types (other than “towns”) was
fairly open and had good visibility, point counts were expected to represent variation in number, with
little effect of differences in detectability. In contrast, ravens in towns were frequently hidden from view
behind buildings, cars, dumpsters, or other obstructions, and this difference in detectability would have
led to a systematic under-estimation of raven numbers. To avoid the confounding effects of differences
in detectability between towns and other resource site-types, the city street surveys consisted of 2 km,
meandering driving transects that incorporated housing and commercial areas. The driving surveys took
approximately 5 min, the same amount of time as the point counts took. All resource sites associated
with a given city were sampled in random order. Patagial-tagged (see below) and unmarked birds were
recorded at each resource site.

To evaluate effects of time of day, site-type, and season on raven abundance, surveys were
conducted in all four seasons in 1996 and 1997 at three times of day in each town. Only in these two
years, surveys at all six site-types were conducted at three times of day in all four seasons. This subset
of the full dataset is referred to as the “year-restricted” dataset. The order of towns surveyed varied in a
randomized block design consisting of 3-day blocks in which each locality was visited at all three times
of day within each block. A minimum of six repetitions of this 3-day pattern was conducted in each of
the four seasons. All six site-types were visited during each repetition. To evaluate annual variation, the
suite of site-types surveyed was narrowed to three (landfill, sewage pond, DC1), time of day to one
(morning) and seasons reduced to only winter from 1994 through 1997 and 1999 through 2000 (site-
type/season-restricted dataset).

Diurnal variation in abundance at the EAFB landfill was determined with day-long surveys. On
13 occasions in 1996 and 1997, surveys were conducted every half hour from sunrise to sunset. An
observer sat in a vehicle at one spot along the edge of the landfill and counted ravens seen within the boundaries of the landfill.

To determine the use of space on a local and regional basis by ravens using the landfill at EAFB, we radio- and wing-tagged ravens. Rocket nets were used on ten occasions between June 1994 and March 1999 at the EAFB landfill to capture a total of 210 ravens. Meat scraps were placed at the capture site every morning for 12 to 31 days prior to trapping to attract and habituate ravens to the trap setup (Camp et al., unpublished data). Captured birds were weighed, measured, and aged. Measurements included wing chord length, tarsus length, and culmen length, width, and height. Age was scored based on a combination of plumage, iris color, wing and tail conditions, and mouth color (Heinrich & Marzluff 1992; Kerttu 1973). A sample of 0.2 ml of blood was drawn from 24 of these individuals and from 27 ravens caught and measured 80 km away (at Fort Irwin, California; Fleischer & Boarman, unpublished data). Sex was determined using a PCR reaction that amplifies the CHD genes on the W and Z chromosomes (Griffiths et al. 1998; Webb et al. 2004). We then developed a discriminant function based on the mass and morphological measurements of these 51 known-sex birds, and used it to predict the sex of the unknown birds (unpublished data).

All ravens caught were affixed with a uniquely numbered, yellow patagial tag on the left wing in 1994 and on both wings in subsequent years. Tag attachment was similar to that described by Kochert et al. (1983). Radio transmitters were attached backpack fashion to a total of 80 birds over the course of this study (Buehler et al. 1995). We attempted to locate radio-tagged birds 2-6 (mean = 3.75) times per week throughout most of the year. UTM coordinates were recorded when the birds were viewed visually, which negated the need to estimate locations by triangulation. On several occasions, searches for radio-tagged birds were conducted up to 250 km away using fixed-wing aircraft with directional antennae affixed to the wings. Locations of sightings of radio- and wing-tagged birds were categorized
by site-type (same categories as for previous analysis, with addition of agricultural areas). We also recorded sightings of radio- and wing-tagged birds observed during the regular surveys at attraction sites described above.

**Analyses**

*Temporal and spatial variation in use of resource sites*

Both datasets (year-restricted and site-type/season-restricted) from the abundance surveys were treated to a three factor generalized linear model, with a Poisson error structure to account for the discrete count data (i.e., analysis of deviance). All statistical analyses were conducted using the R statistical software and extensions (R Development Core Team 2004). Cloud cover and temperature were entered as covariates for each analysis. In all cases, “locality” refers to towns (i.e., Boron, Mojave, and EAFB), whereas “type” refers to the resource site-type (i.e., DC1, DC2, town streets, landfill, sewage ponds, and golf course). For all datasets, year, locality, and resource site-type were entered as main effects. Time of day and season were included as main effects for the year-restricted dataset.

By limiting our attraction site surveys to pre-selected site-types, we may have inadvertently ignored site types that were important to ravens. Therefore, we also identified the sites used by radio-marked ravens to expand our list of attractive sites. At each resighting of a radioed raven we recorded a geographic coordinate and a site name or land-use type. The proportion of resightings that were made in open desert, or at sites that were not included in our attraction site surveys, could be calculated and used to confirm and expand our list of attractive sites in the region. To the extent that ravens used multiple sites repeatedly, the regional importance of particular attraction sites could be gauged.

We used a non-parametric kernel regression to test if abundance across the day at the EAFB landfill varied from a random distribution. Regression models were tested with a randomization test,
which produced both a p-value for the overall test and a confidence band around the null hypothesis of uniform distribution of ravens throughout the day, which could be used to identify when raven numbers differed from the null expectation. Kernel regressions and randomization tests were done with the “SM” extension of the R statistical software package (R Core Development Team 2004), which implements techniques of Bowman and Azzalini (1997).

**Movements**

The regional importance of one focal attraction site, the EAFB landfill, was addressed by characterizing the movements of ravens trapped at the landfill. We characterized their movements by tabulating the distances between the landfill and locations of subsequent resightings of radioed ravens, and by tabulating the average distance of each individual from the landfill.

In addition to these descriptions of distances moved by marked ravens, we estimated the area of influence of the EAFB landfill. Of the 80 radio-marked ravens, 61 were resighted 10 or more times, and these resightings were used to calculate home ranges. Home range boundaries were calculated with the 95% probability contour from a fixed kernel utilization distribution. Individual home ranges were then overlaid to produce a map of ravens whose home ranges overlapped at any point in the study area; the map can be viewed as the regional area of influence of the EAFB landfill. Home ranges were also estimated for each season, so that seasonal changes in the area of influence could be visualized. Although statistical tests of differences among maps were not attempted, we tested whether the dispersion of individual locations varied seasonally by first calculating a measure of dispersion (the square root of the determinant of the variance/covariance matrix for each individual’s UTM coordinates; Legendre & Legendre 1998), and then testing for differences in dispersion among seasons with a one-way ANOVA. Dispersion was log-transformed prior to analysis to improve normality. A Tukey HSD
post-hoc analysis was used to identify which seasons were significantly different from other.

We further explored the regional patterns of inter-connection among attraction sites by testing the relative influence of site-type and distance in explaining which sets of sites individual ravens visited. Because marked individuals were recorded during raven surveys, we could tabulate the number of times that individuals were found at pairs of attraction sites. The study area was composed of expanses of open desert with anthropogenic sites distributed throughout; therefore, a raven searching for food or water may more likely be observed at attraction sites that were near their point of capture. However, sites that contained attractive resource subsidies may more likely be visited, regardless of their distance from the landfill. To test the relative influence of distance and attraction site-type on the likelihood that ravens would be found at any pair of sites, we divided this analysis into two separate datasets. One dataset represented all ravens seen at both the EAFB landfill and one other site (one-legged trips). The other dataset represented all ravens seen at pairs of sites other than the EAFB landfill (two-legged trips). One-legged trips could be represented with a single distance (the distance between the EAFB landfill and the other site) and a single site-type (the site-type of the other site). The number of marked ravens observed were then related to attraction type and distance from the landfill, using an analysis of deviance. Two-legged trips had to be treated differently. Although we did not know the route traveled by ravens among attraction sites, we did know that ravens were trapped at the EAFB landfill, and thus, to be observed at two pairs of sites other than the EAFB landfill (e.g. at the Boron landfill and at the Mojave sewage ponds) a raven would have had to move from the EAFB landfill to one of the sites, and then move between them. The analysis does not assume order, path, or timing of visitations. For two-legged trips, we represented the effect of distance in an analysis of deviance with two variables: the straight-line distance between the EAFB landfill and the nearest of the two sites, and the straight-line distance between the two sites. Additionally, since attraction site-types could differ between the pair, we
included a variable for each attraction site-type.

RESULTS

Temporal and Spatial Variation in Use of Resource Sites

In the analysis of deviance model of the year-restricted dataset, site-type explained considerably more of the deviance than any other first or higher-order effect (Table 1). Significantly more ravens were counted at landfills followed by sewage ponds, towns, golf courses, DC1, then DC2 (Fig. 2). The relative abundance among types within localities was generally the same except for sewage ponds (hence the significant locality x type interaction). The sewage ponds at EAFB were less utilized relative to landfills and towns than were sewage ponds at Mojave and Boron (Fig. 2). The latter two were 3.5 and 3.2 km, respectively, from the nearest landfill; the EAFB sewage pond was 12 km from a landfill. The sewage ponds at Mojave were used much more than the other two sewage ponds. Locality (town) explained little of the deviance and season explained even less (Fig. 3). The two years included in the model differed significantly, but explained very little of the deviance. Raven abundance at attraction site-types varied with time of day, but there was not a consistent overall effect and its proportion of deviance explained was low. Diurnal patterns varied little among seasons and years. Temperature and cloud cover both accounted for small but significant proportions of deviance in raven counts at site-types.

The analysis of deviance model of the site-type/season-restricted database showed similar results (Table 2). Again, site-type was the single most important factor followed by locality and the type x locality interaction. There was also a significant year effect and significant year x site-type and year x locality interactions, all of which can be attributed to a 62% reduction in numbers of ravens between 1995 and 1997 at the EAFB landfill and the Mojave Sewage Pond (Fig. 4). Numbers of ravens leveled
off between 1997 and 2000. Several changes in landfill management at the EAFB landfill were implemented in 1995 and 1996. During that time, operators began to process and compact garbage in a large warehouse, they then move it to landfill in large bailed blocks, and cover it immediately with a canvass tarp.

The average distance of individuals from the EAFB landfill had a skewed distribution, with half of the average distances 5.2 km or less (Fig. 5). The distribution of distances of single observations of marked individuals was also highly skewed, such that 70% of observations fell within 5 km of the landfill. The three modes demonstrated in Fig. 5 correspond to EAFB housing and operations area, Mojave landfill and sewage pond, and agricultural and rural residential areas south and west of EAFB. The 95% kernel home range sizes ranged between 1.67 km$^2$ and 3,515 km$^2$ (Fig. 6).

The diurnal pattern of raven presence at the EAFB landfill showed significant (p<0.01) variation with a marked significant peak in late afternoon when all seasons were combined, although there was a wide scatter of points (Fig. 7). Raven abundance was at its lowest during the morning (0830-1300) and peaked between 1500 and 1700, which was when the landfill closed for the day and workers were leaving or left the site.

**Movements**

Of the 210 ravens marked and released at the EAFB landfill, 26 (12%) were seen at one or more of the six desert reference sites during the abundance surveys. A total of 12 (6%) were located once, 5 (2%) two to three times, and 1 bird (0.5%) was seen 28 times. A total of seven wing-tagged birds out of 210 were found nesting, although never with another tagged bird. Three were near the EAFB landfill, two were in the open desert, and two were in desert habitat, but near a major highway (State Hwy 58). Although 12% of marked ravens were counted at least once at a desert reference site, only 2.5% of the
20,651 observations of radio-marked ravens were in undeveloped desert.

Average number of attraction sites visited by radio-tracked ravens was 2.1 (sd = 1.68, n = 161, range 1-9) including the EAFB landfill site, where all individuals were first captured. Distance and attraction site-type were both significantly associated with the number of times ravens were seen at pairs of sites, for both one-legged and two-legged trips. For one-legged trips, both site-type and distance were significant \( F_{5, 11} = 39.75, \ p \leq 0.0001; \ F_{1, 11} = 184.79, \ p \leq 0.0001; \) respectively, and together they explained 88.9% of the variance in ravens observed. Site-type and distance had nearly identical independent contributions to the model, explaining 42.8% and 43.3% of the deviance, respectively (the remaining 14.2% was explained by the correlated, and therefore statistically confounded, variation between distance and site-type). The site-types that had more marked ravens than expected from distance alone were landfills, towns, and sewage ponds. Desert reference sites and golf courses had fewer ravens than expected, and DC2 had fewer ravens than DC1 sites. For two-legged trips (i.e. birds that were found at two sites away from the EAFB landfill) both site-type and distance were also significant \( F_{5, 140} = 12.3, \ p < 0.0001; \) distance to closest site: \( F_{1, 140} = 138.4, \ p < 0.001; \) distance between sites: \( F_{1, 140} = 62.1, \ p < 0.001 \) but site-type had a smaller independent contribution to the model than distance, explaining 31% and 69%, respectively.

Raven observations were clustered near the EAFB landfill and nearby anthropogenic sites (e.g. housing areas and horse stables), as well as the Mojave landfill and sewage ponds, agricultural areas to the south (particularly dairy farms), and at several dog kennels immediately west of the Base. This pattern of distribution resulted in an area of influence of the EAFB landfill that was densest at the landfill itself, and weighted toward the west and south (Fig. 8). There was significant seasonal variation in the dispersion of locations for individual ravens \( F_{3, 232}=3.86, \ p = 0.01 \). Tukey HSD post-hoc analysis showed that this was due to less dispersion in the winter compared with spring. Summer and fall
dispersions were not significantly different from each other or from winter or spring. Changes in
dispersion of locations among season are reflected in the size and distribution of the EAFB landfill’s
area of influence among seasons (Fig. 9).

DISCUSSION

Landfills are heavily used by ravens in the west Mojave Desert. The three landfills we surveyed
consistently had more ravens at them than any other site type visited (Fig. 2). This was the case
regardless of time of day, season, year, or weather (Tables 1 and 2). The distribution of all locations of
radio-tagged ravens shows the strongest clusters at two (EAFB and Mojave) of the three landfills in the
immediate area (Fig. 8). Although there are ample accounts in the literature of ravens utilizing landfills,
there have been very few that have quantified the predominance landfills often hold over other attraction
sites (e.g., California, Boarman et al., unpublished data; Wyoming, Dorn 1972; Michigan, Mahringer
1970). Sewage ponds had the second highest counts of ravens in our attraction site surveys. However,
one sewage pond in particular, near the town of Mojave, had particularly high numbers of ravens. This
sewage pond was very near the Mojave landfill and the town of Mojave and probably had regular
movements of ravens between all three sites. The EAFB sewage pond had a near absence of ravens,
probably due to it being relatively remote from the landfill and other concentrations of ravens (Fig. 1).
Sewage ponds probably provide both food and water subsidies to ravens. Other sources of both food and
water occur closer to the EAFB landfill (e.g., Base housing and operations areas), but not closer to the
Mojave landfill. Dairy farms, although not included in the attraction site surveys, were revealed by
radio-tracking to be much used by ravens. In all, 48% (81/170) of our tagged birds were seen at least
once at one particular dairy farm, which was 22.6 km south of the EAFB landfill. These three resource
site types appear to be much more important to ravens than any other sites in the vicinity. A fourth site,
also revealed by radio tracking, was a small enclave of houses west of EAFB containing several outdoor kennels for abandoned and abused dogs. The dogs were acclimated to the ravens, and vice versa. The ravens would walk around the yards eating food out of dog bowls; each species seemed acclimated to the presence of the other. In contrast to these, only 2.5% of over 20,000 observations of radio-tagged birds were in the undisturbed desert.

The role of resource subsidies in predator population dynamics has temporal components. Use of different site types by ravens varied with time of day and season, but these two factors taken together still explained little of the deviance in abundance compared to the effect of location and site. In general, counts were highest in the winter and lowest in the spring. We were surveying raven numbers over a fairly extensive area, larger than the home range sizes of the majority of these non-migratory birds, so we were not detecting mass movements of birds into or out of the area. We believe the seasonal differences in overall numbers reflects a concentration at anthropogenic resource sites (particularly landfills and sewage ponds) during the winter followed by dispersal away from these concentration sites to more dispersed breeding territories and less concentrated resource sites during the breeding season. This greater dispersion in spring is also reflected in the area of influence (Fig. 9) of raven presence in the study area. We did not note any marked seasonal changes in use of specific site types. Raven counts also varied through the course of the day. At the EAFB landfill, the difference followed human activity patterns, where raven numbers dipped at midday when human activity was greatest, then peaked in late afternoon after workers left the landfill for the day. A similar diurnal association between ravens and human activity was recorded at another landfill in the central Mojave Desert (Boarman et al., unpublished data). These temporal patterns may have implications in identifying which resource sources to target for management and when to do so.

An important change in garbage containment practices at EAFB was followed by a marked
reduction in raven abundance (Fig. 4). In response to a requirement to reduce the number of ravens present at the landfill, EAFB began to modernize their landfill in 1995 to 1996. Instead of depositing garbage loose at the landfill face and covering it at the end of each day with 38 cm of dirt, they began to bring garbage into a large shed for sorting, compacting, and bailing. Under the updated system, recyclables and compost are removed, and the remaining garbage is compressed and tied into large blocks, which are then trucked to the face. The blocks are then immediately covered with large tarps. After several days, the garbage is then covered with a minimum of 38 cm of dirt. The surveys showed a significant and consistent reduction by 58 to 70% in abundance of ravens at the EAFB landfill in those years followed by a leveling off in 1997. The pattern was also present at the Mojave sewage pond, but not at other sites surveyed. The Mojave sewage pond, 19 km distant, attracted many ravens from the EAFB landfill, so it is not surprising that its numbers would also decline. The fact that other sites, particularly landfills, did not show much of a reduction during the same time period suggests that practices at the EAFB landfill were successful in decreasing available subsidies, but its effects at some other sites were swamped by land uses at a larger regional scale. It is also important to note that there was no corresponding increase in numbers of ravens at any site, indicating that birds did not just move en masse from the EAFB landfill to other locations. The reduction in raven abundance at the EAFB may have been caused by birds diffusing more or less individually to many other sites, or may have represented a true reduction in production of juveniles by ravens nesting in the vicinity of the landfill.

Ravens use attraction sites, and move between them, based on the type of attraction site and the distances between them. The likelihood that a raven will make a trip between their initial point of capture (the EAFB landfill) and one other site was more closely related to the attraction site-type than to the distance between the points. Once they found and used another site, proximity was more important than site-type in predicting their use of a third site. Furthermore, the distance from the EAFB landfill to
the first site had a greater effect than the distance between the first and second site. This suggests that
the probability that a raven will be found at a pair of sites throughout the region depends on whether at
least one of the sites is detected by the raven, and then on whether the attraction site-type is one that is
preferentially used by ravens, such as a landfill or sewage pond. The implication of this is that the closer
resource sites are to major attractants (e.g., landfills), the more likely they are to attract ravens. More
intense management may be necessary at less popular site types if they occur near popular sites.

Because we only trapped and marked birds at the EAFB landfill, the area of influence of the
EAFB landfill was not expected to reflect regional patterns of raven abundance as a whole. However, we
did expect the landfill to be a central point in the distributions of ravens trapped there, with raven home
ranges centered on the landfill, and distributed in all directions around it. Instead we found that the
landfill was an extremely important site for many of the ravens there (in that many were only ever seen
at the landfill or at EAFB housing, kennels, or some other nearby site), and that ravens
disproportionately used areas to the west and south of the landfill. Although we know that ravens were
found in populated areas to the west and north, point counts conducted within the region most heavily
used by ravens (south of Highway 58 and east of Highway 14) also showed a peak abundance at
Edwards, and smaller peaks at the towns of Mojave and Rosamond (Kristan & Boarman 2003). Our
focus on the EAFB landfill was justified by the distribution and abundance patterns of the ravens in the
region.

Our data suggest that attraction sites in the west Mojave form a series of stepping stones through
otherwise inhospitable desert habitat. In addition to our analysis of the effects of distance and attraction
site-type on the distribution of marked ravens at survey locations, radio-tracking data support this
interpretation. For example, although 12% of individual ravens were counted at least once at a desert
reference site during the course of the attraction site surveys, only 2.5% of the 20,651 observations of
radio-marked ravens were in undeveloped desert. The regional area of influence for ravens caught at the EAFB landfill throughout the region shows that ravens move between a small number of attractive sites, including agricultural areas to the south, and Mojave landfill and sewage ponds to the west. There was little movement to the east or north, in spite of the fact that resource subsidies were available at Boron (to the east) and California City (to the north), and both were well within the movement ability of this species. Furthermore, there were very few observations of tagged birds north and east of these two towns. We hypothesize that these movement patterns can be explained by there being less developed land between EAFB and both Boron and California City, and particularly beyond. EAFB may represent the eastern extent of a relatively cohesive raven population occupying the southern Central Valley, 80 km to the west, and the western edge of the Mojave Desert. The spatial scale at which ravens respond to resource distributions is not known, but the effect of distance on movement between attraction sites suggests that ravens did not have equal access to all of the attraction sites that we surveyed. Neatherlin and Marzluff (2004) similarly found that campgrounds in old-growth forests of the Olympic Peninsula acted as stepping stones for the dispersal of American crows (*Corvus brachyrhynchos*) into less-productive, typically uninhabited habitats. Hence, small, relatively unimportant resource site types may actually play an important role in aiding the dispersal of ravens into or through undisturbed habitat.

As a detailed example of how one subsidized predator population makes use of anthropogenic resources, we have demonstrated how human-provided resources are regularly used by ravens in the Mojave Desert. Anthropogenic resources influence seasonal movements, direction of movements, spatial extent of predation risk (Kristan & Boarman 2003), reproductive success (Kristan et al. 2004; Kristan & Boarman, unpublished data), and survivorship (Webb et al. 2004). Food is the most readily observed resource subsidy, with landfills the most used food attraction. Most of our radio-tagged birds also visited dairy farms, dog kennels, alfalfa fields, and other agricultural areas south and west of the
study area, a result consistent with those reported by Knight et al. (1993) in the Mojave desert. In addition, ravens obtained food subsidies from garbage cans and dumpsters, from road kills along paved highways, and from food left out for pets, to name a few sources. Water is an especially important subsidy in an arid environment such as the Mojave Desert. We incidentally observed ravens in the Mojave Desert obtaining water from irrigation structures, ponds, stock tanks, wildlife guzzlers, dripping faucets, and more (see also Knight et al. 1998). Nesting substrate is a third important anthropogenic subsidy utilized by ravens. Out of 225 raven nests recorded in and around EAFB, 58.5 % were on anthropogenic structures such as billboards, power poles, and buildings (Kristan & Boarman 2003). Use of such structures has extended the breeding range of ravens into habitats previously unusable due to a lack of natural nesting substrates. Ravens also take advantage of human-provided structures such as abandoned buildings for shelter from predators and extreme weather, while using telephone lines and high-tension power poles as substrate for nighttime roosting (Boarman et al., unpublished data; Chamblin & Boarman 2004; Engel et al. 1992).

The presence of a species at human-provided resource features is necessary, but not sufficient, to categorize it as a subsidized predator. It must also be demonstrated that the population’s persistence and growth are facilitated by the human-augmented resources. Elsewhere, we demonstrated that raven diet and reproduction are influenced by the presence of anthropogenic resources (Kristan et al. 2004; Webb et al. 2004). Not only do ravens nesting near human habitations eat significantly more anthropogenic foods, but the presence of refuse and roadkills in their diets significantly improved fledging success (Kristan & Boarman, unpublished data; Kristan et al. 2004). Synanthropic birds also have higher fledging success than those living in more remote areas, and their fledglings have greater survivorship up to at least two years of age (Webb et al. 2004). The result of all of these anthropogenic resources is a Mojave Desert raven population that grew by 1000% over a recent 26-year period (Boarman & Berry
Soulé (1990) suggested that ravens in the southwest United States are subsidized predators and we further propose they are the quintessential example.

**Implications**

Ravens are increasingly understood to be subsidized predators, as well as scavengers, in the west Mojave Desert. Landfills, sewage ponds, towns, and agricultural areas are more heavily used than other kinds of anthropogenic sites. Although ravens routinely moved between sites that were up to 23 km apart, they did not travel in all directions equally. Regional impacts of human resources thus are affected by the spatial distribution of attraction sites, with isolated anthropogenic structures serving as stepping stones for movements and dispersal. One way of limiting the penetration of ravens into undeveloped areas may be to avoid providing “stepping stones” that facilitate their spread. This requires concentrating developments, particularly those that provide even small amounts of resources for ravens, rather than spreading them throughout the desert. Although we do not yet know what constitutes a stepping stone, attraction sites that supply constant food and water sources are good candidates. Although roads run between Edwards and both Boron and California City, Edwards ravens were rarely found at either of these sites, in spite of the fact that both towns supported raven populations. Hence, the regional links between raven populations are not simply functions of distance.

Food is the most important resource subsidies humans provide to ravens in the Mojave Desert. Virtually every site with large numbers of ravens can be characterized as having a bounty of food: garbage at landfills, grains at dairy farms, and pet food at large, outdoor dog kennels west of EAFB. Limiting the availability of food at these sites will likely have a significant long-term effect on raven populations in the west Mojave. Our surveys indicated that compacting garbage and covering the blocks with tarps can reduce the number of ravens utilizing a landfill. Refining the garbage containment
practices further, such as repairing tears in the tarp when they occur, is likely to result in the presence of even fewer ravens. However, our data show that ravens at EAFB are part of a population inhabiting a much broader area than the base. Similar garbage containment practices should be implemented at other landfills in the vicinity if ravens numbers are to be reduced. In addition, efforts need to be made to reduce the availability of organic waste at other points in the waste stream. Actions could include reducing the use of garbage bags on garbage pick-up days and ensuring that all dumpsters behind restaurants and markets are self closing. Public education and cooperation with animal welfare and adoption organizations could work to encourage home owners and kennel operators to feed their dogs in a manner that reduces access by ravens to dog food.

ACKNOWLEDGMENTS

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Wildlife Research Center, Animal and Plant Health Inspection Service.


Table 1. The relative importance of site type, locality, time of day, and season at explaining raven abundance at four types of anthropogenic resource sites and the open desert. Analysis of deviance table for year-restricted dataset, which included surveys from 1996 and 1997 at all six site-types (p < 0.001, $R^2 = 0.76$).

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<th>p</th>
<th>% Dev.</th>
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<tr>
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<td>Percentile</td>
<td>p-value</td>
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<td>&lt; 0.001</td>
<td>0.6%</td>
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<td>442</td>
<td>29.5</td>
<td>&lt; 0.001</td>
<td>0.6%</td>
</tr>
<tr>
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<td>30.3</td>
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<td>16542</td>
<td></td>
<td></td>
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</tbody>
</table>
Table 2. The relative importance of site type, locality, and year at explaining variance in raven abundance at two types of anthropogenic resource site and open desert. We used for this analysis the site-type/season-restricted dataset, which consisted of raven abundances in winter surveys, in 6 years (1994-1997, 1999, 2000). Only three attraction site-types that were observed in all years are included in “type,” (p = < 0.001, R^2 = 0.70).

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>deviance</th>
<th>F</th>
<th>p</th>
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<td>4239.81</td>
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<tr>
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<td>1190.6</td>
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<td>10.68</td>
</tr>
<tr>
<td>Year</td>
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<td>154.18</td>
<td>&lt; 0.001</td>
<td>2.77</td>
</tr>
<tr>
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<td>2.68</td>
<td>0.100</td>
<td>0.01</td>
</tr>
<tr>
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<td>4.87</td>
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<td>0.02</td>
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<td>693.18</td>
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<td>12.44</td>
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<td>97.52</td>
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<td>3.50</td>
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<td>636</td>
<td>6531.3</td>
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</table>
Figure 1. Map of study site in the western Mojave Desert at Edwards Air Force Base, California. DC1 = desert reference 1, DC2 = desert reference 2.
Figure 2. Difference in raven abundance (mean number of ravens per survey) among different attraction sites at three localities in and around Edwards Air Force Base, California. Marked ravens are represented by dark bars, unmarked ravens are gray. DC1 = desert reference 1, DC2 = desert reference 2, GC = golf course, lf = landfill, SP = sewage pond.
Figure 3. Difference in raven abundance by season at each locality and at all three combined. Data from 1996, 1997, and 1999 are combined. These are the years with all four seasons surveyed. Bars represent 95% Poisson confidence intervals.
Figure 4. Change in raven abundance between 1995 and 2000 at three landfills in the Mojave Desert. Landfill management methods were changed during 1995 and 1996. DC1 = desert reference 1, SP = sewage pond.
Figure 5. Distribution of mean distances of marked individuals from the EAFB landfill where they were initially captured.
Figure 6. Examples of nine 100% minimum convex polygon home ranges for radio-marked ravens. These are presented sole for the purpose of illustrating how home range sizes can vary by several orders of magnitude. MCP home range sizes were not used in analyses. The home ranges represent the three smallest (individuals that never left the EAFB landfill and housing complex; enclosed within the dotted circle), three that left the west Mojave, and three intermediate-sized home ranges (bold lines) for ravens that moved between three commonly used attraction sites (EAFB sites, Van Dam Farms, and sites at the town of Mojave). EAFB is indicated by grey shading.
Figure 7. Diurnal variation in raven abundance throughout the day at EAFB landfill in 1996 and 1997 combined.
Figure 8. The distribution of overlapping raven home ranges in all seasons combined. Dark areas were within as many as 100% of radio-marked ravens’ home ranges.
Figure 9. Area of influence of the EAFB landfill by season.
Chapter 2: Diet composition of common ravens across the urban-wildland interface of the West Mojave Desert*

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EXECUTIVE SUMMARY OF CHAPTER

In this chapter, we compared diets of nesting ravens near different types of human developments, predicting that the ravens’ diet would reflect differences in available food subsidies. The study took place on and near Edwards Air Force Base in the West Mojave Desert from 1999–2000. The contents of pellets found beneath raven nests were dissected and analyzed to determine diet composition. A total of 1,142 food items from the 560 pellets that were gathered from beneath 98 nests was identified. Food items were then placed into broad categories (mammals, birds, reptiles, amphibians, plants, arthropods, and trash). Diet content was expressed as the percentage of pellets that contained each food type, and a matrix of nests and food item composition was created. Diet composition of birds at each nest was then related to the distance to the nearest road and the distance to the nearest point subsidy (such as ponds, landfills, developments). No tortoise remains were found in the pellets.

We found that ravens nesting close to point subsidies and far from roads had the greatest incidence of trash in their diets, while those nesting near roads but far from point subsidies in natural landscapes had low incidence of trash and higher incidence of mammals and reptiles (presumably road-kills). Ravens nesting in more natural areas far from roads and point subsidies had more plant material and arthropods in their diet, and ravens close to both roads and point subsidies had more birds and amphibians in their diet. Amphibians were found in the last group because the African clawed frogs at the artificially-made Piute Ponds, which was classified as an anthropogenic site. In contrast to diet composition, diet diversity was not related to either distance of nests to roads or distance to point subsidies. Furthermore, fledging success was significantly higher for ravens whose pellets contained trash, which indicates how important human subsidies are for ravens to reproduce successfully. Ravens whose diets consisted of vegetation and arthropods, for example, were at an apparent reproductive
disadvantage compared to those that received a “free lunch” from anthropogenic sources.

Management Implications

Ravens are opportunistic foragers as well as predators. Their generalist diet allows them to take advantage of different kinds of foods that are associated with different human developments. Raven diets having a greater incidence of human-provided foods were associated with increased fledging success; these effects decreased with distance from developments. Therefore, proximity to anthropogenic resources can be seen as the key to raven success. Improved management of waste at landfills and fencing along highways to reduce the incidence of road-kills may help slow the growth of raven populations in and around EAFB. Although no desert tortoise predation was found on Base during this study, high densities of ravens may cause problems for desert tortoise recovery and for nursery programs.

ABSTRACT

Common ravens (Corvus corax) are human-subsidized scavengers and predators in the Mojave Desert. They have increased dramatically in number and have been implicated as contributors to the decline in desert tortoise (Gopherus agassizii) populations. Known patterns of increased fledging success near human developments suggested that food was the most likely resource subsidy received by ravens. Because ravens are opportunistic foragers with a generalist diet, we predicted that the types of resource subsidy provided by different kinds of human developments should be reflected in measures of diet composition of breeding ravens. We estimated diet composition from contents of raven pellets collected at nests and related diet composition to distance of the nests from roads and point sources of resource subsidies, such as towns or landfills. Ravens that nested close to point subsidies far from major
roads had the greatest incidence of trash in their diets. Ravens that nested close to roads but far from point subsidies had a low incidence of trash and a higher incidence of presumably road-killed mammals and reptiles. Ravens far from both roads and point subsidies had more plant material and arthropods, and ravens close to both roads and point subsidies had more birds and amphibians. Diet diversity was not related to distance from roads or developments. Fledging success was correlated with diet composition, such that birds with diets consistent with trash or road-kill subsidies fledged the greatest number of chicks. Our results suggest that ravens forage opportunistically on foods available near their nests, and different kinds of human developments contribute different foods. Improved management of landfills and highway fencing to reduce road-kills may help slow the growth of raven populations in the Mojave.

INTRODUCTION

Common ravens (Corvus corax) are native to the West Mojave Desert but have increased in number concomitantly with increases in human populations (Knight et al. 1993, Boarman and Berry 1995). Ravens are generalists in foraging ecology and diet and are capable of exploiting a variety of anthropogenic resources. The importance of human-provided resources to raven population growth is supported by the observation that proximity to human developments, such as housing, landfills, sewage treatment ponds, and roads, augments raven reproductive success (Kristan 2001, Webb 2001). Increases in availability of adequate nesting sites have led to raven population increases in other areas (White and Tanner-White 1988, Steenhof et al. 1993, Knight et al. 1995), but this was unlikely to explain increases in the West Mojave, because natural nest sites in Joshua trees (Yucca brevifolia) were abundant and were used by the majority of ravens in this part of the West Mojave (Kristan 2001). Taken together, these observations suggest that anthropogenic developments augment raven population growth in the West Mojave primarily through direct food subsidies to ravens. The rapid increase in raven populations
has become a management concern because large raven populations may harm species such as the threatened desert tortoise (*Gopherus agassizii*, Boarman 2003). Threats from ravens may be particularly severe because predators are more likely to cause extinctions in prey when food subsidies allow their populations to remain high as prey populations decline (Andrén 1992, Sinclair et al. 1998, Courchamp et al. 2000). Based on the large but largely circumstantial body of evidence that human-provided food resources promote raven population growth, removal of food resources has been proposed as a nonlethal method of raven population control in the West Mojave (Boarman 2003).

Although it seems obvious that resource subsidies are responsible for raven population growth and that removing food subsidies should therefore slow or possibly reverse raven population growth, different types of human developments are likely to provide different types of resource subsidies. Human development of the West Mojave has produced a clustered pattern of urban and agricultural land uses adjacent to undeveloped desert landscapes, and of roads traversing long stretches of undeveloped desert scrub. Developments associated with urban areas are diverse and can provide a variety of foods that are independent of the natural environment, such as trash found at landfills and housing areas and aquatic prey found at artificial wetlands. Many of these resources could be removed through improved management practices, such as covering exposed trash at houses and landfills. In contrast, the primary food subsidy associated with roads through undeveloped natural landscapes would be road-killed carrion, although trash-dumping at roadsides may occur as well (Camp et al. 1993). If the kinds of food subsidies arising from roads and from towns (and associated landfills, etc.) are different, very different remediation actions will be required to remove them.

Ravens nesting on islands lacking human food sources are forced to hunt arthropods and small vertebrates (Nogales and Hernandez 1994), and we hypothesized that ravens in our study population that attempted to nest in remote areas, far from sources of anthropogenic food subsidies, also would have a
greater incidence of these kinds of prey in their pellets. Finally, we hypothesized that anthropogenically subsidized diets should be associated with increased fledging success. We evaluated these hypotheses by characterizing the diet of ravens, as indicated by contents of pellets collected from beneath raven nests, and by relating raven diet to proximity to roads and human developments, as well as to raven fledging success in the West Mojave Desert.

**STUDY AREA**

The primary study area was within the western half of Edwards Air Force Base (EAFB) and on lands immediately surrounding the base in the West Mojave Desert of California (Figure 1). The study area covered approximately 770 km². The small number of point sources of resource subsidies (features that could be represented by a point on a map, such as towns, artificial water bodies, and landfills) were distributed throughout the area, surrounded by undeveloped shrublands. Vegetation in undeveloped areas was composed of creosote bush (*Larrea tridentata*) and saltbush (*Atriplex* spp.) scrub, often forming a woodland in association with Joshua trees.

Two artificial, permanent water bodies represented sources of water, food, and riparian vegetation (Figure 1). The larger body (Piute Ponds) was an artificial wetland within EAFB that contained well-developed riparian vegetation, including willows (*Salix* sp.), cattails (*Typha* sp.), and rushes (*Juncus* sp.). Piute 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 also were present near towns in the study area, Mojave (population 3,763) and Rosamond (population 7,430).

The military lands outside the cantonment at EAFB are used primarily for military aircraft
training, with little disturbance to the vegetation. Undeveloped lands outside the EAFB boundary were used for a variety of purposes, including recreation and sheep grazing. The housing area within EAFB (population 7,423) and the towns of Rosamond and Mojave all consisted of single-family homes, apartment complexes, and commercial developments (e.g., restaurants, grocery stores, etc.). Solid-waste disposal sites (landfills) were present near EAFB housing and southeast of Mojave.

METHODS

Pellet collection and analysis

Pellet analysis has been successfully used to characterize raven diet composition in several studies (e.g., Marquiss and Booth 1986, Camp et al. 1993, Nogales and Hernandez 1994, 1997) and was used to characterize diet for our study. During springs 1999 and 2000 we collected pellets from beneath known raven nests. Nest locations were known from concomitant studies of raven breeding biology (Kristan 2001). Nest searching was conducted each year from 1996 to 2000; by 1999 we observed 261 nests (of which 150 exhibited some degree of breeding activity), and by 2000 we observed 341 nests (of which 168 exhibited some degree of breeding activity). Nests were distributed throughout the study area (Figure 1). At the beginning of the breeding season in early March, we removed pellets already present from the vicinity of the nest so that pellet collections would reflect foods consumed during the current breeding season. We collected pellets opportunistically during reproductive monitoring, and made collections from 42 nests in 1999 and from 72 nests in 2000; because collections were made from some of the same nests in both years, we made collections from 98 different nests over the 2 years, distributed throughout the study area (Figure 1). The number of pellets from a nest ranged from 1–44, and we analyzed 1,142 items from 560 pellets. In the lab we dissected pellets and identified all food items. We identified plant and animal remains to species when possible, though frequently it was possible to
identify them only at higher taxonomic levels. We interpreted the presence of pieces of paper or plastic or other artificial, nonfood items in a pellet as consumption of trash.

**Statistical analysis**

We expressed diet contents as percent of pellets that contained each food item \((100 \times \frac{\text{number of pellets with the item}}{\text{total number of pellets in collection}})\), and as percent of nests that had the food item in >1 pellets \((100 \times \frac{\text{number of nests with the food item}}{\text{total number of nests}})\).

For statistical analysis, we assigned pellet contents to broad classes: mammals, birds (including egg shells), reptiles, amphibians, plants, arthropods, and trash. We then tallied number of pellets that contained each of these food items for each nest and used the matrix of nests by counts of food items as our diet composition data. We measured distance between each nest and the nearest paved road and nearest point subsidy using Geographic Information System (GIS) maps. “Point subsidies” consisted of any potential source of food found on the study area that could be represented by a point or polygon on a map and included housing developments, landfills, and artificial water bodies (e.g., sewage ponds, artificial wetlands, permanent artificial ponds). We related diet composition to distance to roads and distance to point subsidies using canonical correspondence analysis (CCA; Legendre and Legendre 1998). CCA is an ordination technique that simultaneously orders nests relative to patterns of diet composition and orders food items relative to patterns of occurrence in the sample from each nest. Additionally, because CCA is a direct ordination technique, the ordering of samples and food items was constrained by the distances to roads and human developments. Since we collected different numbers of pellets for each nest, we used a “partial CCA,” in which the number of pellets collected at a nest was included as a covariate and thus was statistically controlled (Legendre and Legendre 1998). Statistical significance of a CCA was determined using a permutation test that compared the observed CCA result
against the distribution of CCA results from a large number (in this case 1,000) of randomly shuffled data matrices (Legendre and Legendre 1998). A significant CCA indicated that diet composition was associated with distance to roads or point subsidies.

An advantage of CCA is that the position of each observation along CCA axes (i.e., their CCA scores) can be used as a numerical representation of diet composition. We used scores from the first and second CCA axes (CCA1 and CCA2) to represent the 2 strongest patterns of diet composition and related fledging success to diet composition by regressing total number of chicks fledged from a nest on the CCA axis scores. Nests were observed for 1–2 years, so we used the number of years observed as a covariate. The strong relationship between years observed and total fledglings observed made the \( P \)-value for the model uninformative; therefore, using a likelihood ratio test, we tested its significance by comparing it with a regression model that only included number of chicks fledged and number of years observed.

We calculated diversity of food items found in the collections from each nest using Shannon’s index (Krebs 1989). Because number of pellets in a collection strongly influences diversity observed, we used standard partial regression approaches to statistically remove the effect of number of pellets before analyzing effects of roads and point subsidies on diet diversity (Legendre and Legendre 1998). This approach involved fitting a linear regression between diversity and number of pellets in a collection (or, in this case, the log of the number of pellets, which resulted in a linear relationship between the variables), and then using the residuals from this regression to analyze effects of distance to roads and distance to subsidies on diet diversity.

**RESULTS**

Raven pellets contained a variety of food items reflecting their opportunistic, generalist diet
We found mammals in 76.5% of pellets and at 92.9% of nests. We found *Dipodomys* sp., the most common single food item, in 50.2% of pellets and at 84.7% of nests. Jackrabbits (*Lepus* sp.) and cottontails (*Sylvilagus* sp.) also were commonly found at nests (18.4% and 26.5% respectively), but were less common per pellet (3.4% and 5.9%, respectively). We found arthropods at 81.6% of nests and in 37.4% of pellets. Trash was present at 57.1% of nests and in 24.2% of pellets.

Nests from which we obtained pellet collections were found up to 8 km from the nearest road and up to 12 km from the nearest point subsidy. The diet composition at nests was significantly associated with distance to roads and distance to subsidies (randomization test of CCA, \( P < 0.01 \); Figure 2). The vectors representing effects of roads and subsidies formed approximately a 90º angle, indicating that their effects on diet composition were independent of one another. The lengths of vectors were proportional to the strength of their association with diet composition. CCA1 was more strongly associated with distance to subsidies, with nests that were distant from subsidies receiving positive CCA1 scores. CCA2 was more strongly associated with distance to roads, with points farthest from roads receiving the largest CCA2 scores. Trash was found most commonly in nests both close to subsidies and far from roads. Nests close to both subsidies and roads had more birds and amphibians. Nests close to roads and far from subsidies had greater numbers of mammals and reptiles. Pellets from nests far from both roads and subsidies had greater amounts of plant material and more arthropods.

Raven diet composition was associated with variation in fledging success (Table 2). We assessed overall model significance by comparing it against a model with only number of chicks fledged and number of years of observation; the model was significant (deviance=7.56, df=2, \( P=0.02 \)). Pairs with more anthropogenically enhanced diets fledged more chicks; CCA2 was positively associated with fledging success, such that a high incidence of trash in the diet was associated with high fledging success. The effect of diet on fledging was fairly large; the difference in maximum and minimum
predicted number of fledged chicks from this model (predicted for one year of observation) was 1.58 chicks (observed number of fledglings ranged from 0–5).

Although there was substantial variation in diet diversity among nests (Figure 3), diet diversity was not related to distance to roads \( (r^2=0.008, \text{df}=1.96, f=0.81, P=0.37) \) or to point subsidies \( (r^2=0.029, \text{df}=1.96, f=2.92, P=0.09; \text{Figure 4 a, b}) \).

**DISCUSSION**

Ravens are highly flexible, generalist predators and scavengers (Boarman and Heinrich 1999). The components of raven diets vary geographically (summarized in Nogales and Hernandez 1997) and seasonally (Harlow et al. 1975, Ewins et al. 1986, Marquiss and Booth 1986, Engel and Young 1989), as well as by habitat within a geographic region (Marquiss and Booth 1986, Stiehl and Trautwein 1991). Although diet studies do not always quantify relative availability of food items consumed by ravens, the strong influence of geographic area and habitat among studies supports the contention that ravens forage opportunistically.

Because ravens are opportunistic, we interpreted patterns of variation in diet composition in the EAFB ravens as patterns of variation in food availability. This type of inference is limited by the known biases in pellet-based diet studies (Marti 1987, Redpath et al. 2001). Since pellets contain indigestible components of food such as bone, feather, and fur, the highly digestible foods such as muscle tissue are underestimated by pellet analysis (Marti 1987). Additionally, small mammals tend to be overestimated and birds underestimated in pellets relative to direct observation of foraging predatory birds (Redpath et al. 2001). We lacked alternative methods for comparison, but we did not find evidence in our pellets of scavenging on large animals, even though we have observed this behavior in this population. However, the set of foods detected in the pellets included a variety of vertebrate taxa, trash, and plant materials, a
range sufficiently broad to reflect effects of human developments. Thus, even in light of suspected biases in pellet analyses, we considered it appropriate to use our data to evaluate the effects of human developments on the relative composition of food items that can be detected in raven pellets.

Even within the same environment, ravens show great variation in diet, and our results indicated several differences from the diets of ravens in the East Mojave Desert (Camp et al. 1993). Animals were the most common food items, but plant materials were found at 46.9% of nests, and in 18.1% of all pellets, compared with 92% of pellets in the East Mojave. We found arthropods in 37.4% of pellets (compared with 85.8% in the East Mojave) and at 81.6% of nests. We did not attempt to distinguish arthropods to genus or species because arthropod identification to the species level is intrinsically more difficult and because arthropod remains in pellets tended to be small, fragmented pieces (Marti 1987). Insects were the most common arthropods in our pellets. Camp et al.’s (1993) study area was less developed than ours (85% of their nests were >5 km from roads compared with our 2%, and only 5% of their nests were within 10 km of landfills compared with our 67%); this difference in degree of development may help explain observed differences in raven diets between the East and West Mojave. Surprisingly, Camp et al. (1993) found a similar frequency of trash in their ravens’ diets: we found trash at 57.1% of nests, and in 24.2% of pellets, which was very similar to the 21.7% trash in pellets in the East Mojave. Whether the trash found in East Mojave raven pellets was distributed among a smaller number of nests is not known.

The diet composition of ravens on our study area was affected by their proximity to human developments, and fledging success was affected by diet composition. These results are consistent with the hypothesis that one of the ways human developments in the West Mojave are affecting raven populations is by providing food subsidies to breeding birds. We have found that ravens nesting near roads and point subsidies have the greatest fledging success (Kristan 2001). From the current study, we
see that ravens nesting near point subsidies that were known sources of food and water had a higher incidence of trash in their pellets, particularly when they also nested far from roads. Sources of trash on the study area included landfills and housing developments, and some of the access roads to these were not considered roads for the purposes of this analysis (i.e., they were unpaved, low-speed, or low traffic-volume roads). Although the large flocks of ravens frequently found at conspicuous sources of trash are generally composed of juveniles and nonbreeding adults (Boarman and Heinrich 1999), trash is a common dietary component of breeding ravens as well (Ewins et al. 1986). Trash has been found at nests up to 14 km away from the nearest source (Restani et al. 2001), and we found trash at nests up to 6 km from roads or point subsidies. Amphibians were also more prevalent near point subsidies, a finding that is an artifact of Piute Ponds, an artificial wetland, being classified for our analyses as an anthropogenic point source. Ravens nesting near roads (i.e., negative CCA2 values) had a variety of reptiles, mammals, and birds in their pellets. However, this variety of vertebrates in collections near roads did not result in greater diversity within nests and instead represented differences in diet composition among nests. Variable diets of ravens near roads have been noted in other studies (Marquiss and Booth 1986). The increased incidence of small vertebrates in pellets near roads is consistent with the hypothesis that roads primarily subsidize raven reproduction via road-killed carrion because these animals commonly are killed on roads (Forman and Alexander 1998, Caro et al. 2000).

We also hypothesized that ravens nesting in the most remote parts of the study areas, far from both roads and point subsidies, would have the greatest need to hunt, and would therefore also have a high incidence of small vertebrates. Although we found a low incidence of trash at remote nests, these pellets had an increased incidence of plant materials and arthropods rather than small vertebrates. This pattern was observed by Nogales and Hernandes (1994) in ravens on the Canary Islands, which eat a high proportion of plants on islands that lack sources of carrion or trash. Furthermore, invertebrates were
eaten extensively only when vertebrates were rare (Nogales and Hernandes 1997). Ravens nesting far from human developments, and with diets containing relatively little human-provided foods, reproduced poorly in the Mojave Desert.

It was possible that hunting live vertebrate prey was substantially less successful for ravens in remote areas than scavenging road-killed carrion was for ravens nesting near roads, which was then reflected as a high incidence of vertebrates near roads. Because of this, there is extensive overlap in diet composition among nests, and the patterns of change in diet composition reflect changes in relative frequencies of food items rather than complete substitutions of food items. For example, >1 pellets from the 16 most remote nests contained mammals, and 5 of 16 contained birds, but the proportion of pellets with birds or mammals was lower in remote nests than in nests near roads or near subsidies. The reduced incidence of human-associated foods from pellets in remote areas suggested that the food consumed came from the area near the nests. If Nogales and Hernandez (1994) are correct that plants and invertebrates are eaten primarily when carrion and small vertebrates are not available, it appears the East Mojave and remote parts of the West Mojave represent poor foraging habitat for breeding ravens.

Although both human subsidies and roads represent sources of food subsidies for ravens, they provide different kinds of foods. Interestingly, while roads and point subsidies increase raven fledging success, ravens do not nest preferentially near roads (Kristan 2001). This may reflect differences in the persistence and predictability of the food subsidies provided by these different anthropogenic developments. Trash is available at the same places throughout the year at landfills and housing developments. Road kill is affected by the ecology of the adjacent animal communities and will therefore be seasonably available, peaking during the breeding season or during prey dispersal (Forman and Alexander 1998). Additionally, locations of road kills are variable, and road-killed carrion may be an intrinsically less predictable food source than are the resources at landfills and housing areas. Thus, it
is possible for carrion to increase raven fledging success, even if it is not sufficiently predictable to influence nest-site choice.

MANAGEMENT IMPLICATIONS

Diets with a greater incidence of human-provided foods were associated with increased fledging success for ravens, and these effects decreased with distance from developments. Such a large population of ravens as currently exists in the West Mojave Desert probably could not be sustainable if fewer anthropogenic resource subsidies were available. Reducing the availability of food subsidies to ravens may reduce predation pressure on the threatened desert tortoise population, thereby aiding in its recovery. Covering trash in receptacles and thorough and regular covering of garbage at landfills may be effective methods for reducing food subsidies from refuse dumping. Reducing food subsidies provided by roads would require actions that prevent road kill, such as fencing (Boarman and Sazaki 1996). In the lightly populated parts of the Mojave, small, spatially restricted towns should also have spatially restricted effects, but effects of roads crossing undeveloped areas are distributed over large areas. Current road-fencing projects aimed at reducing wildlife mortality could have the associated benefit of reducing food subsidies to ravens.

ACKNOWLEDGMENTS

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LITERATURE CITED


Nogales, M., and E. C. Hernandez. 1994. Interinsular variations in the spring and summer diet of the


Table 1. Contents of pellets collected from common raven nests in the west Mojave Desert.

<table>
<thead>
<tr>
<th>Class</th>
<th>Order</th>
<th>Contents</th>
<th>Num. pellets(^a)</th>
<th>% of pellets(^a)</th>
<th>Num. nests(^b)</th>
<th>% of nests(^b)</th>
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<tr>
<td>Amphibia</td>
<td></td>
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<td>Anura</td>
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<sup>a</sup> The number of pellets that contained one or more of the item.

<sup>b</sup> The number of nests that contained one or more of the item.

<sup>c</sup> Italics represent the broadest categories that could be consistently identified. Bold denotes categories used for ordination analyses.

<sup>d</sup> Insects and isopods were classified as “arthropods” for ordination analyses.
Table 2. The relationship between numbers of chicks fledged from a nest and the diet composition estimated from pellets found at the nest.

|                  | Estimate | Std. Error | z value | Pr(>|z|) |
|------------------|----------|------------|---------|----------|
| Intercept        | -1.04    | 0.28       | -3.76   | < 0.01   |
| CCA1\(^a\)      | -0.04    | 0.04       | -1.17   | 0.24     |
| CCA2\(^a\)      | 0.05     | 0.02       | 2.53    | 0.01     |
| Years observed\(^b\) | 1.12     | 0.17       | 6.54    | < 0.01   |

\(^a\)The scores from the first two axes of a canonical correspondence analysis of diet composition, which are numerical representations of variation in diet.

\(^b\)The number of years (one or two) that a nest was used in this study.
Figure 1. Map of raven nests observed in the West Mojave Desert, spring 1999 and 2000. Lines represent major roads, numbers are sources of human food subsidies, small dots are the locations of raven nests, and crossed circles are nests from which pellets were collected. 1 = Mojave, 2 = North Edwards, 3 = Mojave sewage pond, 4 = Mojave landfill, 5 = Edwards Air Force Base landfill, 6 = Edwards Air Force Base housing, 7 = Rosamond, 8 = Pond, 9 = Piute Ponds wetland.
Figure 2. Partial canonical correspondence analysis biplot that positions nests (open circles) relative to axes of change in diet (CCA 1 and CCA2), controlling for the number of pellets from each nest. Food items are positioned near the nests in which they were most common. The variables that constrain the ordination are represented by vectors from the origin of the plot. The length of the vector is proportional to the magnitude of the effect of that variable on the CCA axes, and the direction of the vector indicates the direction of the relationship between the variable and the CCA scores. Data are from raven nests observed in the West Mojave Desert, spring 1999 and 2000.
Figure 3. Histogram of the Shannon diversity index residuals for collections of pellets at each raven nest, corrected for differences in the number of pellets among nests. Collections are from raven nests in the West Mojave Desert, spring 1999 and 2000.
Figure 4. Shannon diversity index residuals relative to distance (m) from roads (a) and distance (m) to point sources of resource subsidies (b). Data are from pellet collections made at common raven nests in the West Mojave Desert, spring 1999 and 2000.
Chapter 3: Anthropogenically enhanced reproductive success in West Mojave ravens

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EXECUTIVE SUMMARY OF CHAPTER

The fact that ravens benefit directly from food and water near human developments is well accepted. However, physical alterations of the desert habitat by humans provide an important though less obvious benefit. For example, ravens routinely use artificial structures as nest substrate. The relative effects of different kinds of subsidies on raven populations are not known, yet have important implications for managing raven populations in the Mojave. In this study, we evaluate how reproductive performance and nest site distribution are related to proximity to anthropogenic developments.

Specifically, our research attempted to answer the following three questions: 1. What are the relative influences of proximity to anthropogenic resources and of variation in natural habitat variables on raven reproduction?; 2. Do ravens nest disproportionately near sources of anthropogenic resources?; and 3. Are the effects of human developments on fledging primarily direct, such as through food or water subsidy, or indirect, through physical changes in the desert habitats?

The study took place on the western half of EAFB and adjacent lands. We attempted to find all raven nests in the study area by scanning suitable substrate while driving through the area, between March and June of 1996 through 2000. We made several reproductive measures during weekly visits to each nest, representing different aspects of breeding biology: nest site occupancy, initiation of breeding, clutch size, clutch initiation date, fledging date, and number of chicks fledged. We then measured selection of nest sites relative to roads and point subsidies by comparing the spatial distribution of raven nests to randomly located points in raven nesting habitat. In addition, we examined the relative independent effects of groups of natural and anthropogenic variables using generalized linear models and explored whether anthropogenic effects on reproduction were expressed.
We found that ravens selected areas near point subsidies to build nests, but that they did not selectively build nests near roads. The lack of nests near roads was in contrast to other studies, a fact that may be explained by the abundance of Joshua trees and the raven’s apparent preference to build nests in this substrate when it was available. In general, ravens were not always responsive to anthropogenic cues in their investment decisions (choices about where to nest), even though anthropogenic variables had the greatest impact on the performance consequences of these decisions. For example, distance from major roads had a greater effect on fledging than either distance from point subsidies or the degree of urbanization in several years, but did not affect investment. Roads probably increase raven reproductive success by providing road-killed carrion, however carrion may be less consistently present when ravens are selecting nest sites than are the food and water found at point subsidies, and may thus be less useful as a nest site selection cue. We also found that direct effects of anthropogenic factors were more important than indirect effects in each year of the study.

Management Implications

Ravens can persist and increase in inhospitable environments when human resources are available. Anthropogenic developments enhance raven reproductive success, and probably allow rapid raven population growth in the west Mojave. Limiting raven access to resources near human developments at EAFB may help reduce their populations and, in turn, the predation pressure they exert on prey, especially the threatened desert tortoise.

In addition, it is important to note that the effects of anthropogenic resources on raven populations and desert tortoises are not limited to the immediate areas surrounding human developments. Many occupied raven nests were found far from roads and human developments, presumably because territories close to subsidies were occupied. Breeding raven pairs in undeveloped areas are a concern.
because these areas are relatively undisturbed and therefore may be high-quality desert tortoise habitat. As human developments in the region promote the spread and persistence of ravens in areas that are marginal breeding habitat, human activities can indirectly affect sensitive prey far from the actual developments. Consequently, efforts to manage ravens to promote tortoise recovery should also attempt to control ravens in remote areas.
ABSTRACT

Anthropogenically subsidized predators are expected to be able to continue to impact prey at low population densities. Common Ravens (Corvus corax) have increased in number over the last 3-4 decades in the Mojave Desert, where they are considered human commensals. Between 1996-2000, we examined: a) how anthropogenic features associated with urbanization (i.e., roads, or food and water subsidies from urban areas) affected raven reproduction, b) whether ravens nest disproportionately near human developments, and c) whether anthropogenic developments represented primarily direct subsidies to ravens, or indirectly benefited ravens by providing high-quality nesting habitat. Both roads and point sources of subsidies (such as towns, landfills, ponds) increased fledging success, but ravens only disproportionately selected nests near point subsidies. Presence of the previous year's nest in a territory at the beginning of the breeding season (a natural, environmental cue) affected whether ravens initiated breeding, and anthropogenic factors affected the timing of initiation. The direct effects of anthropogenic factors on fledging success were more consistent over time than indirect effects via changes in natural factors, and direct effects were usually stronger within a year; consequently, it is likely that anthropogenic factors primarily affect raven reproduction through direct resource subsidies. Ravens were found throughout the study area up to 8-10 km from developments, and thus the restricted spatial distribution of roads and point subsidies on the study area did not restrict the distribution of breeding ravens to areas near anthropogenic sites. Ravens nesting in undeveloped areas far from resource subsidies would need to subsist on prey found near the nest, and the impacts of commensal populations of ravens on sensitive vertebrates can thus be considered indirect effects of anthropogenic development that extends far from roads and beyond city limits.

Key words: Common Raven, Corvus corax, subsidized predator, urbanization
INTRODUCTION

Subsidized predators can have disproportionate impacts on prey, since their numbers are not limited by prey numbers (Polis et al. 1997, Sinclair et al. 1998). Hunting by domesticated predators, such as house cats (*Felis domesticus*), is a well-known example of predation mortality associated with the presence of humans that extends beyond developed areas and into adjacent undeveloped habitats (Churcher and Lawton 1987, Coleman and Temple 1993, Crooks and Soulé 1999). A similar case can be made that prey mortality from wild predators which are maintained at artificially large numbers by human-provided subsidies are also an indirect impact of human developments. There are several documented cases of increased predation in anthropogenically fragmented habitats, involving opportunistic generalist species ranging from coyote (*Canis latrans*) and raccoon (*Procyon lotor*, Crooks and Soulé 1999), to avian nest predators such as jays and magpies (Andrén and Angelstram 1988, Andrén 1992). Although the dependence of domestic predators on humans is clear, it is generally less clear whether wild predator populations are increased by human activities, or are simply redistributed by the presence of readily available resources.

Although Common ravens (*Corvus corax*) are known primarily as scavengers, they are also capable hunters that prey on a variety of small animals, including the threatened desert tortoise (*Gopherus agassizii*) in the Mojave Desert (Boarman, 1993, Boarman and Heinrich 1999). Ravens have increased in number by up to 1500% over the last several decades in the Mojave (Boarman and Berry 1995, Sauer et. al. 2000), and observations that implicate expanding human development as the cause of raven population growth include concomitant increases in raven and human populations (Boarman 1993), and that ravens feed in large numbers on human refuse and breed in urban areas (Knight et al. 1993, Boarman and Heinrich 1999). The strong association of ravens with, and apparent reliance on, human resources in the Mojave make ravens behave as a human commensal in this habitat (Knight et al.
Although it appears obvious that anthropogenic developments subsidize raven populations, the manner in which 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 where ravens are found in association with anthropogenic features, such as roads (Austin 1971, Knight and Kawashimi 1993) and urban areas (Knight et al. 1993). Human developments provide food and water, both of which could limit raven population growth in a desert environment, and continued expansion of ravens throughout the Mojave may depend both on the pattern of urbanization and on the extent to which the Mojave supports raven populations in the absence of these subsidies. However, urbanization is a complex phenomenon, and direct food and water subsidy represents only one possible effect of human development. Ravens also make extensive use of physical alterations of the desert habitat, such as extensively using artificial structures as nest platforms (Austin 1971, Knight and Kawashima 1993, Knight et al. 1993, 1995, White and Tanner-White 1988). If artificial platforms provide better protection from predators, shade for nestlings, or in some way represent better nesting substrate than the available natural alternatives, they may also promote population growth. The relative effects of these different kinds of human modification to the desert on raven populations is not known, yet has important implications for managing raven populations in the Mojave.

We address these questions by evaluating how reproductive performance and nest site distribution is related to proximity to anthropogenic developments that are known food or water sources. We further distinguished between effects of urbanization that represented manipulation of “natural” cues that are potentially relevant to ravens selecting nest sites or breeding territories, and the “anthropogenic” cues that are novel features of human activities, which allowed us to evaluate the relative importance of
direct effects of urbanization, and of indirect effects via physical changes in the desert habitat.

METHODS

Study Area

The primary study area centered on the western half of Edward Air Force Base (EAFB) in the west Mojave Desert (Figure 1). Vegetation on the study area primarily consisted of creosotebush (Larrea tridentata) and saltbush (Atriplex spp.) scrub, both of which often formed a woodland with Joshua tree (Yucca brevifolia). Creosotebush is larger than saltbush, standing 1.5-3 m and < 1 m in height respectively, and individual creosotebush plants were more widely spaced. Joshua tree is an agave with the growth form of a tree, averages 6-9 m in height, and is used extensively for nesting by ravens and other bird species.

Several 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, Kristan et al., in prep.), 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).

The military lands outside the cantonment at EAFB are used primarily for military aircraft training, with little disturbance to the vegetation. 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. Like Rosamond and Mojave, the housing area within EAFB (pop. 7,423) consisted of single-family homes, apartment
complexes, and commercial developments (e.g. restaurants, grocery stores, etc.). Solid waste disposal sites (landfills) were present near EAFB housing and near the town of Mojave.

**Research Questions**

Because adult ravens spend most of their time, and do most of their foraging, within 400 m of their nests during breeding (Sherman 1992, Boarman and Heinrich 1999) nestling survival was expected to be strongly influenced by nest site characteristics. Raven nests occurred throughout the study area, thus the spatial extent of effects of anthropogenic subsidies on raven populations should be easiest to detect during the breeding season, since spatial variation in reproductive success should reflect the local habitat quality. Additionally, since urbanization is a complex process that alters many aspects of the environment, the effects of anthropogenic resources could be direct (e.g. food and water subsidies), or indirect (e.g. altering natural variables that ravens use when choosing territories).

To address the interacting effects of natural and anthropogenic variables on reproductive investments (i.e., choices about where to nest) and performance we posed several specific questions:

1. What are the relative independent influences of proximity to anthropogenic sources of food and water and of variation in natural habitat variables on raven reproduction?
2. Do ravens nest disproportionately near sources of anthropogenic resources?
3. Are the effects of human developments on fledging primarily direct, such as through food or water subsidy, or indirect, through physical changes in the desert habitats?

**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 were conspicuous, and most nests were visible from several hundred meters. We attempted to find all raven nests in the study area by scanning all suitable platforms while driving throughout the area, between March and June of 1996 through 2000. The study area had an extensive network of primitive roads and trails, and it was possible to travel within 0.5 - 1 km of all points within the area containing potential nesting habitat. When nests were found they were assigned unique identifiers and their positions were recorded to within 10 m using global positioning system (GPS) units. New breeding territories were discovered each year, and thus the number of nests under observation increased with time. In 1999 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 most of the territories on the study area (we believe 90% or more, based on the distribution of nests and the territorial spacing of ravens), and that we had not under-sampled any portion of the study area.

We made several reproductive measures during weekly visits to each nest, representing different aspects of breeding biology: nest site occupancy, initiation of breeding, clutch size, clutch initiation date, and number of chicks fledged. Occupancy (the presence of one or more adult ravens at the nest site during the breeding season), initiation (including any breeding activity from laying on), and fledging success (whether at least one chick fledged from the nest) could be observed from the ground without access to the nest bowls, as could the number of chicks fledged in most cases. Clutch size was only recorded from nests with bowls that we could observe, either by climbing or by using a mirror attached to a telescoping pole. We recorded fledging date and clutch initiation date to the nearest week. When nests were found before clutches were completed we estimated initiation date by subtracting the number of eggs present when the 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 estimated
initiation date based on the date of other events, such as hatching or fledging (Boarman and Heinrich 1999). Except in cases where nests fail early in the cycle, ravens make only one breeding attempt per year (Boarman and Heinrich 1999), and thus all known nests were checked weekly until it became too late for a pair to breed successfully (mid-May). Nests without breeding activity by mid-May were checked once more in early June to confirm that no late nesting attempts were made. Nests of pairs that initiated breeding were checked weekly until the fate of the breeding attempt was known.

_Natural variables_

Variables to which ravens might respond in the absence of anthropogenic effects were considered "natural" variables. Because we wanted to evaluate how human development affected habitat, natural variables included non-natural elements that represented anthropogenic manipulations of a natural cue. For example, the suitability of a nesting substrate is expected to be relevant to nest site selection in any habitat, which made substrate a natural variable. Anthropogenic substrates, such as poles and buildings, were thus considered a manipulation of a natural variable, which made anthropogenic addition of nesting substrate a candidate for an indirect effect of human development. In addition to nest substrate we recorded the species of the dominant shrub (creosote bush, saltbush, both species, or neither) in the immediate vicinity of the nest, with a lack of native shrub cover typical of nests within housing developments. Substrate and shrub cover were unchanged during the duration of the study for each nest, and were recorded once. Nests in artificial platforms potentially had different persistence rates than those in natural substrates, and we searched for nests early enough in 1999 and 2000 to record whether the previous year's nest was present at the beginning of the breeding season. We also recorded the presence of standing water, both artificial and natural, within sight of the nest at the time when breeding was initiated in 2000.
Anthropogenic variables

We differentiated between three kinds of anthropogenic developments: point subsidies, roads, and local levels of urbanization (called “urbanization” from now on). Point subsidies were spatially restricted, permanent developments that could be represented by a single point (such as a landfill or pond) or polygon (such as housing areas) on a map, and that were sources of food or water. We confined our analysis of roads to the highways and major paved roads ringing the core study area, but omitted the lightly-used dirt roads covering much of the scrub habitat. Distances of nest sites from point subsidies and roads were measured using a GIS. For the categorical 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). Ravens in the Mojave are within 400 m of their nests 90% of the time (Sherman 1993), so we scored this variable within a 400 m radius circle centered on the nest to represent the raven territory. The “urbanization” variable allowed us to include the effects of unmapped features such as single isolated houses that were embedded within an otherwise natural surrounding.

Statistical Analyses

Spatial distribution of nests

We measured selection of nest sites relative to roads and point subsidies by comparing the spatial distribution of raven nests to randomly located points in raven nesting habitat. We generated 5000 random points within the study area, then omitted points that fell in areas without nesting habitat, such as dry lake beds, which left 4345 points. Distances to roads and point subsidies from raven nests and random points were calculated from GIS maps.
We assessed both the numerical abundance of nests relative to distance from anthropogenic sites, and selection of areas near anthropogenic sites, with selection defined as disproportionate use of particular distances (Manley et al. 1993). We measured selection by calculating a selection ratio (log[proportion used/proportion available]), using kernel density estimates (Bowman and Azzalini 1997) to measure proportional use (nest sites) and proportional availability (random sites) as a function of distance from roads and point subsidies. The log of the ratio of these density estimates is symmetrical around zero, with zero indicating use in proportion to availability, and thus no selection.

**Independent effects of natural and anthropogenic factors on reproduction**

We related natural and anthropogenic factors to occupancy, initiation of breeding, clutch size, and numbers of chicks fledged within a year. We analyzed performance over time using the number of years that nests were occupied or produced one or more chicks, but because new nests were discovered each year we included the number of years that the nest was observed as a covariate in this analysis. This had the disadvantage that the strong relationship between numbers of years either occupied or successful and numbers of years of observation guaranteed a significant overall model. We therefore analyzed these variables 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 numbers of successful years over all five years, but analyzed occupancy within a year beginning with 1997, since most nests in the first year of the study (1996) were found occupied and thus presented very little variation to explain. We only analyzed initiation in 1999 and 2000, because early nest checking in these years increased the reliability of this measurement.

We examined the relative independent effects of groups of natural and anthropogenic variables using generalized linear models. We used logistic regression to model binary variables (initiation of
breeding, occupancy), and used Poisson regression to model count variables (clutch size, number of chicks fledged, numbers of years successful, number of years occupied). We first evaluated whether a significant relationship existed between a reproductive variable and the full set of natural and anthropogenic variables, and then the relative independent contribution of the groups of natural and anthropogenic variables was assessed by comparing the fit of models that included all of the variables to ones that omitted one of the groups of variables. Significant independent effects of a group were tested by calculating the decreases in model fit when a group of variables was omitted, which was then tested using likelihood ratio tests. The relative importance of each variable from a significant group were further analyzed with a regression model including only the significant group.

**Indirect effects of anthropogenic variables on fledging via changes in natural variables**

An indirect effect of urbanization via changes in natural variables would be contained in the joint, correlated effect of anthropogenic and natural variables, which was not measured by the previous analysis. To address this, we used a procedure analogous to partitioning the spatial component of ecological variation (Borcard et al. 1992), and that has been used to estimate the relative effects of current and past land uses on shrubsteppe birds (Knick and Rotenberry 2000). We partitioned the effects of anthropogenic and natural variables on the number of chicks fledged and numbers of successful years into components that were direct effects of the set of anthropogenic variables (depicted as the shaded region A in Figure 2A), direct effects of the set of natural variables (Figure 2A, shaded region C), and indirect effects of anthropogenic variables via changes in natural variables (Figure 2A, shaded region B). The area of all of the shaded regions in Figure 2A (i.e. A+B+C) represents the model deviance from a model including both natural and anthropogenic groups of variables. The region A+B represents the model deviance from a model including only anthropogenic variables, and the region B+C represents the
model deviance from a model including only natural variables. Region A then was calculated by subtracting the model deviance for natural variables alone from the model deviance with all variables. Similarly, region C was calculated by subtracting the model deviance for anthropogenic variables from the model deviance with all the variables. Region B was calculated by subtracting the model deviance with all of the variables from the sum of the model deviances with only anthropogenic or with only natural variables. Region B represents the portion of the effects of natural and anthropogenic variables that are correlated, and since anthropogenic variables could alter natural variables, but not the converse, we considered this correlated variation to be primarily an indirect effect of anthropogenic variables on reproduction. Chance correlations between anthropogenic and natural variables could also contribute to this component, such as would occur if creosote bush was closer to roads than saltbush. These effects were assumed to be small compared to the large changes imposed by urbanizing native habitats, but where possible we checked this assumption by looking for associations between the natural elements of natural variables and the anthropogenic variables.

We explored whether anthropogenic effects on reproduction were expressed by affecting the timing of breeding by partitioning the effects of initiation date on fledging into components that were associated with anthropogenic and natural variables (Figure 2B, shaded regions D, F, and G), and a component that was independent of anthropogenic and natural factors (Figure 2B, shaded region B).

RESULTS

Nest site selection

Raven nests were most common near point subsidies (Figure 3a) and near roads (Figure 3b), and declined in abundance with increasing distance from both. However, habitat near subsidies was relatively uncommon compared with habitat near roads, leading to differences in selection of these two
features. Ravens selected nest sites within 2 km of point subsidies, and did not select areas that were 
over 2 km from point subsidies (Figure 4). In contrast, ravens selected nests that were over 2 km from 
routes and did not select areas that were within 2 km of roads (Figure 4).

**Independent effects of anthropogenic and natural factors on reproduction**

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 successful years 
(Table 1). Natural factors were also significant in 1997 and 2000. Numbers of chicks fledged declined 
with increasing distance to roads in every year but 1998, and declined with increasing distance to point 
subsidies in 1998 (Table 2). The number of years successful declined with distance to both roads and 
point subsidies (Table 2). Degree of urbanization had significant, independent effects on the number of 
chicks fledged only in 2000 (chicks fledged per nest: urban = 1.92 (n = 13), mixed = 1.67 (n = 9), 
natural = 0.81 (n = 123)).

In the years that natural variables affected fledging success, shrub cover and substrate were both 
significant in 1997, but only shrub cover was significant in 2000 (Table 3). In 1997, the mean number of 
chicks fledged was 1.00 (n = 2) for nests in buildings, 0.00 (n = 2) for cliff nests, 1.35 (n = 45) for 
Joshua tree nests, 0.67 (n = 45) for pole nests, and 1.13 (n = 15) for tree nests. In 1997, the mean number 
of chicks fledged was 0.57 (n = 28) for nests in creosote bush, 1.17 (n = 48) for nests in saltbush, 1.35 (n 
= 14) for nests with both dominant shrub species, and 1.00 (n = 19) for nests with neither shrub species. 
In 2000 the mean number of chicks fledged was 0.42 (n = 24) in creosote bush, 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.

Nest site occupancy models were significant in 1997, 1998 and 2000 (Table 4). Natural variables
had greater effects on occupancy in 1998 and 2000, and anthropogenic variables had a greater effect 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 presence of the previous year's nest affected occupancy (Table 5). This variable was not recorded prior to 1999, and 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 (p = 0.057 and 0.075, respectively), and both had greater effects than urbanization (p = 0.96), but none had significant effects independent of the others.

Initiation of breeding in occupied territories was associated with natural variables in both 1999 and 2000, but not with anthropogenic variables (Table 6). In both years the presence of the previous year's nest at the beginning of the breeding season significantly increased the probability of initiation (Table 7), with initiation increasing from 28.9% to 71.0% in 1999 and from 1.4% to 62.2% in 2000 when nests were present. Nest substrate was also significantly associated with initiation in 1999, with initiation occurring in 75% of nests in buildings (n=4), all nests in cliffs (n=4), 56.8% of nests in Joshua trees (n=125), 57.5% of nests in poles (n=80) and 57.6% of nests in 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), with the larger classes (Joshua trees, poles, and trees) exhibiting similar initiation rates. The previous year's nest was present in 75% of building nests, 100% of cliff nests, 78% of Joshua tree nests, 61% of pole nests, and 69% of tree nests (deviance = 17.36, df = 4, p = 0.001).

Clutch size was unaffected by either natural or anthropogenic factors in all years (range of p – values: 0.13-0.86).
Indirect effects of anthropogenic variables on fledging via changes in natural variables

The amount of direct and indirect effect of anthropogenic variables on fledging success varied among years, but the direct effect was greater than the indirect effect within every year (Table 8). The direct effects of natural factors was more variable, and exceeded the direct effects of anthropogenic factors in 1997 and 2000.

Fledging success declined with later laying 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 (Table 9). In 1999 nests that were near roads initiated earlier, and in 2000 nests near subsidies initiated earlier. Additionally in 2000, nests in urbanized habitats were initiated earlier than nests in mixed or natural habitats. Initiation date accounted for 59.4% of the combined effect of anthropogenic factors, natural factors, and initiation date on fledging success in 1999, and 41.6% of their combined effect in 2000. The indirect effect of anthropogenic factors via initiation date was 11.8%, all of which was also associated with natural factors, whereas 8.3% was attributable to anthropogenic factors in 2000, of which 4.6% was associated only with anthropogenic factors and 3.7% was associated with both anthropogenic and natural factors (Table 10). Small negative estimates of variance components occurred in this analysis, and were set to zero.

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). Nests with different shrub cover types had different distances to roads (F = 2.70, df = 3, 350, p = 0.045), and to point subsidies (F = 9.80, df = 3, 350, p < 0.0001). This was because urban nests (n = 35) did not have either dominant shrub, and were closer to roads and subsidies
than were nests with either dominant shrub type. Distances did not differ between creosote bush and saltbush.

Shrub cover varied with degree of urbanization, since nests within urban areas had no native shrub cover, and all shrub classes (saltbush, creosote, and both) occurred in natural habitat. 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), as well as 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

Nest site selection

Ravens in the Mojave are typically associated with urban and agricultural areas (Knight and Kawashima 1993), and roads (Knight et al. 1993). Likewise, raven nests on our study area were most common near roads and point subsidies (which included urban areas, Figure 3a and 3b), with 59% of nests falling within 2 km of a road and 38% falling within 2 km of a point subsidy. However, we found that ravens selected nests within 2 km of point subsidies (Figure 4), and over 2 km from roads (Figure 4). In both cases this means that the majority of individuals occupied habitat that was not selected at a population level. Raven populations were dense in the relatively small urbanized portions of our study area, such that available territories may have been limited, forcing individuals to nest in marginal habitats. In contrast, ravens did not select nests near roads in our study, in spite of the positive effects of roads on fledging success. This result contrasts with populations in Idaho, Nevada, and the eastern Mojave that overwhelmingly used artificial platforms along roads and power lines (White and Tanner-White 1988, Steenhof et al. 1993, Knight et al. 1995). Although the roads on our study area did have
artificial platforms associated with them, we believe the difference in our results is due to the large proportion of nests we found in Joshua trees. Joshua trees were common throughout the study area, and nest sites appear to have been sufficiently plentiful that artificial platforms did not concentrate ravens at roadsides.

**Independent effects of anthropogenic and natural factors on reproduction**

We observed different effects of anthropogenic and natural variables on different measures of reproduction, but this was unsurprising since different measures of reproduction represent different biological phenomena. Nest site choice, territory occupancy, and breeding initiation are all under facultative control, and reflect reproductive investment decisions. Clutch size is in principle also an investment decision, although it is not known if clutch size is fixed in this species (Boarman and Heinrich 1999). In contrast, events occurring after laying would be strongly constrained by the position and local characteristics of the territory, and the consequences to a pair of misjudging factors such as resource levels or predator risk would be inescapable for chicks in the nest. Consequently, the completion of a clutch marks the beginning of a decrease in a pair's control over the fate of their offspring, and fledging success represents a performance consequence of the investment decisions of a breeding pair.

Given this framework, ravens were not always responsive to anthropogenic cues in their investment decisions, even though anthropogenic variables had the greatest impact on the performance consequences of these decisions. For example, distance from major roads had a greater effect on fledging than either distance from point subsidies or the degree of urbanization in several years, but did not affect investment. Roads probably increase raven reproductive success by providing road-killed carrion, particularly roads passing through otherwise natural habitat (Austin 1971, Camp et al. 1993).
Road-killed carrion may be less consistently present when ravens are selecting nest sites than are the food and water found at point subsidies, and may thus be less useful as a nest site selection cue.

Territory occupancy 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). Natural variables had significant effects in 1998 and 2000, but different variables in this group 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 presence of a nest 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 because unoccupied territories could either represent a resident pair's choice to forgo breeding, a vacancy due to a mortality, or (in spite of the fact that we visited unoccupied nests repeatedly) a false negative. Thus, occupancy was potentially a mix of several different processes, each of which could be influenced differently by anthropogenic and natural variables.

Initiation of breeding was determined only for territories that were known to be occupied in a year, and was more likely than occupancy to consistently represent investment choices. 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 the relationship with breeding success was not known. We hypothesize that the nest may either act as a cue that stimulates breeding behavior, or that the presence of a usable nest may reduce the amount of energy required to prepare for egg laying. However, the presence of the previous year's nest did not affect fledging once breeding was initiated.
Indirect effects of anthropogenic variables on fledging via changes in natural variables

We partitioned fledging success into components that represented direct effects of anthropogenic or natural variables, and the correlated effect of the two. We interpreted direct anthropogenic effects as the effects of food subsidies for several reasons. First, by partialling out the effects of physical changes in the environment, we excluded a large number of possible alternative explanations for the effects of developments. Second, point subsidies include a heterogeneous collection of anthropogenic sites, including artificial water bodies, housing developments, and landfills, that were grouped together because they are known sources of food, and therefore consistent effects of point subsidies on fledging are likely to be due to this common characteristic. Finally, the diets of these ravens are affected by roads and point subsidies in predictable ways (Kristan et al., in prep.). Ravens that nested near roads but far from point subsidies had a greater incidence of (presumably road-killed) mammals and reptiles in their diets, and a lesser incidence of refuse, whereas ravens near both roads and point subsidies had a greater incidence of refuse (Kristan et al., in prep). In contrast, ravens nesting far from both roads and subsidies had a disproportionate amount of plant material in their diets, which is consistent with a limited access to carrion and human subsidies (Nogales and Hernandez 1994). Similarly, although the shared components of our variance partitioning could in principle be due to spurious correlations, the nature of the relationships between anthropogenic and natural variables suggests that the shared component represents an indirect effect of anthropogenic developments. By design, natural variables included large effects of anthropogenic modifications, and the measured associations between natural and anthropogenic variables show that these effects dominated the relationships between them. For example, shrubless territories were primarily found near roads or point subsidies, but the native shrub types (creosote bush and saltbush) did not differ in their distances to roads or point subsidies.

The direct effects of anthropogenic factors exceeded the indirect effects each year. Additionally,
although the direct effects of natural factors on fledging twice exceeded the direct effects of anthropogenic factors (1997 and 2000), they were less consistent among years. In both 1997 and 2000 nests in creosote bush scrub areas did poorly, fledging 0.57 and 0.42 chicks, respectively, compared with nests in saltbush scrub, which fledged 1.17 and 1.12 chicks, respectively. This parallel difference between habitats in 1997 and 2000 was not explained by differences in distance from roads or point subsidies, and accordingly the indirect effect of anthropogenic factors via natural factors was smallest in those years (Table 8). We hypothesize that the differences between creosote bush and saltbush nests are due to periodic differences in prey availability, but data on prey abundance and habitat-specific raven foraging behavior would be needed to confirm this. However, in years that this difference in fledging success is expressed, it overwhelms the indirect effects of anthropogenic variables via changes in natural variables.

One way that anthropogenic factors affected raven reproduction was through changes in clutch initiation date. Nests near roads or subsidies or in urban areas initiated earliest; 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, and approximately 20% of this effect was attributable to anthropogenic factors in both years (Table 5). Benefits of early breeding observed in ravens breeding in undeveloped habitats in Grand Teton National Park, Wyoming have been associated with mild winters, which either improved raven body condition or advanced the availability of food (Dunk et al. 1997). It is also possible that resource subsidies available at anthropogenic sites bring individuals into breeding condition sooner. Early breeding could have large benefits to ravens nesting in the Mojave Desert. The earliest clutches in 1999 and 2000 were laid in the first or second week of March, and the latest were laid in the last week of May. The earliest chicks fledged before the latest clutches were completed, and the expected 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 that can use shade and drink surface water can avoid temperature extremes and pant to cool themselves without risking dehydration. In contrast, nestlings in poorly shaded nests may overheat, and even in shaded nests they may dehydrate if their parents do not provide enough prey to meet the water requirements for 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.

Conservation Implications

Ravens can persist and increase in inhospitable environments when human resources are available (Restani et al. 2000). Anthropogenic developments enhance raven reproductive success, and probably allow rapid raven population growth in the west Mojave. Direct effects of roads and point sources of food and water subsidies are the most consistent, although indirect effects via changes in habitat are important in some years. Although the type of subsidy probably differs between different types of developments (e.g. roadkill, refuse from landfills), in both cases food subsidies are likely to be contributing to the increased reproductive success.

The spatial clustering of high-quality breeding habitat near roads and human developments did not restrict raven populations to developed areas, and we found many occupied raven nests far from roads and human developments in spite of the low probability of success. The birds that attempted to breed in remote areas would primarily forage in the habitat surrounding the nest (Sherman 1993), and successful pairs in undeveloped areas increase predation risk near the nests (Kristan and Boarman. 2003). Ravens are effective predators as well as opportunistic scavengers, and may impact sensitive
vertebrate species living within their breeding territories, notably the desert tortoise. As human developments in the region promote the spread and persistence of ravens in areas that are marginal breeding habitat, human activities can indirectly affect sensitive prey far from the actual developments.

ACKNOWLEDGMENTS

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LITERATURE CITED


Table 1. Independent effects of groups of anthropogenic and natural variables on numbers of chicks fledged within a year and on numbers of successful years.

<table>
<thead>
<tr>
<th></th>
<th>All</th>
<th>Anthropogenic</th>
<th>Natural</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dev.</td>
<td>DF</td>
<td>P</td>
</tr>
<tr>
<td>1996</td>
<td>38.5</td>
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</tr>
<tr>
<td>1997</td>
<td>39.6</td>
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<td>1998</td>
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<td>52.8</td>
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<tr>
<td>Yrs.</td>
<td>53.1</td>
<td>11</td>
<td>&lt;0.001</td>
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</table>

Technical variables: A = distance to roads, B = distance to point subsidies, C = urbanization, D = nest substrate, E = shrub cover, F = presence of previous year's nest, G = presence of standing water at initiation.
Table 2. Independent effects of individual anthropogenic variables on number of chicks fledged within a year and numbers of successful years.

<table>
<thead>
<tr>
<th>Year</th>
<th>Roads (df 1) Coeff.</th>
<th>Dev.</th>
<th>P</th>
<th>Subsidies (df 1) Coeff.</th>
<th>Dev.</th>
<th>P</th>
<th>Urbanization\textsuperscript{a} (df 2) Coeff.</th>
<th>Dev.</th>
<th>P</th>
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<td>-0.0002</td>
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<td>1.62, 1.52</td>
<td>3.67</td>
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<td>1997</td>
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<td>5.21</td>
<td>0.022</td>
<td>-0.0001</td>
<td>2.75</td>
<td>0.100</td>
<td>0.09, 0.42</td>
<td>2.41</td>
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<td>-0.0034</td>
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<td>&lt;0.001</td>
<td>-0.58, -0.24</td>
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<td>8.03</td>
<td>0.018</td>
</tr>
<tr>
<td>Years succ.</td>
<td>-0.0001</td>
<td>10.10</td>
<td>0.001</td>
<td>-0.0001</td>
<td>15.19</td>
<td>&lt;0.001</td>
<td>-0.38, -0.19</td>
<td>2.21</td>
<td>0.332</td>
</tr>
</tbody>
</table>

\textsuperscript{a} Urbanization is a dummy-coded categorical variable. The coefficients are for the “urban” and “natural” categories, with the coefficient for the “mixed” category set to zero.
Table 3. Independent effects of individual natural variables on number of chicks fledged.

<table>
<thead>
<tr>
<th>Year</th>
<th>Effect</th>
<th>Df</th>
<th>Dev.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>Substrate</td>
<td>4</td>
<td>15.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Shrub cover</td>
<td>3</td>
<td>9.0</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>2000</td>
<td>Substrate</td>
<td>3</td>
<td>0.6</td>
<td>0.891</td>
</tr>
<tr>
<td></td>
<td>Shrub cover</td>
<td>3</td>
<td>28.4</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Nest</td>
<td>1</td>
<td>2.0</td>
<td>0.162</td>
</tr>
<tr>
<td></td>
<td>Water at initiation</td>
<td>1</td>
<td>0.5</td>
<td>0.467</td>
</tr>
</tbody>
</table>
Table 4. Independent effects of groups of anthropogenic and natural variables on nest site occupancy.

<table>
<thead>
<tr>
<th>Year</th>
<th>All</th>
<th>Anthropogenic</th>
<th>Natural</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dev.</td>
<td>DF</td>
<td>P</td>
</tr>
<tr>
<td>1997</td>
<td>24.5</td>
<td>11</td>
<td>0.010</td>
</tr>
<tr>
<td>1998</td>
<td>46.3</td>
<td>11</td>
<td>&lt; 0.000</td>
</tr>
<tr>
<td>1999</td>
<td>17.3</td>
<td>12</td>
<td>0.140</td>
</tr>
<tr>
<td>2000</td>
<td>66.3</td>
<td>12</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Yrs. succ.</td>
<td>7.2</td>
<td>11</td>
<td>0.780</td>
</tr>
</tbody>
</table>

¹ Independent variables: A = distance to roads, B = distance to point subsidies, C = urbanization, D = nest substrate, E = shrub cover, F = presence of previous year's nest, G = presence of standing water at initiation.
Table 5. Independent effects of individual natural factors on occupancy of a nest site by one or more adult ravens.

<table>
<thead>
<tr>
<th>Year</th>
<th>Effect</th>
<th>DF</th>
<th>Deviance</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>Shrub cover</td>
<td>3</td>
<td>15.64</td>
<td>&lt; 0.000</td>
</tr>
<tr>
<td></td>
<td>Substrate</td>
<td>4</td>
<td>24.26</td>
<td>0.000</td>
</tr>
<tr>
<td>2000</td>
<td>Shrub cover</td>
<td>3</td>
<td>6.24</td>
<td>0.100</td>
</tr>
<tr>
<td></td>
<td>Substrate</td>
<td>4</td>
<td>6.41</td>
<td>0.170</td>
</tr>
<tr>
<td></td>
<td>Nest</td>
<td>1</td>
<td>51.97</td>
<td>&lt; 0.000</td>
</tr>
</tbody>
</table>
Table 6. Independent effects of groups of anthropogenic and natural variables on initiation of breeding.

<table>
<thead>
<tr>
<th>Year</th>
<th>All</th>
<th>Anthropogenic</th>
<th>Natural</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dev.</td>
<td>DF</td>
<td>P</td>
</tr>
<tr>
<td>1999</td>
<td>51.9</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2000</td>
<td>124.4</td>
<td>13</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

1 Independent variables: A = distance to roads, B = distance to point subsidies, C = urbanization, D = nest substrate, E = shrub cover, F = presence of previous year's nest, G = presence of standing water at initiation.
Table 7. Independent effects of individual natural variables on initiation of breeding.

<table>
<thead>
<tr>
<th>Year</th>
<th>Effect</th>
<th>DF</th>
<th>Deviance</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>Substrate</td>
<td>4</td>
<td>12.1</td>
<td>0.020</td>
</tr>
<tr>
<td></td>
<td>Shrub cover</td>
<td>3</td>
<td>7.56</td>
<td>0.060</td>
</tr>
<tr>
<td></td>
<td>Nest</td>
<td>1</td>
<td>35.32</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>2000</td>
<td>Substrate</td>
<td>4</td>
<td>8.26</td>
<td>0.080</td>
</tr>
<tr>
<td></td>
<td>Shrub cover</td>
<td>3</td>
<td>1.4</td>
<td>0.710</td>
</tr>
<tr>
<td></td>
<td>Nest</td>
<td>1</td>
<td>56.49</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td></td>
<td>Water at initiation</td>
<td>1</td>
<td>2.05</td>
<td>0.150</td>
</tr>
</tbody>
</table>
Table 8. The relative magnitude of direct effects of anthropogenic factors, natural factors, and indirect effects of anthropogenic factors on fledging success.

<table>
<thead>
<tr>
<th>Variable</th>
<th>All included</th>
<th>Anthropogenic direct</th>
<th>Natural direct</th>
<th>Anthropogenic indirect</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>38.5</td>
<td>22.2 (0.577)</td>
<td>11.6 (0.301)</td>
<td>4.6 (0.119)</td>
</tr>
<tr>
<td>1997</td>
<td>39.6</td>
<td>13.6 (0.343)</td>
<td>27.6 (0.697)</td>
<td>0.0 (0.000)</td>
</tr>
<tr>
<td>1998</td>
<td>22.7</td>
<td>12.8 (0.564)</td>
<td>2.9 (0.128)</td>
<td>7.0 (0.308)</td>
</tr>
<tr>
<td>1999</td>
<td>27.7</td>
<td>15.6 (0.563)</td>
<td>4.3 (0.155)</td>
<td>7.7 (0.278)</td>
</tr>
<tr>
<td>2000</td>
<td>52.8</td>
<td>17.8 (0.337)</td>
<td>34.0 (0.644)</td>
<td>1.0 (0.019)</td>
</tr>
<tr>
<td>Years</td>
<td>34.6</td>
<td>21.8 (0.630)</td>
<td>9.3 (0.269)</td>
<td>3.6 (0.104)</td>
</tr>
<tr>
<td>successful</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 9. Independent effects of individual anthropogenic variables on dates of initiation of egg laying.

<table>
<thead>
<tr>
<th>Year</th>
<th>Effect</th>
<th>Coefficient</th>
<th>SS</th>
<th>DF</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>All</td>
<td>1644.0</td>
<td>4, 118</td>
<td>2.8</td>
<td>0.031</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Roads</td>
<td>0.0012</td>
<td>683.5</td>
<td>1</td>
<td>4.6</td>
<td>0.034</td>
</tr>
<tr>
<td></td>
<td>Subsidies</td>
<td>0.0001</td>
<td>88.6</td>
<td>1</td>
<td>0.6</td>
<td>0.441</td>
</tr>
<tr>
<td></td>
<td>Urbanization&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-11.44, -4.53</td>
<td>436.0</td>
<td>2</td>
<td>2.9</td>
<td>0.057</td>
</tr>
<tr>
<td>2000</td>
<td>All</td>
<td>2605.0</td>
<td>4, 141</td>
<td>4.1</td>
<td>0.004</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Roads</td>
<td>0.0002</td>
<td>278.0</td>
<td>1</td>
<td>1.7</td>
<td>0.189</td>
</tr>
<tr>
<td></td>
<td>Subsidies</td>
<td>0.0009</td>
<td>1018.0</td>
<td>1</td>
<td>6.4</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td>Urbanization&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-8.07, 3.36</td>
<td>1309.1</td>
<td>2</td>
<td>4.1</td>
<td>0.019</td>
</tr>
</tbody>
</table>

<sup>a</sup>Urbanization is a dummy-coded categorical variable. The coefficients are for the “urban” and “natural” categories respectively, with the coefficient for the “mixed” category set to zero.
Table 10. The relative effects of groups of natural and anthropogenic variables and clutch initiation date on fledging success.

<table>
<thead>
<tr>
<th>Component</th>
<th>1999</th>
<th>Amount of total effect (percent)</th>
<th>2000</th>
<th>Amount of total effect (percent)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthropogenic (A)</td>
<td>10.29</td>
<td>(24.1%)</td>
<td>11.43</td>
<td>(17.0%)</td>
</tr>
<tr>
<td>Initiation date (B)</td>
<td>14.94</td>
<td>(35.0%)</td>
<td>15.32</td>
<td>(22.8%)</td>
</tr>
<tr>
<td>Natural (C)</td>
<td>5.32</td>
<td>(12.5%)</td>
<td>31.13</td>
<td>(46.3%)</td>
</tr>
<tr>
<td>Anthro. via Date (D)</td>
<td>-0.97</td>
<td>(0.0%)</td>
<td>3.09</td>
<td>(4.6%)</td>
</tr>
<tr>
<td>Anthro. via Natural (E)</td>
<td>2.68</td>
<td>(6.3%)</td>
<td>-3.3</td>
<td>(0.0%)</td>
</tr>
<tr>
<td>Natural via Date (F)</td>
<td>5.34</td>
<td>(12.5%)</td>
<td>7.03</td>
<td>(10.5%)</td>
</tr>
<tr>
<td>Anthro. via Natural and Date (G)</td>
<td>5.03</td>
<td>(11.8%)</td>
<td>2.5</td>
<td>(3.7%)</td>
</tr>
<tr>
<td>Total date (B+D+F+G)</td>
<td>25.31</td>
<td>(59.4%)</td>
<td>27.94</td>
<td>(41.6%)</td>
</tr>
<tr>
<td>Total anthro. via date (D+G)</td>
<td>5.03</td>
<td>(11.8%)</td>
<td>5.59</td>
<td>(8.3%)</td>
</tr>
</tbody>
</table>
Figure 1. A map of the study area. The gray polygon is dry lake bed, which provides no breeding habitat for ravens.
Figure 2. Partitioning effects of anthropogenic variables, natural variables (A), and date of initiation of breeding (B) on fledging success. In both panels, region A and C are the direct effects anthropogenic and natural variables on fledging. Panel A, region B represents the indirect effects of anthropogenic variables via changes in natural variables. Panel B, region B represents the direct effects of initiation date. The remaining lettered regions represent the indirect effects of anthropogenic variables via changes in initiation date (D) or changes in natural variables (E), the indirect effects of natural variables via changes in initiation date (F), and the effects of anthropogenic variables via changes in both natural variables and initiation date (G).
Figure 3. 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. 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 4: Common raven juvenile survivorship in a human augmented landscape*

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EXECUTIVE SUMMARY OF CHAPTER

In this study, we investigated whether increased juvenile survivorship contributes to raven population increases near human subsidies. Specifically, we asked whether juvenile survival from birth to the time of departure from the natal territory is related to factors such as nest proximity to human resources, distance between nests, nest substrate and juvenile condition. We also asked whether raven juvenile survival after departure from the natal territory (between fledging and the third year) could be predicted by time-since-fledging, year of hatching, and sex.

The study took place on EAFB and in surrounding communities during the spring of 1999 and 2000. We selected a random subset of known raven nests in different substrates and at varying distances from anthropogenic influence. A total of 240 raven nestlings from 98 nests were marked with individually-coded patagial tags, and a subset (102) of these received radio transmitters. We monitored marked juveniles by returning to their natal territories at intervals of 1-3 times per week until the juveniles were known to have died or left their respective natal territories. Juveniles that survived natal departure were relocated by radio telemetry and by visually searching the study area. We investigated the survival rate of juvenile ravens to dispersal in relation to environmental and morphological parameters, and conducted a mortality analysis to compare the relative contributions of anthropogenic and natural sources to pre-departure mortality.

The survival rate to juvenile departure was 38%, with nearest point subsidy being a significant variable in predictive models. Ravens nesting within 1.0 km of a point subsidy experienced survival rates to juvenile departure of nearly 60%, while those nesting farther than 1.5 km survived only 10-30% of the time.

We also tracked individuals that survived to departure for 33 consecutive months. The best-fitting mark-recapture models predicted post-departure survival as a function of time-since-fledging,
nearest point subsidy, and year hatched. Annual survival was 47% for first year, 88% for second year, and 88% for third year birds. Sources of juvenile mortality were recorded through March 2002 for 82 individuals found dead, with 12 cases of unknown source (15%) and 70 cases distinguishable between natural or anthropogenic sources. Most of the observed mortality (71 of 82 cases, or 87%) occurred prior to departure from natal territories, and predation accounted for the majority of the known causes (52 of 70 cases, or 74%). Mammalian predation was the primary identifiable source of mortality (44 of 70 cases, or 63%). Although nest distance to human activity did not significantly predict mortality prior to juvenile departure, it did predict whether the source of mortality was anthropogenic or natural.

The positive correlation between survival to juvenile departure and proximity to point subsidy supports our hypothesis that anthropogenic resources increase raven recruitment. A physiological or behavioral threshold may exist for Mojave ravens in regards to nest distance from resources. Nest distance of 1.5 km from nearest point subsidy represented a cutoff between high and low survival rates, and another study in eastern Mojave observed that nesting ravens usually foraged within 1.5 km of their nest. Nesting closer to anthropogenic resources probably reduces the physiological costs of foraging, may allow for increased food delivery rates, and increased adult vigilance against predators.

**Management Implications**

This study supports our hypothesis that anthropogenic resources subsidize the western Mojave raven population. In areas like the western Mojave where resource levels are naturally low, the impacts of artificial resources can be dramatic, and their influence helps explain increased raven abundance. Since the human presence in the region will likely increase, land managers should expect raven numbers to grow in parallel, unless raven access to anthropogenic resources is diminished. Management practices at EAFB should attempt to eliminate raven access to anthropogenic resources to reduce raven
population density and its impacts on biodiversity in the western Mojave.

ABSTRACT

Anthropogenic resource subsidies have contributed to the dramatic increase in the abundance of Common Ravens (Corvus corax) in the western Mojave Desert, California, during the past 30 years. To better understand the effects of these subsidies on raven demography, we examined whether survival to juvenile departure from the natal territory could be predicted by a set of environmental and morphological variables, such as nest proximity to anthropogenic resources and juvenile condition. We captured 240 juvenile ravens over 2 years and marked them prior to fledging. Nest proximity to anthropogenic resources and earlier fledging dates significantly predicted raven juvenile survival to departure from the natal territory. The best-fitting mark-recapture models predicted postdeparture survival as a function of time since fledging, nest proximity to anthropogenic resources, and year hatched. The positive effect of nest proximity to anthropogenic resources influenced postdeparture survival for at least 9 months after fledging, as revealed by the mark-recapture analysis. Annual survival was 47% for first-year, 81% for second-year, and 83% for third-year birds. Our results support the hypothesis that anthropogenic resources contribute to increasing raven numbers via increased juvenile survival to departure as well as increased postdeparture survival. We expect raven numbers to grow in concert with the growing human presence in the Mojave Desert unless raven access to anthropogenic resources is diminished.

Key words: Common Raven, Corvus corax, dispersal, juvenile dispersal, juvenile survival, juvenile survivorship, mark-recapture, Mojave Desert.
INTRODUCTION

Avian populations grow in response to increased availability of resources such as food supply and nesting substrates (Lack 1966, Braun and Balda 1989, Newton 1998). Human-modified landscapes may provide increased opportunities for generalist species, especially wide-ranging ones capable of exploiting both anthropogenic resources and those provided by surrounding, less disturbed landscapes (Hansson 1997). An example of such a species is the Common Raven (*Corvus corax*) in arid areas of southern California. Coinciding with an increasing human presence in the western Mojave Desert (U.S. Census Bureau 2000), annual Breeding Bird Surveys conducted by the U.S. Fish and Wildlife Service show a tenfold increase in Common Raven sightings in the region (Boarman and Berry 1995). The human population increase is significant because ravens forage at anthropogenic sites (Conner and Adkinson 1976, Boarman 1993, Knight et al. 1993, Restani et al. 2001).

Potential demographic mechanisms for the higher raven abundance as a function of anthropogenic resource subsidies include increased reproductive success (e.g., higher clutch sizes, hatching rates, fledging rates), increased immigration, decreased emigration, increased survival, or various combinations of these alternatives. Of these, juvenile survival and the associated limiting factors are notoriously difficult to study (Pulliam et al. 1992), due in part to the logistical constraints of mark-recapture studies. Raven abundance in the western Mojave provides a unique opportunity to study juvenile survival and the associated limiting factors because ravens occur in high density and can carry longlasting radio-transmitters.

The distribution of anthropogenic resources in the western Mojave is also favorable for studying their influence on the survival of juvenile ravens. Most forms of anthropogenic resources (hereafter, point subsidies) in the region (e.g., sewage ponds, landfills) form distinct oases of rich, artificially maintained resources set within an otherwise resource-limited landscape. Breeding ravens construct
nests throughout the landscape, and many feed their young at least partially with forage obtained at point subsidies (Kristan 2001).

We hypothesized that raven juvenile survival (to leaving the natal territory; hereafter, juvenile departure), could be predicted by a set of individual parameters (e.g., sex, mass) and environmental characteristics including nest proximity to point subsidies. We describe the relatively brief process of permanent emigration of fledglings from the natal territory as juvenile departure in order to distinguish it from natal dispersal *per se*, which encompasses the period between fledging and the first breeding attempt (Greenwood 1980), and which in ravens may not occur until 4 years after fledging (Boarman and Heinrich 1999). Since nutrition and other conditions prior to juvenile departure may affect postdeparture survival (Lack 1966, Dewey and Kennedy 2001), we extended our survival analysis into the postdeparture period. Since proximity to humans influences the risks of mortality in some species (Koenig et al. 2002, Rubolini et al. 2001), we also asked if nest proximity to anthropogenic activities such as roadways increased the risk of mortality, and whether any sources of anthropogenic mortality were either additive or compensatory (Nichols et al. 1984).
METHODS

Study Area

The study site consisted of Edwards Air Force Base (348389N, 118869W) and surrounding communities in the western Mojave Desert, occupying approximately 4000 km2, and lies within the Mojave Desert floristic province (Fig. 1; Hickman 1993). Mean annual precipitation is 112 mm, and falls mainly in the form of rain between November and March (MacMahon 2000). Mean annual temperature is 18.18°C, with hot summers (mean monthly daytime temperature 25–30°C, June–August), and cool winters (10–15°C, December–February; MacMahon 2000). The most common natural community types are Mojave creosote bush (*Larrea tridentata*) scrub and desert saltbush (*Atriplex* spp.) scrub. The most common anthropogenic community types include residential areas, agriculture, and ranching operations.

Ravens in the western Mojave Desert build nests in or on a variety of natural and anthropogenic substrates. The most common natural substrates are Joshua trees (*Yucca brevifolia*) and cliffs (Kristan 2001). Anthropogenic substrates include billboards, power poles, storefronts, and landscaped trees. Clutches consist of 1 to 5 eggs, laid in March or early April (Boarman and Heinrich 1999). Raven nestlings are altricial and fledge at approximately 5 weeks of age. Throughout the nesting period, adult ravens vigorously defend their territories against intruders. This aggressive behavior serves as an important clue to identifying active territories and their boundaries.

During the spring of 1999 and 2000, we conducted random searches for raven nests located in various substrates and distances from anthropogenic influence. Locations of nests were measured in universal transverse mercator (UTM) coordinates and plotted on a study site map constructed from ground observations, USGS 7.5- minute digital topographic maps, and USGS 7.5- minute digital
orthophoto quarter quadrangles. For each nest we determined the distance to the nearest point subsidy
and nearest human activity using mapping software (ESRI 1999). The nearest point subsidy to each nest
was identified using a priori observations of the types of anthropogenic resources utilized by ravens
foraging in the study site, including residences, artificial wetlands, landfills, sewage ponds, livestock
feedlots, shopping areas, agricultural fields, and golf courses. The nearest human activities to each nest
included residences, paved roads, industry, etc. Thus, the distance to the nearest human activity was
usually less than, but occasionally equal to, the distance to the nearest point subsidy.

**Mark-recapture**

We captured and marked a total of 240 (1999, \(n = 108\); 2000, \(n = 132\)) raven nestlings from 98
nests at approximately 4.5 weeks of age, which was just prior to fledging. All nestlings were marked
with individually coded patagial tags. Wings tags were applied to nestlings in the patagial area of both
wings using either plastic clips or pop rivets. Wing tags were handmade from white, lightweight vinyl-
coated nylon (‘‘Herculite,’’ Herculite Industrial Fabrics, Emigsville, Pennsylvania) cut into thin strips
(170 x 26 mm) widening into teardrop-shaped ends (55 mm at the widest point). The general shape and
application of the wing tags were similar to the methods of Stiehl (1983), but the wing tags were
considerably narrower.

A subset (102) of the marked juveniles received radio-transmitters (ATS, Holohil Systems Ltd.,
Carp, Ontario, Canada), attached with a backpack-style harness (Buehler et al. 1995). Each harness was
composed of two teflon ribbons (40 x 1 cm) threaded through each end of the unit casing. The rear
ribbon passed behind the wings and the front ribbon draped over the shoulders. After fitting the ribbons
beneath the contour feathers, we secured the four ends together near the furcula with an aluminum J-clip
and high-strength adhesive. The transmitters used in this study weighed 22 g (approximately 3% of a
fledgling’s body mass) with a typical battery life of 18–24 months. We also took the following measurements from all captured juvenile ravens: mass, wing chord length, tarsus length, tarsus height, culmen length, culmen width, and culmen depth. All capture and experimental techniques strictly followed guidelines described by Gaunt and Oring (1997).

Since male and female ravens are morphologically indistinguishable, we used molecular techniques to identify sex. During visits to the nests, two small, growing feathers were sampled from each nestling, and sex was determined using a PCR reaction that amplifies the CHD genes on the W and Z chromosomes (Griffiths et al. 1998).

We monitored marked juveniles by returning to their natal territories 1–3 times per week until the juveniles were either known to have died, or had left their natal territories. The identity of all marked juveniles was confirmed by reading their wing tags with the aid of a spotting scope and binoculars. Since adult ravens vigorously defend active nesting territories against intruders, natal territories were defined as the area centered at the nest and defended by the nesting adult ravens. During repeated visits to each nesting territory, we observed that researchers, conspecifics, and heterospecifics such as Red-Tailed Hawks (*Buteo jamaicensis*) were typically intercepted by the resident pair between 0.5 and 1.0 km from the nest. Our estimates of natal territory sizes based upon such observations of adult defensive behavior were similar to the mean radius (1.0 km) between adjacent raven nests independently observed by Kristan (2001).

The natal territories of marked juveniles were monitored on a regular basis until each juvenile was located at least several kilometers outside the natal territory (*n* = 90), found dead (*n* = 141), or declared missing (*n* = 9). Juveniles were considered to have survived only if they were resighted alive outside their natal territories. To minimize the number of missing birds, each territory was thoroughly checked for signs of dead juveniles once all obvious signs of juvenile occupation had stopped. When
juveniles turned up missing, radio-transmitters greatly aided the search for them. Survival checks were also greatly aided by strong juvenile preference for anthropogenic habitat (Webb 2001). The vast majority of surviving juveniles were first resighted outside their natal territories at point subsidies. Juveniles that were never resighted at point subsidies were usually found dead within their natal territory. Only nine marked juveniles were never relocated. Based on their continued absence from point subsidies throughout the region, these few missing juveniles were considered to have perished.

Juveniles that survived natal departure were relocated by radio-telemetry and by searching the study area (Kenward 1987, White and Garrot 1990, Winterstein et al. 2001). The entire study area was visited and searched monthly between June 1999 and February 2002, with the goal of maintaining an approximately uniform search effort throughout the study. Relocation of radiotagged juveniles was conducted mainly by motorized vehicle telemetry. Signals were detected using dual 3-element Yagi antennas attached to a vehicle’s roof by 1-m swiveling masts, in tandem with an ATS R2000 portable scanning radio receiver (Advanced Telemetry Systems 1993). Handheld portable 3-element and 2-element Yagi antennas were also used to search for radio-tagged juveniles by foot. On three occasions, we flew a Cessna 185 equipped with dual wingmounted, 3-element Yagi antennas to conduct a large-scale aerial search for missing transmitter signals. Detectability of transmitter signals ranged from 1–50 km, depending upon the search mode (vehicle, foot, or aircraft), topography, and behavior of the individual birds.

The source of mortality was assessed as best as possible for all dead juveniles. In general, most cases of known mortality were classified as either natural or anthropogenic. The classification was further refined depending upon the amount of additional evidence, such as the location and timing of death, condition of the remains, and any markings left by predators.

We investigated the survival rate to departure of juvenile ravens in relation to environment and
morphology. The environmental parameters included the distance from each nest to the nearest point subsidy, the distance from each nest to the nearest human activity, individual fledging date, nest substrate, air temperature during the nestling period, and attachment of a radio-transmitter. The point subsidies considered for the analysis consisted of permanent sources of food or water. The human activities included in the analysis were those posing potential harm to wildlife such as vehicle traffic and railroads. The morphological parameters included the measurements taken at capture. Juvenile departure was defined as movement from the natal territory, followed by subsequent observer detection.

**Statistical Analyses**

Analysis of juvenile survival to departure was conducted using logistic regression (SAS PROC LOGISTIC; SAS Institute 1999) with forward selection predicting the outcome (surviving or not surviving) from the set of predictor variables. We substituted a condition index for each individual, composed of the residual from a regression of mass on tarsus length rather than using the entire suite of morphological parameters because most were highly correlated (e.g., $r = 0.64$ for mass vs. tarsus length). In addition, we extended our survival analysis into the postdeparture period using open-population mark-recapture analyses (Cormack 1964, Jolly 1965, Seber 1965). We chose nest proximity to the nearest point subsidy as a factor because prefledging resource availability has been shown to affect avian juvenile survival (Perrins 1965, Van Der Jeugd and Larsson 1998). Although survival rates may decrease with age, we expected the postdeparture survival rate to increase with time as juveniles matured. We chose sex as a factor because we suspected that fledgling males and females might have different dispersal patterns (Wheelwright et al. 1995).

A mortality analysis was conducted to compare the relative contributions of anthropogenic and natural sources to predeparture mortality. We used logistic regression (SAS PROC LOGISTIC) with
forward selection to predict the outcome (mortality by natural vs. anthropogenic means) in relation to
nest distance from the nearest human activity.

We used program MARK (White and Burnham 1999) to build and test mark-recapture models to
compare parameters between sexes, among years, and in relation to the individual covariate of nest
distance to the nearest point subsidy (Williams et al. 2002). Our models were constructed using 3-
months recapture intervals corresponding to the four seasons of the year. Program MARK estimates
model parameters such as survival through numerical maximum likelihood techniques. We used
Akaike’s information criterion (Akaike 1973) corrected for small sample size (AIC.) and overdispersion
(QAIC.) to select the best model from the list of a priori models, and the model with lowest AIC. or
QAIC. was used for statistical inference and parameter estimation (Burnham and Anderson 1998).

Because of differences in detection probabilities, we analyzed juveniles marked with transmitters
separately from juveniles that were marked with wing tags only. Although transmitters increased the
recapture probability for raven juveniles, data obtained from radio-transmitters in our study did not meet
the assumptions of known fate data because ravens are highly mobile and the radio-transmitters were
relatively weak in comparison to the size of the study area. Thus, the data from radio-tagged juveniles
were incorporated in a Burnham joint live recaptures and dead recoveries analysis (Burnham 1993),
while the recaptures-only data from juveniles with wing tags only were used in a Cormack-Jolly-Seber

Survival and recapture rates were our parameters of interest for both the CJS and Burnham
analyses. CJS models estimate two parameter types: survival rate (Φ), and recovery rate (ρ), and provide
only minimum estimates of true survival because mortality is confounded with permanent emigration.
The parameter space for Burnham models includes four parameter types: survival rate (S), recapture rate
(ρ), recovery rate (r), and site fidelity (F). Since survival and recapture rates were our primary
parameters of interest, we did not constrain recovery rate or site fidelity in the Burnham analysis. Mark-recapture analyses were conducted by testing the global models and then constraining parameters according to our *a priori* hypotheses. Model notation follows that of Lebreton et al. (1992) and Franklin et al. (2000). We constrained parameters as functions of time ($t$), sex, age, the individual covariate of nest distance to the nearest anthropogenic resource (*proximity*), and constancy ($\cdot$). We evaluated the impact of nest distance to the nearest anthropogenic resource with an ANODEV test (Skalski et al. 1993, White and Burnham 1999), which compared the amount of deviance explained by a covariate against the amount of deviance not explained by the covariate.

Goodness-of-fit tests are typically used to confirm that data analyzed in information-theoretic models met the assumptions of those models (Anderson et al. 2001). Program MARK provides a parametric bootstrapping approach (White and Burnham 1999) for goodness-of-fit testing for most types of models with the notable exception of models containing individual covariates. We created our own goodness-of-fit program for the CJS analysis that emulates the parametric bootstrapping approach in MARK. However, a similar program for Burnham analyses is not currently available.
RESULTS

Predeparture Juvenile Survival

The overall survival rate to departure was 38% (90 of 240 marked individuals). Significant predictors of survival to departure included nest distance to the nearest anthropogenic resource ($x^2 = 16.8, P < 0.001$) and fledging date ($x^2 = 18, P < 0.001$; Fig. 2). Sixty percent of juvenile ravens nesting within 1.0 km of anthropogenic resources survived to depart from their natal territory, while only 10–30% of those nesting farther than 1.5 km survived. Juvenile ravens fledging prior to 28 May in 1999 experienced greater than 70% survival while those fledging after 18 June experienced only 15% survival (Fig. 3). A similar pattern of survival occurred in 2000, with higher survival for juvenile ravens fledging prior to 26 May, and lower survival for juvenile ravens fledging later than 3 June. Nonsignificant predictors of survival to departure included the condition index, sex, nest substrate, year, distance to the nearest human activity, and transmitter attachment (all $P > 0.05$). Thus, ravens fledging earlier in the season and closer to the nearest point subsidy were more likely to survive to depart from their natal territories.

It was unlikely that juveniles that survived to depart from their natal territories escaped detection. The vast majority of survivors were relocated within 2 months after fledging. Only two individuals located for the first time outside their natal territories were found dead at that time.

Postdeparture Juvenile Survival

We tracked 90 ravens for 33 consecutive months between June 1999 and March 2002, obtaining 2451 postdeparture locations. Overall, juvenile ravens survived better during the postdeparture period if their nests had been closer to anthropogenic resources. Those fledging in 2000 survived better than those
fledging in 1999. The best-fitting CJS and Burnham models were both functions of time, nest distance to the nearest anthropogenic resource, and year (Table 1, 2). The effect of distance to the nearest anthropogenic resource was detectable for up to 9 months after departure. The best CJS model predicted survival as a function of nest distance to the nearest anthropogenic resource for three recapture intervals (9 months) after fledging, followed by time-dependence alone. This model was over four times as well supported as the next best model, and the individual covariate of nest distance from the nearest anthropogenic resource explained a highly significant proportion of the deviance (ANODEV $F_{2,87} = 4.5$, $P < 0.001$). The best Burnham model predicted survival as an additive function of nest distance to the nearest point subsidy, and was over 42 times as well supported as the next best model. The individual covariate of nest distance to the nearest point subsidy accounted for a highly significant proportion of the deviance (ANODEV $F_{4,53} = 5.2$, $P < 0.001$).

No support was found for any models incorporating differences in survival or recapture between the sexes. Burnham survival estimates (based upon radio-equipped birds) were generally higher than CJS estimates, suggesting that CJS methods underestimated true survival rates. Seasonal survival estimates were typically higher than 75%, with the lowest values usually occurring during the winter. Cumulative survival was estimated from the product of seasonal survival estimates calculated separately for CJS and Burnham estimates and then averaged. Mean annual survival was 50% for hatch-year, 81% for second-year, and 83% for third-year birds. After 33 months, an estimated 28% of the juvenile Common Ravens that survived departure were still alive (Fig. 4).

**Causes of Mortality**

Juvenile mortality was recorded through March 2002. A total of 82 mortalities were recorded, with 12 cases of unknown source (15%) and 70 cases distinguishable between natural or anthropogenic...
sources. Most of the observed mortality (71 of 82 cases, or 87%) occurred prior to departure from natal territories, and predation accounted for the majority of the known causes (52 of 70 cases, or 74%). Mammalian predation was the primary identifiable source of mortality (44 of 70 cases, or 63%), and of these, coyotes (Canis latrans) were the most common (16 of 21 cases, or 73%). Although nest proximity to the nearest human activity was not a significant overall predictor of mortality prior to juvenile departure, nest proximity to the nearest human activity did significantly predict whether the source of mortality was either anthropogenic or natural. Juveniles fledging from nests closer to human activities were more likely to die from an anthropogenic source ($\chi^2 = 9.79, P < 0.02$). Thus, anthropogenic sources of mortality compensated for natural sources of mortality rather than adding to the overall mortality rate (Nichols et al. 1984).

DISCUSSION

The positive correlation between survival to juvenile departure and nest proximity to the nearest point subsidy supports our hypothesis that anthropogenic resources increase raven recruitment. A physiological or behavioral threshold may exist for Mojave ravens in regards to nest distance from resources. Working in the eastern Mojave, Sherman (1993) observed that nesting ravens usually foraged within 1.5 km of their nest. In the western Mojave, nesting ravens forage at anthropogenic resources near their nests (Kristan 2001), and a nest distance of 1.5 km from the nearest point subsidy appears to represent a cutoff between high and low survival rates. Nesting closer to anthropogenic resources probably reduces the physiological costs of foraging, and may allow for increased food delivery rates and permit increased adult vigilance against predators. Although nesting near anthropogenic resources is a successful strategy, the distribution of nest distances from point subsidies does not appear strongly leptokurtic. This suggests ravens are reluctant to contract their territories simply in order to nest near
point subsidies, even though the natural resources within their territories may be scarce. Point subsidies are larger than a single nesting pair can defend and therefore must be shared with unrelated ravens. Marzluff and Neatherlin (unpubl. data) observed a similar conflict between raven territorial behavior and increased reproduction and survival associated with proximity to anthropogenic resources on the Olympic Peninsula, Washington, a substantially different ecological setting.

Closer proximity to anthropogenic resources may increase juvenile survival through increased opportunity for adult vigilance against predators prior to juvenile departure (Arcese and Smith 1988, Dewey and Kennedy 2001), the period when juvenile ravens are most susceptible to predation. Raven juveniles are particularly vulnerable between fledging and first successful flight, spending considerable time on the ground, and appear generally naïve to threats from intruders. The lack of dense vegetation near most nesting substrates probably reduces the ability of juvenile ravens to hide from predators before they can fly. When present, adult nesting ravens display aggressively toward observers prior to juvenile departure. The relatively low survival rate of juvenile ravens to departure (38%) was in large part due to predation by coyotes, also a human-subsidized predator (Tigas-Lourraine et al. 2002).

A negative relationship between the probability of recruitment and breeding date has been observed in several species and attributed to various causes including food availability (Daan et al. 1989), parental quality (Spear and Nur 1994), and predation pressure (Naef-Daenzer et al. 2001). The pattern of decreasing juvenile survival and fledging date parallels the seasonal trend of increasing air temperature in the western Mojave. Survival rates plummeted when air temperatures regularly exceeded 30ºC during the late stages of the nesting season in June and July. Extreme air temperature probably restricts adult foraging activities, causes additional adult energy expenditure during brooding, and slows juvenile development (Peterson et al. 1986).

Heat stress is probably increased by the lack of cover found in most natural nesting substrates
such as Joshua trees and cliffs compared to anthropogenic substrates like billboards and landscaped trees. Steenhof et al. (1993) attributed higher raven nesting success in transmission-line towers in comparison to natural substrates to better protection from heat. Nesting substrate was not a significant predictor of raven juvenile survival to departure in our study, however, perhaps because the differential insulation between natural and anthropogenic substrates affected the nestling stage more strongly than the fledgling stage. Nestlings from late-season nests were unlikely to survive to fledging age, and thus could not be included in the study.

The population dynamics of many species are sensitive to juvenile survival (Levin et al. 1987, Kushlan 1988, Davis and Levin 2002). It is likely that anthropogenic resources have contributed to the increase in raven abundance, at least in part through increased juvenile survival. However, the relative impact of juvenile survival on raven population dynamics in the western Mojave is unclear because other demographic parameters such as the mean lifespan, age of first reproduction, and emigration and immigration rates are poorly documented (Boarman and Heinrich 1999).

**MANAGEMENT IMPLICATIONS**

This study supports our hypothesis that anthropogenic resources subsidize the western Mojave raven population. Moreover, it indicates that one demographic mechanism by which this is achieved is increased juvenile survival (both survival to departure from the natal territory and postdeparture survival) as nest proximity to anthropogenic resources increases. In areas like the western Mojave where resource levels are naturally low, the impacts of artificial resources can be dramatic, and their influence helps explain the increased abundance of ravens. Unfortunately, ravens have been implicated as human-subsidized predators (Soule’ 1988) of sensitive species, including the federally threatened desert tortoise (*Gopherus agassizii*) in the Mojave Desert (Camp et al. 1993), and thus their sustained high abundance
is of considerable conservation concern. Land managers should expect raven numbers and conflicts with humans to grow in parallel to the human population, unless raven access to anthropogenic resources is diminished. Eliminating or altering management practices that inadvertently provide resource subsidies to ravens should reduce their population density and associated negative impacts on biodiversity in the western Mojave.

ACKNOWLEDGMENTS

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LITERATURE CITED


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Table 1. Ranking of juvenile raven CJS models. Notation: Phi = survival; P = recapture; 
t = time; (.) = constancy term; NPS = nest distance to the nearest point subsidy; g= sex differences; 
(*) = interaction term; (+) additivity term; a2 = two age groups,(#) = months for interaction.

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Table 2. Ranking of juvenile raven Burnham models. Notation: S = survival; p = recapture; t = time; () = constancy term; NPS = nest distance to the nearest point subsidy; g= sex differences; (*) = interaction term; (+) additivity term; a2 = two age groups; r = recovery rate; F = site fidelity; (#) = months for interaction.

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Figure 1. Location of the Mojave Desert study area in California. The dark polygons within the study area represent anthropogenic habitat, and the light portions represent natural habitat.
Figure 2. Survival to departure from the nest territory and nest distance to the nearest anthropogenic resource (e.g., sewage pond, landfill) for juvenile Common Ravens hatched in 1999 and 2000. Increments increase above 2.0 km for descriptive purposes because sample sizes were smaller at these distances. Numbers above bars are sample sizes (individuals).
Figure 3. Survival of juvenile ravens to departure from the natal territory in relation to fledging date and the mean daily maximum temperature during the nestling period in 1999 and 2000. The fledging group dates are organized by weeks mainly for descriptive purposes, but also represent the relative number of juveniles fledging in the population. Numbers above bars are sample sizes (individuals).
Figure 4. Seasonal survivorship estimates for juvenile ravens. Seasons were defined as spring (March, April, and May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). A Burnham model was used to estimate survivorship for juvenile ravens carrying radio transmitters, and a CJS model was used for ravens without transmitters. Burnham models estimate survivorship for each season, while CJS models estimate survivorship between seasons. (A) Burnham survivorship estimates for juveniles with transmitters and hatched in 1999. (B) CJS survivorship estimates for juveniles without transmitters and hatched in 1999. (C) Burnham survivorship estimates for juveniles with transmitters and hatched in 2000. (D) CJS survivorship estimates for juveniles without transmitters and hatched in 2000.
Figure 5. Annual survivorship estimates for juvenile Common Ravens during the first three years. Values are the product of seasonal survival estimates. Estimates for the first and third year are based on data from the summer, fall, and winter seasons for birds hatched in 2000 and 1999, respectively. Third year data was not available for birds hatched in 2000. The mean values combine both CJS and Burnham estimates.
Chapter 5: Juvenile common ravens (Corvus corax) optimize their movements using multiple cues

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EXECUTIVE SUMMARY OF CHAPTER

Raven populations in the Mojave Desert have increased dramatically in recent years. As part of our effort to understand the reason for their increase, we examined the movement of juvenile ravens. Prior to this study, little was known about this critical period between the birds’ dispersal from their natal territory and their becoming breeding, territorial adults.

We made predictions based on two models that have been proposed to explain the ultimate causes of juvenile dispersal. The first model, that movement patterns are based on inbreeding avoidance, predicts that there will be a sex bias or evidence of heritability in movement behavior, and that movements will occur with respect to siblings. The second model is that distribution of resources is the primary ecological mechanism driving movement. It predicts that the movements of ravens will reflect resource availability within the landscape.

We used radio telemetry to evaluate the movements of juvenile ravens in the context of these models by marking and following 2 years of juvenile ravens in the western Mojave Desert. We investigated habitat use, looked for heritability in movement behavior, tested for sexual dimorphism in movements, and characterized interactions between siblings. We interpreted our findings with the aim of contributing to an improved general understanding of the mechanisms driving natal dispersal.

Over the 2 years of the study, 90 individuals survived to natal departure and radio tracking resulted in 2451 relocations. Both sub-adult and juvenile common ravens were found to rely heavily on anthropogenic resources (such as landfills and sewage ponds) and concentrate in anthropogenic habitat. Movement patterns were not found to be heritable, and no differences were found in the movement patterns of males and females. Instead, the ravens’ initial movement was towards flocks of conspecifics.
Raven juveniles optimize their movements using multiple cues including resources, conspecifics, and close relatives. Their movement patterns lend some support for the common dispersal models considered. The relative philopatry of raven juveniles and their selection of resource-rich anthropogenic habitat uphold the predictions of resource competition models of natal dispersal. Behavioral models based on inbreeding avoidance were not supported by the absence of a sex bias and the low heritability for movement distance. Both ecological and behavioral mechanisms influenced the tendency for juveniles to use anthropogenic habitats mostly in the presence of conspecifics. The locations of raven juveniles after departure show that siblings tend to associate more than unrelated individuals. Sibling association provides evidence for individual recognition which may serve proximate social functions and ultimately prevent inbreeding.
ABSTRACT

Common models for explaining avian natal dispersal invoke behavioral and ecological mechanisms. We evaluated the movements of juvenile Common Ravens in the context of these models. We marked and followed two annual years of juvenile ravens in the western Mojave Desert. We investigated habitat use, looked for heritability in movement behavior, tested for sexual dimorphism in movements, and characterized interactions between siblings. Raven juvenile movements were relatively philopatric, and displayed little sexual dimorphism. Habitat use reflected the distribution of anthropogenic resources. Low heritability in movement behavior and a lack of sexual dimorphism did not support predictions of dispersal based on behavioral models. Association of siblings outside of the natal territory suggests the ability to recognize close relatives and, if recognition plays a role in inbreeding avoidance, may lend support to behavioral explanations. Juvenile philopatry and patterns of habitat selection related to resource abundance supported some predictions based upon ecological models. However, the direction of initial movements from the natal territory to the nearest large flock rather than the closest anthropogenic resource suggests juvenile movements are influenced by conspecifics. Overall, raven juvenile movements resembled an optimization process, rather than a strictly patterned behavior. Raven juvenile movements reflected the distribution of resources as well as conspecifics. Key words: natal dispersal, juvenile dispersal, Common Raven, Corvus corax, avian dispersal, individual recognition, kin recognition, conspecific attraction.
INTRODUCTION

Natal dispersal, "the permanent movement from birth site to first breeding or potential breeding site" (Greenwood 1980: 1141), is a life history trait with important ecological, genetic, and social implications for populations. It is a demographic process relevant to the distribution and abundance of organisms (Johnson and Gaines 1990), and an understanding of the dynamics of dispersal is increasingly important for conservation biology (Simberloff 1997). An increased understanding of dispersal is relevant for maintaining dwindling populations of threatened species, as well as efforts to understand the impact and expansion of predator and pest species (Macdonald and Johnson 2001).

Natal dispersal has not been well documented, especially in long-lived species, such as the Common Raven (Corvus corax). Ravens have an extended juvenile period and delayed reproduction. Captive ravens (Corvus corax) have attempted breeding as early as their second year (Gwinner 1965), but the age of first breeding for wild ravens is not well documented. Most wild ravens probably do not attempt breeding until later than their third year (Boarman and Heinrich 1999, Webb et al. 2004).

Because the ontogeny of raven breeding behavior is unknown, it is difficult to predict when the behavior of raven natal dispersal begins. One possibility is that raven natal dispersal begins early, and occurs throughout the juvenile period, and therefore the entire pre-breeding period is synonymous with natal dispersal behavior (Figure 1). However, another possibility is that natal dispersal behavior is delayed. In this scenario, the behavior of the pre-breeding period are distinct in character and temporally separated from natal dispersal behavior (Figure 2). Furthermore, since it is difficult to predict when the behaviors associated with true natal dispersal might begin for juvenile ravens, we substitute the term juvenile movements to describe
the pre-breeding behavior of juvenile ravens. Juvenile movements defined here can be understood in terms of natal ranging (Dingle 1996) or gross dispersal (Greenwood 1980), rather than true natal dispersal or effective dispersal (Greenwood 1980).

We assumed that juvenile movements during the birds’ first two or three years adequately characterized the nature of their pre-breeding movements. Based upon related studies in the same system (Boarman, *unpub. data*), we have no reason to suspect that raven juvenile movements defined here would strictly differ from the movements of older pre-breeding individuals. Both sub-adult and juvenile Common Ravens in the western Mojave appear to heavily utilize anthropogenic resources (such as landfills and sewage ponds) and concentrate in anthropogenic habitat.

Although it is possible that juvenile movements may differ from natal dispersal in timing and function, there are no existing hypotheses specific to juvenile movements. We cannot effectively distinguish between juvenile movements and natal dispersal at this time. Thus, the existing hypotheses regarding natal dispersal remain the most relevant body of knowledge for evaluating juvenile movements. Accordingly, we used the mechanisms of natal dispersal theory as an initial framework to evaluate raven juvenile movements. The mechanisms of natal dispersal theory can be likened to a spectrum of causes (Figure 3) ranging from the mostly behavioral to the mostly ecological, where none of the mechanisms are mutually exclusive.

Behavioral explanations (Howard 1960, Horn 1983) invoke inbreeding avoidance as the primary mechanism driving natal dispersal behavior. The assumption is that an animal's movements are primarily an adaptation to avoid inbreeding, and they are driven by cues which are either mostly innate or mostly environmental. If inbreeding avoidance influences raven juvenile movements through innate cues (Greenwood 1980), then we expected to observe a sex
bias or evidence of heritability in movement behavior. If inbreeding avoidance is mediated by environmental cues such as the presence of siblings, (Pusey and Wolf 1996, Wheelwright and Mauck 1997), then we expected movements to occur with respect to siblings.

The distribution of resources is often cited as the primary ecological mechanism driving natal dispersal (Murray 1967, Waser 1985, Walls and Kenward 1994, Lambdin 1994, Lambdin et al. 2001). This mechanism predicts that movements should occur with respect to resource distribution in the landscape. If resource distribution influences raven juvenile movements, then we expected the initial movements of fledgling ravens to reflect resource availability, and raven juvenile habitat use thereafter to reflect resource availability within the landscape.

In this study, we evaluated the movements of juvenile Common Ravens in the context of the spectrum of natal dispersal models by marking and following two annual years of juvenile ravens in the western Mojave Desert. We investigated habitat use, looked for heritability in movement behavior, tested for sexual dimorphism in movements, and characterized interactions between siblings. We interpreted our findings with the aim of contributing to an improved general understanding of the mechanisms driving natal dispersal.

**METHODS**

The study site was comprised of Edwards Air Force Base (34° 38' N, 118° 6' W) and surrounding communities and natural habitats in the western Mojave Desert, approximately 4000 km² (Figure 4), which lie within the Mojave Desert Floristic Province (Hickman 1993). The habitat consists of a mixture of natural and anthropogenic types (CNDD 1999). Mean annual precipitation is 112 mm, and falls mainly in the form of rain between November and March (MacMahon 2000). Mean annual temperature is 18.1 °C, with hot summers (mean monthly
maximum temperature 25-30 °C, June, July, and August), and cool winters (mean maximum temperatures 10–15 °C, December, January, February) (MacMahon 2000). The most common natural community types are Mojave Creosote Bush (*Larrea tridentata*) Scrub and Desert Saltbush Scrub (*Atriplex spp.*). The most common anthropogenic community types include residential areas and various kinds of agriculture, ranching, and military flight-support operations.

The distribution of anthropogenic resources in the western Mojave is favorable for studying their influence on the movements of juvenile ravens. Most forms of anthropogenic resources (hereafter, point subsidies) in the region (i.e. sewage ponds, landfills) form distinct point sources of rich artificial subsidies set within a resource-limited arid landscape. The patchy distribution of point subsidies is propitious for evaluating the relative influence of resource availability on movements and habitat use.

During the spring of 1999 and 2000, raven nests were located and a total of 240 nestlings from 98 nests were marked at approximately 4.5 weeks of age, just prior to fledging which typically occurs during the 5th week (*unpubl. data*). All nestlings were marked with individually-coded patagial tags. Wing tags were applied to nestlings in the patagial area of both wings using either plastic clips or pop rivets. A subset (102) of the marked juveniles received radio transmitters (ATS, Holohil Systems Ltd.) attached with a backpack-styled harness (Buehler et al. 1995). The transmitters used in this study weighed 22g and were approximately 3 % of the average fledgling’s body mass. All capture and experimental techniques strictly followed guidelines described in Gaunt and Oring (1997).

Since male and female ravens are morphologically indistinguishable, molecular techniques were used to differentiate individuals of either sex. During visits to the nests, two
small growing feathers were sampled from each nestling, and sex was determined using a PCR reaction that amplifies the CHD genes on the W and Z chromosomes (Griffiths 1998).

We monitored marked juveniles by returning to the vicinity of their nests at intervals of 1-3 times per week. Since adult ravens vigorously defend active nesting territories against intruders, natal territories were defined as the area centered at the nest and defended by the nesting adults. In most cases this area extended between 0.5 and 1.0 km from the nest. We returned to the natal territories until the juveniles were found dead, declared missing, or were resighted at least several kilometers outside the natal territory. We describe the relatively brief process of permanent emigration of fledglings from the natal territory as natal departure in order to distinguish it from natal dispersal which encompasses the time period between fledging and the first breeding attempt (Greenwood 1980).

Juveniles that survived natal departure were relocated by radio tracking and by visually searching throughout the study area (White and Garrot 1990, Millspaugh and Marzluff 2001). The entire study area was visited and searched monthly between June 1999 and February 2002, with the goal of maintaining an approximately uniform search effort throughout the study. Relocation of radio-tagged juveniles was conducted mainly by motorized vehicle. Signals were detected using dual 3-element Yagi antennas attached to the vehicle roofs by 1-m high swiveling masts, in tandem with an ATS R2000 portable scanning radio receiver (Advanced Telemetry Systems, 1993). Hand-held portable 3-element and 2-element Yagi antennas were also used to search for radio-tagged juveniles by foot. On three occasions, we flew a Cessna 185 equipped with dual wing-mounted, 3-element Yagi antennas to conduct a large-scale aerial search for missing transmitter signals. Detectability of transmitter signals ranged from one to 50 km, depending upon the search mode (vehicle, foot, or aircraft), topography, and behavior of the
individual birds. On numerous occasions, we used vehicle-based radio receiving equipment to search outside the study site.

Locations of juveniles were recorded in Universal Transverse Mercator (UTM) coordinates utilizing hand-held Global Positioning System (GPS) units (Magellan GPS 300, Rockwell PLGRs). The DOD-issued PLGR maintained an accuracy of less than +/- 10m. The PLGR was used until selective availability was discontinued, after which the Magellan (less than 15m error) was utilized. Locations of juveniles were plotted on a study site map constructed using GIS (ESRI 1999). In order to document raven social ecology, we also visually estimated the number of conspecifics within 100m of the marked juveniles, and also noted the locations of raven flocks within the study site.

We measured several movement indices including the mean, initial, and maximum distance individuals were located from their nests during the time each bird was monitored. The movement indices also included the mean distance moved between locations, the rate of movement between locations (velocity), home range, and Sheilds’ (1982) criteria for relative philopatry. Sheilds’ criteria uses a distance equivalent to 10 home ranges to classify individuals as either dispersive or philopatric. We classified juvenile ravens as philopatric or dispersive by comparing their mean movement distance with the diameter of 10 mean adult home ranges. We estimated the diameter of the mean adult raven home range based upon the mean distance between nests (Kristan 2001). For simplification, we assumed a circular adult home range. We tested for sex-related differences in movement indices t-tests (SAS PROC TTEST).

Home ranges of marked juveniles were calculated in Arcview 3.1 using the Animal Movements program (Hooge et al. 1999) and implementing a 95% fixed kernel estimator (Seaman et al. 1999). A fixed kernel estimator was chosen because kernel methods free the
utilization distribution estimate from parametric assumptions and provide a means of smoothing locational data (Worton 1989). The smoothing parameter was chosen using least squares cross-validation (Seaman et al. 1999).

If there was a strong genetic component to movement behavior, then we expected similarities in the movements between siblings, especially those of the same sex. We estimated the heritability of movement behavior using the regression coefficient from paired observations of mean movement distances between same-year siblings (SAS PROC UNIVARIATE; Price and Burley 1993, Greenwood et al. 1979). Only those individuals with at least 5 locations outside the natal territory were included in the analysis. To account for the possibility of sex biased movements, we also separately analyzed the regression coefficient from same sex and opposite sex sibling pairings.

If siblings and unrelated marked juveniles randomly assorted themselves after departure, then we expected to find them at similar distances from each other. We investigated the degree of association between siblings that survived natal departure by comparing the spacing between siblings and non-siblings. We compared the spacing between siblings located on the same day with the spacing of a randomly selected pair of unrelated juveniles located on the same day as the sibling pair. In the case of nests with more than two survivors, the sibling pair included in the analysis was randomly chosen. Each sibling pair was used only once in the analysis. The date used for each sibling pair was randomly selected from the set of days in which the sibling pair and at least 5 additional unrelated juveniles were located on the same day. From the random date, two non-sibling juveniles were randomly selected. The distances among the sibling and non-sibling pairs were compared using a Wilcoxon’s matched-pairs signed ranks test (SAS PROC UNIVARIATE).
If inbreeding avoidance influences movement behavior through environmental cues, then we expected the frequency of sibling association to differ between same sex and opposite sex pairs and we expected to observe a greater distance between opposite sex and same sex pairs during same day sightings. To investigate the role of sex in sibling associations, we compared the proportion of opposite sex pairs involved in same day sightings with the overall proportion of opposite sex pairs in the tagged juvenile population (SAS PROC FREQ). Only those sibling pairs for whom both members had a reasonable chance of detection were included in the analysis (5 or more locations for both siblings). Furthermore, if inbreeding avoidance influences movement behavior through the presence of close relatives, then we expected the overall movement distances to be greater for opposite sex sibling pairs than same sex pairs. To test for this, we compared the mean movement distance of same sex pairs with opposite sex pairs.

If resource distribution influences raven juvenile movements, then we expected the habitat use of juvenile ravens to reflect resource availability in the landscape. To characterize habitat use, proportions were calculated for the amount of habitat available and the amount of habitat used. Since the proportions of use and availability were very low for many categories, the habitats were lumped into 3 categories: natural, urban, and agricultural. Habitat use was determined by comparing the proportions of habitat use and availability (SAS PROC FREQ; White and Garrot 1990). A habitat map of the study site was constructed using GIS (ESRI 1999). Raven juvenile locations were plotted onto the digital map and each location was classified by habitat type.

If the distribution of resources influenced juvenile movements, then we also expected the initial movements of juveniles to reflect the resource availability. Specifically, we expected to find juveniles to initially depart to the nearest point subsidy if resource availability alone dictated
initial departure movements. To adequately capture the initial movements, we only included those juveniles that we initially resighted within the first 7 weeks after tagging.

Data on habitat type were obtained from the California Gap Analysis Project (Davis et al. 1998), which classifies habitat types according to plant communities recognized by the California Natural Diversity Database (CNDD 1999). The GAP data were ground-truthed for accuracy and combined with USGS 7.5-Minute Digital Raster Graphics (DRG’s) and USGS 7.5 -Minute Digital Orthophoto Quarter Quadrangles. Overall, 20 uniquely identifiable habitat types occurred within the study site.

RESULTS

Including both years, 38% (90 individuals) survived to natal departure (Webb et al. 2004). A total of 2451 relocations were obtained by tracking surviving raven juveniles from May 1999 until February 2002. The mean movement distances from the nest ranged from 1-27 km (Table 1). No sex-related differences were observed for movement distances, including the mean, initial, and maximum distance located from the nest (Table 1). No significant sex-related differences were observed for the mean distance moved between locations, the rate of movement between locations (velocity), or home range (Table 1). The majority of juveniles were philopatric in their movements (Table 1), according to Shields’ criteria. The mean movement distances for both males and females were less than half of Sheilds’ criteria (19 km). Only 13% of the juveniles (3 females and 2 males from 39 total) had mean movement distances large enough to classify them as dispersive. No individuals were known to leave the study site based upon occasional long-range searches accomplished by driving and flying outside the main study site.

The regression for mean movement distance indicated low heritability for movement
behavior by opposite-sex pairs ($r^2 = 0.07$, df = 23, $p > 0.21$, SAS PROC REG, Figure 5). The regression for mean movement distance for same sex pairs was also non-significant ($r^2 = 0.22$, df = 12, $p > 0.22$).

The spacing between all sibling pairs regardless of sex was significantly less than non-sibling pairs regardless of sex ($n = 22$, $S = -70.5$, $p < 0.01$). Although the sample size of same day sightings for opposite sex pairs ($n = 6$) and same sex pairs ($n = 16$) was too small for statistical comparison of spacing, we were able to compare the overall frequency of same day sightings for same sex and opposite sex pairs relative to their proportion in the tagged juvenile population. The frequency of opposite sex pairs sighted within the same day was not significantly less than expected ($n = 6$ of 22 total, $\chi^2 = 1.69$, $p > 0.19$) based upon the proportion of opposite sex sibling pairs with 5 or more post departure locations ($n = 11$ of 24). Furthermore, same-sex and opposite-sex sibling pairs moved similar distances ($n = 46$; $t = 0.60$; $p > 0.55$).

Juveniles utilized anthropogenic habitat (urban and agricultural habitats) more than expected, while under-utilizing natural habitats ($\chi^2 = 142.32$, $p < 0.01$). Only 3% of the total post-dispersal juvenile locations occurred in natural habitat in comparison to the number of locations in urban (64%) and agricultural habitat (33%). There was no significant relationship between the initial departure distance and nest proximity to the nearest point subsidy ($n = 28$, $r^2 < 0.01$, $p > 0.99$). There was a significant relationship between the initial departure distance and nest proximity to the nearest communal flock of ravens foraging at a point subsidy ($n = 28$, $r^2 = 0.60$, $p < 0.01$). The mean number of ravens visually estimated within a 100m radius of each relocated juvenile was 75 birds.
DISCUSSION

Unknown ontogeny

The unknown ontogeny of raven breeding behavior might explain some of our observations, including the lack of sex-biased movements. Although they reach sexual maturity after their first year, most wild ravens probably do not attempt breeding until later than their third year (Boarman and Heinrich 1999, Webb et al. 2004). Thus, the full expression of any potential sexual dimorphism in raven natal dispersal may not occur until breeding activity commences, which is outside the scope of the current investigation. At the completion of this study, the 1999 and 2000 years began their 3rd and 2nd years, respectively. No individuals were known to have attempted breeding. However, based on related studies of sub-adult and breeding ravens (Boarman, *unpub. data*), we have no reason to suspect that the pattern of juvenile and adult movements significantly differ in the western Mojave.

Resource models

The movements of juvenile ravens supported predictions based upon ecological resource models in the pattern of habitat use after departure. The null hypothesis of habitat use in proportion to availability was rejected; the great majority of juvenile post-departure locations were found in resource-rich anthropogenic habitat, either in urban or agricultural areas. This pattern is probably driven by the abundance of anthropogenic resources in these areas compared to the resource limited Mojave Desert. Sewage ponds, landfills, refuse dumpsters, and irrigation water represent some of the diverse urban resources utilized by raven juveniles. Agricultural resources occur in the form of livestock feed, manure, irrigation water, livestock carcasses, and
others. Similar patterns were reported for adult ravens (Boarman et al. in prep., Engel and Young, Heinrich et al. 1994. The relative philopatry of raven juveniles also upholds the predictions of resource models since greater movement away from abundant resources would present greater risks.

**Conspecific attraction**

Behavioral models that predict a strong innate influence in movements that function to prevent inbreeding were not supported by the low heritability in movements nor the lack of a sex-bias in movements. Movements were not driven to avoid inbreeding by environmental cues in the way that was anticipated by opposite sex siblings avoiding each other. Instead, the presence of conspecifics influenced the movements of juvenile ravens in ways not predicted by the most common behavioral models. Juveniles apparently bypassed anthropogenic resources nearby their natal territories in favor of more distant communal food resources shared by large flocks. The presence of conspecifics in a patch of habitat serves as public information (Valone 1989, Marzluff et al. 1996, Danchin et al. 2001) for foraging suitability and presents the opportunity for social interactions thought to be important for non-breeding ravens, including mate finding and forming social networks (Heinrich 1989). It is possible that some juveniles were excluded by territorial adults from some point subsidies nearby their natal territories, but the abundance and large size of many of these resources (such as sewage ponds and landfills) suggests that most point subsidies were too large for territorial defense by single pairs.

**Kin and individual recognition**

If dispersal does not function to prevent inbreeding, then selection should favor the
evolution of other inbreeding avoidance mechanisms. Kin recognition is one mechanism that may play an important role in inbreeding avoidance (Keller 1997). Discrimination of kin from non-kin has been demonstrated in a number of animal species including mammals, birds, reptiles, amphibians, social insects, colonial invertebrates and others. Evidence suggests that recognition and avoidance of close relatives as mates occurs in a variety of animals (Pusey and Wolf 1996, Radesater 1976, Burger 1998, Palestis and Burger 1999). Individuals choosing mates avoid siblings, littermates, or nestmates for breeding. Sibling recognition has been established in a number of birds (Burger 1998), and may represent a mechanism of sibling avoidance for the purpose of breeding (Keller 1997).

Individual recognition is probably an important aspect of the social ecology of ravens. During the extended pre-breeding period, the proximate benefits of individual recognition would include the ability to form hierarchies and search for mates. In this study, numerous vagrant flocks occurred throughout our study site, and frequently contained a number of marked juveniles. Although dispersed juveniles were located throughout the study site, we observed that siblings often joined the same vagrant flock. Although floater flocks are large and contain several marked individuals, we frequently observed siblings within floater flocks to be in close physical proximity to each other. Therefore, it is reasonable to expect that ravens posses the ability to recognize individual conspecifics, and one of the ultimate drivers for this capacity might include inbreeding avoidance. In this study, the physical proximity of dispersed raven siblings suggests active sibling association, and sibling recognition -which may ultimately function in part for the purpose of inbreeding avoidance.
Plasticity in dispersal

Numerous variables affect bird movements and interspecific variation complicates the likelihood for development of a unifying theory (Lambdin et al. 2001). Recent authors (Newton 1991, Verhulst 1997) suggest that problems related to dispersal models may stem from the treatment of dispersal as a fixed trait while ignoring the ability of animals to respond to environmental cues. Researchers argue that individuals use multiple cues during dispersal and recent development in this field treat dispersal as an optimization process rather than as a fixed trait (Lambdin et al. 2001, Danchin et al. 2001). However, it is likely that no single mechanism can explain the motivations for dispersal either within a population at a given time or within a given species (Dobson and Jones 1985, Clarke et al. 1997). A comprehensive understanding of dispersal may only come from considering a combination of models.

CONCLUSIONS

Raven juveniles optimize their movements (sensu Wiens 2001) using multiple cues including resources, conspecifics, and close relatives. Their movement patterns lend some support for the common dispersal models considered. The relative philopatry of raven juveniles and their selection of resource-rich anthropogenic habitat uphold the predictions of resource competition models of natal dispersal. Behavioral models based on inbreeding avoidance were not supported by the absence of a sex bias and the low heritability for movement distance. Both ecological and behavioral mechanisms influenced the tendency for juveniles to use anthropogenic habitats mostly in the presence of conspecifics. The locations of raven juveniles after departure show that siblings tend to associate more than unrelated individuals. Sibling association provides evidence for individual recognition which may serve proximate social
functions and ultimately prevent inbreeding.

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LITERATURE CITED


California Natural Diversity Database. 1999. List of California Terrestrial Natural Communities. State of California Department of Fish and Game Wildlife and Habitat Analysis Branch.


Table 1. Movements of juvenile Common Ravens in the western Mojave Desert.

<table>
<thead>
<tr>
<th>movement variable</th>
<th>males (n=24)</th>
<th></th>
<th>females (n=15)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>s.e</td>
<td>mean</td>
<td>s.e</td>
<td>t</td>
<td>p</td>
</tr>
<tr>
<td>Home range (km²)</td>
<td>142</td>
<td>71</td>
<td>188</td>
<td>10</td>
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<td>0.70</td>
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<tr>
<td>Home range width (m)</td>
<td>8890</td>
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<td>3073</td>
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<td>0.68</td>
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<tr>
<td>Mean Distance (m)</td>
<td>8584</td>
<td>1242</td>
<td>8846</td>
<td>1998</td>
<td>-0.04</td>
<td>0.97</td>
</tr>
<tr>
<td>Maximum Distance (m)</td>
<td>17828</td>
<td>2320</td>
<td>18362</td>
<td>3627</td>
<td>0.13</td>
<td>0.90</td>
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<tr>
<td>Initial Distance (m)</td>
<td>5778</td>
<td>1387</td>
<td>5984</td>
<td>1908</td>
<td>0.09</td>
<td>0.93</td>
</tr>
<tr>
<td>Between Relocations (m)</td>
<td>2897</td>
<td>518</td>
<td>4100</td>
<td>1256</td>
<td>0.89</td>
<td>0.39</td>
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<tr>
<td>Velocity (m/day)</td>
<td>624</td>
<td>136</td>
<td>576</td>
<td>181</td>
<td>-0.21</td>
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<tr>
<td>Shields’ criteria (m)*</td>
<td>19000</td>
<td></td>
<td>19000</td>
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<td>Philopatric individuals</td>
<td>22</td>
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<td>12</td>
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<td>3</td>
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</tr>
</tbody>
</table>

*Calculated as 10 x diameter of the mean nesting territory
Figure 1. Depiction of one alternative scenario for the development of natal dispersal behavior and juvenile movement behavior where natal dispersal and juvenile movements are synonymous; occurring at the same time.
Figure 2. Depiction of one alternative scenario for the development of natal dispersal behavior and juvenile movement behavior where juvenile movements occur prior to natal dispersal and the two behaviors are different.
Figure 3. Diagram of the mechanisms, cues and tests explaining natal dispersal behavior. The mechanisms range from the mostly ecological to the mostly behavioral, and are generally not considered mutually exclusive. The distribution of resources, siblings, and innate tendencies are some of the proximate cues hypothesized by various proposed mechanisms. Heritability in movement behavior, sex bias in movements and the presence of conspecifics and siblings were tests used to evaluate mechanisms and their proposed cues.
Figure 4. Location of the study area in California, USA. The dark polygons within the study area represent anthropogenic habitat, and the light portions represent natural habitat.
Figure 5. Regression of mean movement distances between the nest and post departure locations for pairs of sibling juvenile Common Ravens with 5 or more locations outside the natal territory.
Chapter 6: The spatial distribution of risk of desert tortoise (Gopherus agassizii) predation by common ravens (Corvus corax)*

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EXECUTIVE SUMMARY OF CHAPTER

In the Mojave Desert, large numbers of non-breeding common ravens live in and around human communities, while breeding ravens are more evenly distributed across the landscape. We used Styrofoam tortoise models to examine the spatial distribution of risk of raven predation on tortoises. The models, which resembled juvenile tortoises about 2 inches long, were placed at 100 sampling points on and around EAFB. Raven attacks left distinctive punctures in the top or long cuts around the sides of 29 of these bait tortoises. After 4 days, the tortoise models were retrieved and assigned scores by whether they had raven bill impressions. A computer model for risk of raven predation on desert tortoises was developed based on these data and on surveys of raven abundance at the sampling points.

Our findings suggest that areas of elevated predation risk occur under two different circumstances. First, predation risk was close to 100 percent near large groups of ravens that were distant from successful nests, usually near roads and landfills. These raven groups may have exerted a higher predation pressure than if the same area was occupied by a territorial pair of ravens because they were densely concentrated and did not spend time and energy defending resources. Second, predation risk was between 44 and 59 percent near successful nests that had relatively small numbers of ravens in the vicinity. In this case, the breeding ravens may not have spent a lot of their time defending their territory against intruders, therefore they became more effective predators. An alternative explanation is that there was an increased demand for prey near successful nests, and to meet the demand, adult ravens either spent a greater proportion of their time hunting or perhaps choose an available prey item that they might otherwise not target. Where large numbers of intruders occurred near successful nests, a rare circumstance, predation risk was 0 percent, possibly indicating that increased effort devoted to territorial defense reduced the time devoted to hunting prey by the territorial birds.
Management Implications

Desert tortoises face predation pressure from both large groups of ravens and breeding pairs; consequently, decreasing the regional raven population may be the only way to alleviate impacts on declining tortoise populations. Furthermore, areas that concentrate large number of ravens, such as landfills, may exert a disproportionate amount of raven predation on nearby tortoise populations. Such areas should be managed to reduce their use by ravens. Also, because increased raven reproductive success increases the risk of tortoise predation, features such as roads, which promote raven reproduction by providing road-killed animals as a food subsidy, may be risk factors for tortoises. Roads may provide an important subsidy in more remote areas, because, unlike towns and landfills, roads are distributed throughout both developed and undeveloped desert. To be effective, raven management must be implemented at a broad, regional level.
ABSTRACT

Common Ravens (Corvus corax) in the Mojave Desert of California, USA are subsidized by anthropogenic resources. Large numbers of nonbreeding ravens are attracted to human developments and thus are spatially restricted, whereas breeding ravens are distributed more evenly throughout the area. We investigated whether the spatial distribution of risk of predation by ravens to juveniles of the threatened desert tortoise (Gopherus agassizii) was determined by the spatial distribution of (1) nonbreeding ravens at human developments (leading to “spillover” predation) or (2) breeding individuals throughout developed and undeveloped areas (leading to “hyperpredation”). Predation risk, measured using styrofoam models of juvenile desert tortoises, was high near places attracting large numbers of nonbreeding ravens, near successful nests, and far from successful nests when large numbers of nonbreeding ravens were present. Patterns consistent with both “spillover” predation and “hyperpredation” were thus observed, attributed to the nonbreeding and breeding segments of the population, respectively. Furthermore, because locations of successful nests changed almost annually, consistent low-predation refugia for juvenile desert tortoises were nearly nonexistent. Consequently, anthropogenic resources for ravens could indirectly lead to the suppression, decline, or even extinction of desert tortoise populations.

Key words: anthropogenic resources; California; Common Raven; Corvus corax; desert tortoise; Gopherus agassizii; hyperpredation; Mojave Desert; prey decoy; spatial distribution of risk; spillover predation.

INTRODUCTION

Common Ravens (Corvus corax) in the west Mojave Desert of California, USA are strongly
associated with human developments (Boarman 1993, Kristan 2001). Ravens nest preferentially near anthropogenic features like housing developments and landfills, and raven reproduction is poor in isolated desert habitat, far from anthropogenic resource subsidies (Kristan 2001, Webb 2001). Large numbers of this native species are only consistently found at anthropogenic sites in the Mojave (Knight et al. 1993; W. I. Boarman, unpublished data), and raven numbers have increased 1500% over the last several decades, concomitant with urban growth in the region (Boarman 1993, Sauer et al. 2000). Strong association with, and apparent reliance on, human resources in the Mojave Desert makes the common Raven a human commensal in this habitat (Knight et al. 1993).

Although raven populations are most dense in rural and urban areas (Knight and Kawashima 1993, Knight et al. 1993; W. I. Boarman, unpublished data), the limited availability of urban nest sites in lightly populated parts of the Mojave Desert means that 62% of ravens nest .2 km from human resource subsidies in undeveloped desert (Kristan 2001). Ravens scavenge when refuse and carrion are available, but they are also capable hunters that prey on small vertebrates and invertebrates, including the threatened desert tortoise (Gopherus agassizii; Camp et al. 1993, Boarman and Berry 1995, Boarman and Heinrich 1999). Ravens have been observed to attack and kill juvenile tortoises from within experimental enclosures (Morafka et al. 1997). Juvenile tortoise shells are also commonly found beneath raven nests in this area (W. I. Boarman, unpublished data). Because of their large numbers and conspicuous predation of tortoises, ravens have been implicated as a contributor to tortoise population declines, and as a potential impediment to tortoise recovery (Boarman 1993, United States Fish and Wildlife Service 1994).

Predators reduce prey numbers and, in some circumstances, can contribute to their extinction (Smith and Quinn 1996, Polis et al. 1997, Sinclair et al. 1998, Namba et al. 1999). The greatest predatory impact should come from subsidized generalist predators such as corvids (Andrén et al. 1985,
Andrén 1992), whose numbers remain high when prey populations decline, and which continue to depredate a species that is at very low densities (Polis et al. 1997, Sinclair et al. 1998). However, differences in the spatial distributions and behavior of breeding and nonbreeding ravens in the Mojave complicate predictions of their impacts on prey. Anthropogenic sites such as landfills provide superabundant, continuously replenished food (Restani and Marzluff 2001), and the large groups of well-fed ravens found at landfills may not need to hunt in surrounding lands. However, if these groups of ravens do hunt, they are most likely to impact prey populations through “spillover” predation into adjacent undeveloped areas (Holt 1984, Chapman et al. 1996, Schneider 2001). In contrast, breeding ravens are broadly distributed throughout both developed and undeveloped habitats. Although territorial behavior keeps breeding densities low compared with densities of nonbreeding birds, most breeding ravens do not have anthropogenic subsidies within their territories, and they may be forced to hunt rather than scavenge. The large breeding population throughout undeveloped habitats would produce a pattern of predation consistent with “hyperpredation” (Erlinge et al. 1983, Crooks and Soulé 1999, Courchamp et al. 2000). Both patterns of subsidized predation have the potential to contribute to tortoise population declines. However, spillover predation would remain spatially restricted as long as anthropogenic sites remain spatially restricted, whereas hyperpredation could affect prey throughout the prey’s habitat. These different effects suggest different remediation strategies. Thus, understanding patterns of predation is important for understanding the population biology of, and appropriate conservation strategies for, their prey.

Predation risk, the probability of being killed by a predator in a given interval of time (Lima and Dill 1990), is an important determinant of predation pressure. Attack rates are good measures of predation risk for species that have a limited ability to escape an attack, such as juvenile desert tortoises. We investigated whether the different spatial distributions of breeding and nonbreeding ravens are
associated with differences in predation risk for their prey. We measured predation risk using artificial juvenile desert tortoise models as bait, placed throughout a 770 km² area, and related raven attacks on baits to the distribution of ravens, raven nests, and anthropogenic developments. Based on these relationships, we mapped predation risk throughout the study area to examine its spatial variation and to evaluate whether there are areas of low predation that could act as refugia for raven prey.

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 western Mojave Desert of California (Fig. 1). The study area covered 770 km². The small number of human developments, such as towns, artificial water bodies, and landfills, were distributed throughout the area, surrounded by undeveloped shrublands. Shrubland vegetation was composed of creosote bush (*Larrea tridentata*) and salt bush (*Atriplex* spp.) scrub, often forming a sparse woodland in association with Joshua tree (*Yucca brevifolia*).

Artificial, permanent water bodies were sources of water, food, and riparian vegetation. The larger body (Piute Ponds) was an artificial wetland within EAFB that contained well-developed riparian vegetation, including willows (*Salix* spp.), cattails (*Typha* spp.), and rushes (*Juncus* spp.). Piute 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 (population 3763) and Rosamond (population 7430).

The military lands outside the cantonment at EAFB are used primarily for military aircraft training, with little disturbance to the vegetation. Undeveloped lands outside of the EAFB boundary
were used for a variety of purposes, including recreation and sheep grazing. The housing area within EAFB (population 7423) and the towns of Rosamond and Mojave consisted of single-family homes, apartment complexes, and commercial developments (e.g., restaurants, grocery stores, etc.). Solid waste disposal sites (landfills) were present near EAFB housing and southeast of Mojave.

**Raven Populations**

During the spring, the raven population consisted of breeding birds distributed throughout the study area and nonbreeding birds that aggregated in conspicuous flocks near anthropogenic developments. Most of the known nests were in Joshua trees (57%), but were also found in telephone and electrical utility poles (27%), trees (ornamental landscaping; 13%), buildings (1.5%), and cliffs (1.5%). Nests were located by searching the study area each spring in the years 1996–2000. Nests were commonly reused between seasons, but new nests were discovered each year. By 2000, we were monitoring 305 nest sites within the study area, of which 225 were occupied by ravens for at least part of the nesting season (between March and early July).

**Experimental Protocol**

*Selection of sampling points*

We established sampling points (n = 100) in scrub habitat throughout the study area in March 2000. Points were selected to provide even coverage of the region. Distances between sampling points averaged 1497 m, which is slightly greater than the average spacing between occupied territories (1134 m). Because breeding ravens spend 90% of their time within 400 m of their nests (Sherman 1993), the spacing between points prevented double counting of individuals during raven counts, and prevented individual ravens from encountering multiple baits during predation risk trials. No points were placed in
the dry lake bed (Fig. 1) because we considered it unsuitable habitat for ravens and desert tortoises. At each point, we collected data on the number of ravens present, distance to anthropogenic sites and raven nests, and raven predation. Sampling points were embedded within the area where we searched for raven nests in order to avoid introducing edge effects into our distance measures.

**Raven distributions**

Locations of raven nests were known because of concommittant reproductive monitoring. We characterized the distribution of raven individuals using 10-minute unlimited-radius point counts, conducted within four hours of dawn (Ralph et al. 1995). Both the total number of ravens observed and the number observed within 200 m of the sampling point were recorded. Counts were conducted on either the first or the last day of a predation risk trial to ensure that they accurately represented the distribution of raven individuals at the time of the trial. All counts were conducted between 30 March 2000 and 25 May 2000.

**Predation risk trials**

We standardized the measurement of relative risk of attack by ravens across a large area. We chose to use baits, placed throughout the study area, as our measure of relative predation risk. This had the advantage that we did not have to rely on error-prone estimates of the distribution of particular prey to estimate predation risk. Because ravens have flexible foraging behaviors (including both hunting and scavenging; Boarman and Heinrich 1999) and an eclectic diet (including refuse, small mammals, arthropods, birds, plants, reptiles, and carrion of all kinds; Camp et al. 1993; Kristan, W. B. III, W. I. Boarman, and J. Crayon, unpublished manuscript), we considered attacks on baits to be a reasonable approximation of predation risk to any vulnerable animal encountered by a raven.
Artificial baits were selected following attempts in 1999 to use baits made of foods (dog biscuits) that were disrupted by nontarget species, such as canids and small mammals. We selected styrofoam models of the desert tortoise as our baits because tortoises were known to occur on the study area, are eaten by ravens (Boarman 1993), and are a threatened species. Desert tortoises are diurnal, and their most active season coincides with the raven breeding season (Berry and Turner 1986, Ernst et al. 1994). We obtained the baits from the USDI Bureau of Land Management, which originally made them to study tortoise trampling by livestock by placing known numbers of models in areas of grazed desert scrub. During that study, ravens were observed attacking the models (G. Goodlett and P. Frank, personal communication), leading us to believe that the models could be used to estimate raven attack rates. The models were shaped like tortoise shells and were painted to resemble desert tortoises. Ravens are only known to depredate juvenile desert tortoises with carapace lengths, 100 mm or less, usually by piercing the carapace with their bills or biting at the head or limbs (Boarman and Heinrich 1999). Our models were made from a single mold and were 62 mm long, which is within this vulnerable size range. Raven attacks on the baits left distinctive punctures in the top or long cuts around the sides. Red-tailed Hawks (Buteo jamaicensis) were also present in the area at much lower numbers than ravens, but raptors have sufficiently different bill morphology and eating modes that misidentification was unlikely. None of the models used in this study showed signs of attack from other species, avian or mammalian.

Styrofoam tortoise baits were attached to 10-inch (25.4-cm) spikes in the ground with pieces of adhesive backed industrial Velcro (Velcro USA, Manchester, New Hampshire, USA). Baits were placed within the shrub habitat at the sampling point, in areas that provided an unobstructed view from above. Each week between 27 March and 25 May 2000, single baits were placed at 10–15 sampling points and were left for four nights. This period is in the middle of the raven nesting season, with 63% of initiated breedings occurring after 27 March and 71% of successful fledging occurring after 25 May 2000.
Kristan 2001). The points were not visited during the four-day sampling interval to avoid affecting the behavior of the ravens, and each point was sampled only once to avoid conditioning ravens to avoid the inedible baits. The spacing between sampling points (see Selection of sampling points) minimized the chances that individual ravens would encounter multiple baits and learn to avoid them. 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, such as towns, landfills, and water bodies, were identified from USGS Geographical Names Information System data, augmented by sites that we identified in the field. Roads were associated with increased raven reproductive success (Kristan 2001); because road-killed carrion potentially could also attract individual ravens, we considered roads to be potential risk factors for raven prey. Locations of paved roads with high traffic volume 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 were most likely to produce enough carrion to subsidize raven reproduction (Kristan 2001).

**Distance measurements**

Distances from sampling points to anthropogenic sites and nests were measured using a geographic information system (ArcView 3.2 [ESRI 2000]; GRASS 5.0 [Neteler and Mitasova 2002]). We scored each nest by whether it was occupied (adults present in the territory), whether breeding was initiated (presence of eggs, incubation, etc.), and whether successful fledging was observed. Mean distances to the five nearest occupied nests or nests with breeding initiated were calculated for further analyses, but the distance to the single nearest successful nest was used because of
the smaller number of successful nests. Finally, we also scored each point by the number of chicks fledged from the closest successful nest.

**Statistical Analysis**

*Distribution of raven individuals*

The association between counts of individual ravens and proximity to anthropogenic sites and raven nests was evaluated using Poisson regression (the most appropriate error structure for discrete count data; Venables and Ripley 1994). We modeled both the total number of ravens observed at a point and the subset of ravens that were within 200 m of the point. Distances to anthropogenic point subsidies and roads were used in all models. For this analysis, we wished to evaluate whether local breeding activity contributed to variation in raven numbers throughout the area, and whether one of the four alternative measures of local breeding activity was best at explaining variation in raven numbers. We addressed these questions by comparing the relative effects of the breeding status of the nearest nests (occupied, breeding initiated, successful, number fledged) on raven counts. We compared the statistical support for models that included nests of each breeding status to one model that included no measure of breeding activity (i.e., only roads and point subsidies). Model support was assessed using Akaike’s Information Criterion values, AIC (Burnham and Anderson 1998). The strength of support for each model was evaluated using Akaike weights, \( w \) (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 with \( w \geq 0.9 \) is considered to be best supported, but lacking a best supported model, models that are within four AIC units of the model with the highest \( w \) are considered plausible explanations for the data, and worth further consideration. Lack of a model with \( w \geq 0.9 \) can occur either when different models make similar
predictions or when sample sizes are inadequate to distinguish models that make distinct predictions.

_Determinants of raven predation risk_

We modeled raven attacks on styrofoam tortoise baits by using logistic regression. We compared the AICs of models including different combinations of distances to anthropogenic sites, counts of raven individuals, distances to raven nests of different breeding status, or the number of chicks fledged from the nearest successful nest. The last variable was used to evaluate whether the risk of predation from breeding ravens was related to the food requirements of their brood. We constructed an initial set of models that included the number of ravens observed within 200 m of the sampling point, a measure of human development (either distance to roads or point subsidies), and a measure of raven breeding activity (territory occupied, breeding initiated, successful breeding, number of chicks fledged). Additional models were then generated by omitting interaction terms and variables from the original set to see whether simpler models were better supported.

_Spatial distribution of raven predation risk_

We mapped the probability of attack predicted from the best supported predation risk models to assess whether the spatial structure in anthropogenic sites and association of ravens with those sites resulted in areas of low predation risk within the study area. Values for each independent variable were derived using GIS. The number of ravens was estimated by interpolating pointcount data using regularized spline with tension techniques (Mitášová and Mitáš. 1993).
Consistency of breeding activity over time

Although predation risk trials were only conducted during 2000, breeding activity at nests varies over time. The consistency of spatial variation in predation risk over time consequently could depend on the consistency of breeding activity at known raven nests over time. The number of years that territories were occupied and the number of years of successful reproduction were related to the number of years observed, distance from roads, and distance from anthropogenic subsidies. Because nests were observed for different numbers of years, regression models were used to predict the number of years that territories were occupied and the number of years they were successful out of five years of observation at the minimum (0 m) and maximum (10 500 m) observed distances from roads and at the minimum (0 m) and maximum (14 000 m) observed distances from anthropogenic subsidies.

RESULTS

Distribution of Raven Individuals

The number of ravens in unlimited-radius counts was $2.49 \pm 3.55$ individuals (mean $\pm$ 1 SD) and the number within 200 m of the sampling point was $0.55 \pm 1.17$ individuals. Raven numbers declined with increasing distance from point subsidies in all models, and no other variable made significant, unique contributions to raven numbers in all models for unlimited-radius counts (Table 1). The best supported overall model (i.e., the model with the lowest AIC) included the number of chicks fledged from the nearest successful nest, but distance to nests with breeding initiated received moderately strong support (i.e., the $\Delta$AIC was within four units of the best model, and the $wi$ for the best model was less than 0.90; Burnham and Anderson 1998).

Although model $R^2$ values ranged from 0.24 for Model 4 to 0.28 for Model 1 for unlimited-
radius counts, model $R^2$ values 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 nests with breeding activity initiated (Table 2, Model 2), but the model including the mean distance to the five nearest occupied nests resulted in similar AIC values (Table 2, Model 1). Distances to occupied nests and to initiated nests were strongly correlated ($r = 0.91$), and this redundancy is reflected in the similar statistical support; omitting Model 1 from the set raised the $w_i$ for Model 2 to 0.84, with the next best supported model (Model 3) having $w_i$ of 0.07. Ravens declined in number with increasing distance from point subsidies in each model. Distance from roads did not affect raven counts in any model.

**Determinants of Raven Predation Risk**

Of the 100 baits used in this study, 29 were attacked by ravens. Attack rates declined slightly, but significantly, over time ($x^2 = 3.85$, df = 1, $P = 0.049$), and date was included as a nuisance covariate in subsequent analyses. Statistical support was moderately strong for two models, with all other models receiving $\Delta$AIC greater than four units. The model with the largest $w_i$ included 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 3). The next best supported model added distance to anthropogenic point subsidies to the first model, and all of the two-way interactions between the three variables. The interaction between distance from successful nests and numbers of ravens was well supported (i.e., the AIC increased substantially, and the model became nonsignificant when the interaction term was omitted) and indicated a nonlinear relationship between these variables and predation risk. All univariate models were poor predictors of predation risk. Models including nest success measures (i.e., distance to successful nest or number of chicks fledged) were better supported than models including breeding
initiation or nest site occupancy.

The nonlinear relationship between predation risk and the number of ravens observed and the distance from successful nests is best displayed graphically (Fig. 2). Near successful nests (i.e., within 1 km), predation risk decreased as the number of ravens observed increased. Far from successful nests (i.e., >2–3 km), predation risk increased with an increasing number of ravens. Between these distances, predation risk became insensitive to variation in raven numbers. Within the range of variation observed in numbers of ravens and distance to successful nests, the predicted probability of attack changed from <0.1 to >0.9. The next best supported model included distance from anthropogenic point subsidies (Fig. 3). The greatest effect of point subsidies can be seen when few ravens were observed; being near point subsidies increased the probability of attack near successful nests (distance to subsidies = 0 km; Fig. 3A), and being far from point subsidies decreased the probability of attack near successful raven nests (distance to subsidies = 8 km; Fig. 3C).

Spatial Distribution of Raven Predation

The largest area with maximum estimated numbers of ravens was near the Edwards housing area and landfill, with pockets of elevated numbers near other point subsidies, such as the ponds in the southeast and southwest and the Mojave landfill in the northwest (Fig. 4).

Predicted risk levels from the two best supported models were very similar (Figs. 5 and 6) and highly correlated ($r = 0.947$). Areas that had large numbers of ravens but were far from successful nests received the highest predicted risk, and these areas occurred near the landfills (Figs. 5 and 6). Pockets of elevated risk were also found in the vicinity of successful nests in remote areas. The predicted number of ravens at successful nests ranged from 0.012 to 7.119 individuals, which resulted in an estimated predation risk at successful nests (i.e., distance from successful nest = 0) that ranged from 0.004 to
Adding distance to subsidies did not change the locations of high and low risk, but reduced the probability of attack in the most isolated areas. At successful nests, the estimated probability of attack ranged from 0.004 to 0.595.

**Consistency of Breeding Activity Over Time**

The number of years that a territory was occupied was not affected by distance to roads or by distance to point subsidies (deviance = 3.44, df = 2, \( P = 0.179 \)), but the number of years of successful reproduction was greater near roads and near subsidies (deviance = 38.31, df = 2, \( P < 0.001 \)). Predictions of the number of years of occupation were therefore relatively similar across the distances to roads or subsidies, but the predicted number of years of success was greater near roads and subsidies, with subsidies having the larger effect (Table 4).

**DISCUSSION**

**Determinants of Raven Numbers**

Greater numbers of ravens were observed near human developments. Although our sampling was not stratified by land-use types, this result reflects the association of large groups of ravens in the Mojave Desert with anthropogenic sources of food and water (Knight et al. 1993; W. I. Boarman, *unpublished data*), such as landfills and artificial water bodies. However, because many developments did not attract ravens, regressions of raven counts on distance to human developments, independent of measures of nesting activity, were poorly supported (Model 4 in Tables 1 and 2) in spite of the consistent association of flocks of ravens with human developments. We believe that this is due to a strong influence of raven social structure on the distribution of individuals. Nonbreeding ravens are gregarious and use conspecifics as cues of food availability (Marzluff et al. 1996). In our study
population, fledging chicks move to anthropogenic resources that have flocks of ravens, even if other anthropogenic resources are closer (Webb 2001). This conspecific attraction leaves some sites unoccupied in spite of the resources available.

The effect of breeding ravens on the distribution of individuals was well supported, although different measures of breeding activity were associated with ravens observed within 200 m of the sampling point than with those observed in an unlimited radius. Breeding ravens maintain large exclusive territories (5.1 km² in coastal southern California; Linz et al. 1992), but their territorial defense can be overcome by large numbers of intruders (Dorn 1972, Boarman and Heinrich 1999). In our study, breeding ravens apparently were not able to defend anthropogenic subsidies, even when the subsidies were small enough to fall entirely within a typical raven territory, such as the Mojave landfill. Furthermore, proximity to occupied nests had relatively little influence on observed numbers of ravens in an unlimited radius (Table 1), whereas proximity to both occupied nests and nests with initiated breeding influenced the numbers of ravens observed within 200 m (Table 2). We believe that this is because areas far from anthropogenic subsidies typically do not attract large groups of nonbreeding individuals, and the only ravens that are commonly observed in isolated parts of the study area are breeding individuals. Individuals that are outside of defended territories and at distant resource subsidies could be included in unlimited-radius counts, thereby weakening the effect of local breeding activity.

Determinants of Raven Predation Risk

The effect of raven abundance on predation risk depended on distance from the nearest successful nest (Figs. 2 and 3). Proximity to successful nests was not strongly associated with variation in counts of ravens; thus, successful nests represented a source of predation risk distinct from the effect of raven abundance at a sampling point. Predation risk increased with increasing raven numbers far from
successful nests, but decreased with increasing raven numbers close to successful nests. The nonlinear relationship between predation risk, raven numbers, and distance to successful nests can be understood in the context of the social structure of raven populations. Only the breeding adults would pose a predation risk within a successfully defended territory, with risk increasing closer to the nest. Counts of raven individuals typically would be low in most parts of a defended territory, because only the breeding adults would be present. Intruding birds could increase the numbers counted, but intruders are actively chased by the territory holders, and would therefore have little opportunity to contribute to predation risk. Under these circumstances, predation risk would be insensitive to the number of ravens observed, as was seen at intermediate distances from nests. Low predation risk in the presence of large numbers of intruders near successful nests could indicate that increased effort devoted to territorial defense reduced the time devoted to foraging by the territorial birds. However, the combination of close proximity to successful nests and large counts of ravens was rare, and this interpretation is thus tenuous. Points with large counts far from nests, and therefore outside of defended territories, would be subject to predation risk from all of the ravens observed; accordingly, we found that predation risk increased with increasing numbers of ravens when points were far from successful nests.

Although two models with different measures of breeding activity had similar effects on counts of ravens, the two models of predation risk with the greatest support both included distance to successful nests (Table 3). This result is consistent with the need for territorial, breeding ravens to rely more heavily on natural prey than on anthropogenic food subsidies. While chicks are in the nest, ravens behave like central-place foragers and spend most of their time within 400 m of their nests (Sherman 1993). Ravens that either did not initiate breeding, or initiated breeding and failed early in the nesting cycle, would be less strongly tied to a nest site and would be released from satisfying the food requirements of a brood. Thus, even though ravens were known to be present at nests classified as
“occupied” and “breeding initiated,” these nest sites did not represent predictable predation risk factors.

At the outset, we hypothesized that anthropogenic sites that only occasionally attracted small numbers of ravens, but did not consistently attract large flocks of birds, could still expose prey to elevated predation risks. However, we found that proximity to an anthropogenic site had a weak relationship with predation risk compared with the effects of large, persistent flocks of ravens. Although anthropogenic developments are a precondition for the presence of large populations of ravens in the region, not all developments attract large, conspicuous groups of ravens, and thus are not intrinsic risk factors for raven prey.

Predation risk is defined as the probability of being killed by a predator in some defined period of time (Lima and Dill 1990). Attack rates are a component of predation risk that includes both the probability that ravens will encounter the bait and the probability that they will attack it once they find it. The final component of predation risk, the probability that prey will be killed, given a raven attack, is not directly modeled by our methods. However, we assumed that attack rates on our artificial baits were a reasonable index of desert tortoise predation risk because of the varied diet and opportunistic foraging habits of ravens (Engel and Young 1989, Stiehl and Trautwein 1991, Camp et al. 1993, Sherman 1993, Nogales and Hernandez 1997), and because of the limited ability of juvenile tortoises to escape ravens during an attack (Ernst et al. 1994). Predation risk for other species may also be indexed by attacks on our baits, although encounter and attack rates vary by prey species, depending on crypsis and palatability (Brodie 1993). However, to derive quantitative estimates of predation risk for the desert tortoise or any other raven prey species (e.g., for use in predator–prey models), attack rates on artificial baits would need to be related to encounter, attack, and escape rates for living animals.
Spatial Distribution of Raven Predation Risk

Although proximity to anthropogenic subsidies was supported as an important factor in determining predation risk (Table 3), the effect was small and parallel to the effects of observed raven numbers. The predicted values from the models that included anthropogenic subsidies (Fig. 6) and excluded anthropogenic subsidies (Fig. 5) were so similar ($r = 0.95$) that we will hereafter discuss the two patterns simultaneously.

Areas of elevated predation risk occurred near large groups of ravens that were distant from successful nests, as well as near successful nests that had relatively small numbers of ravens in the vicinity (Figs. 5 and 6). Observed numbers of ravens had the greater effect, with probability of attack nearing 1.0 (100%) near the largest raven groups at landfills. However, the probability of raven attack at successful nests reached 0.44 and 0.59 for predictions that excluded or included distance from anthropogenic sites, respectively. Because human developments are maintaining such artificially high raven populations (Boarman 1993), we considered predation risk that was attributable to ravens to be, by definition, an artificially elevated predation risk by a subsidized predator. Although both breeding and nonbreeding ravens were associated with elevated predation risk, the distinctly different patterns of predation risk from nonbreeding vs. breeding ravens suggest different patterns of effect on prey populations.

For a species such as the desert tortoise, which has limited ability to evade ravens, the spatial distribution of predation risk should be closely related to spatial variation in mortality and predation pressure. Different theories relate predation pressure from subsidized predators to prey population dynamics, depending on the degree of spatial segregation between predator and prey. The high predation risk observed near large, persistent flocks of ravens at anthropogenic sites is likely to act as “spillover” predation (Holt 1984, Schneider 2001). If the predator’s habitat is sufficiently intermixed with the prey’s
habitat, then spillover predation can extirpate prey (Holt 1984, Schneider 2001). However, as long as the predator’s habitat remains small relative to the area of habitat that is unsuitable for the predator, this pattern of predation will leave refugia of low predation risk (Chapman et al. 1996). Breeding ravens also appear to produce a spatially restricted risk of predation within a breeding season (Fig. 5). However, the spatial distribution of breeding activity is much less consistent over time than the spatial distribution of groups of nonbreeding ravens, and is less likely to leave prey refugia. For example, 62% of the 305 nests that we observed were occupied every year that they were observed (range 1–5 years of observation), but only 18% of the 54 nests observed in all five years of the study were occupied every year. None of the nests occupied for five years was successful every year, and only 10% were successful for four years out of the five (Kristan 2001). Our results suggest that as the spatial distribution of successful nests changes over time, the location of areas of high predation risk due to breeding ravens also changes from year to year. Juvenile desert tortoises have soft shells and are within the vulnerable size range for raven predation for 5–6 years (Ernst et al. 1994). Consequently, the effects of raven predation risk would average over several years, further reducing the effectiveness of refugia, and the only potential refugia would be in areas far from human developments and in habitat that is unattractive to ravens.

Predators that occupy the same habitat as the prey can still be subsidized if the prey base is sufficiently diverse (Erlinge et al. 1983), or if alternative prey species that are more tolerant of heavy predation are available to sustain a large predator population (Courchamp et al. 2000). This pattern of predation has been called “hyperpredation,” because the predator population is insensitive to reductions in the target prey population size, and the predator can continue to depredate the target prey at very low prey population sizes. Ravens in the Mojave are supported by human resources, but breeding ravens occupy expanses of undeveloped habitat, where their predatory effects will more closely resemble hyperpredation than spillover predation. Models of the effects of predation pressure on prey populations
usually make the simplifying assumption that all individuals of a predator species exhibit the same predatory behavior (Holt 1984, Courchamp et al. 2000, Schneider 2001). Our results suggest that behaviorally flexible species can simultaneously produce more than one pattern of predation, and may thus impose a greater threat of extinction for their prey.

Conservation Implications

Anthropogenic point subsidies and roads affect raven breeding success (Kristan 2001), but do not increase predation risk unless these developments are associated with large groups of ravens. Maintaining large areas of undeveloped habitat should protect prey from these large groups of ravens. Single successful raven nests pose a comparatively smaller direct threat to prey, but raven nests are more evenly spread through the landscape and over time may have similar overall impacts on a prey population. Decreasing the regional raven population size, or decreasing raven reproductive success in tortoise habitat, may be necessary to reduce the predation risk from breeding ravens.

We do not know that ravens have contributed to the decline of desert tortoises in our study area. However, abundant predators are capable of suppressing population growth of even highly productive prey such as rabbits when they are at low population levels (Newsome et al. 1989). Likewise, the commensal raven populations supported by human activities in the West Mojave Desert may inhibit recovery of desert tortoise populations. To the extent that human activities facilitate raven occupation of this area, the impacts of both breeding and nonbreeding Common Ravens on desert tortoises can be considered an indirect effect of human developments in the desert.

ACKNOWLEDGMENTS

Funding was provided by Edwards Air Force Base and the USGS Biological Resources Division.
This manuscript benefited from comments from J. T. Rotenberry, M. V. Price, J. Lovich, and two anonymous reviewers. M. Hagan, W. Deal, G. Goodlett, and T. Okamoto provided invaluable logistical and field support.

LITERATURE CITED


ESRI. 2000. ArcView 3.2. ESRI, Redlands, California, USA.


Table 1. The effects of point subsidies, roads, and distances to nests of ravens of different breeding status on numbers of ravens observed in unlimited radius point counts.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Coefficient</th>
<th>Std. Error</th>
<th>z</th>
<th>P</th>
<th>AIC a</th>
<th>ΔAIC b</th>
<th>w_i c</th>
</tr>
</thead>
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<td></td>
<td></td>
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<td>-8.24</td>
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<td>Roads</td>
<td>4.08E-05</td>
<td>4.37E-05</td>
<td>0.93</td>
<td>0.351</td>
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<td>427.0</td>
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<td>Number fledged</td>
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<td>Point subsidies</td>
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<td>4.11E-05</td>
<td>-8.46</td>
<td>&lt; 0.001</td>
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<td></td>
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</tr>
<tr>
<td>Roads</td>
<td>8.19E-06</td>
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<td>0.18</td>
<td>0.856</td>
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</table>

*a Akaike's Information Criterion

*b The difference between the model AIC and the smallest AIC in the set under consideration

*c Akaike weights
Table 2. The effects of point subsidies, roads, and distances to nests of ravens of different breeding status on numbers of ravens observed within 200 m of the sampling point.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Coefficient</th>
<th>Std. Error</th>
<th>z</th>
<th>P</th>
<th>AIC a</th>
<th>∆AIC b</th>
<th>wi c</th>
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<td>Model 1</td>
<td></td>
<td></td>
<td></td>
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<td>211.4</td>
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<td></td>
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<td>Roads</td>
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<td>0.554</td>
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<td></td>
<td></td>
<td>209.8</td>
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<td>0.61</td>
</tr>
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<td>-2.55</td>
<td>0.011</td>
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<td>214.8</td>
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<td>215.4</td>
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<td>0.04</td>
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<td>-0.74</td>
<td>0.462</td>
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<td></td>
<td>216.2</td>
<td>6.4</td>
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<td>-5.05E-05</td>
<td>1.03E-04</td>
<td>-0.49</td>
<td>0.625</td>
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a Akaike's Information Criterion

b The difference between the model AIC and the smallest AIC in the set under consideration
c Akaike weights
Table 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. All models include the date of the predation risk trial as a nuisance covariate.

<table>
<thead>
<tr>
<th>Model</th>
<th>DF</th>
<th>P</th>
<th>AIC&lt;sup&gt;a&lt;/sup&gt;</th>
<th>ΔAIC&lt;sup&gt;b&lt;/sup&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
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<td>Close ravens*successful nest</td>
<td>4</td>
<td>0.01</td>
<td>115.19</td>
<td>0.0</td>
<td>0.57</td>
</tr>
<tr>
<td>Close ravens*subsides +</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>close ravens*successful nest +</td>
<td>7</td>
<td>0.02</td>
<td>118.59</td>
<td>3.4</td>
<td>0.11</td>
</tr>
<tr>
<td>subsidies*successful nest</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Close ravens<em>subsides</em>successful nest</td>
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<td>0.03</td>
<td>119.82</td>
<td>4.6</td>
<td>0.06</td>
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<td>Close ravens<em>roads</em>successful nest</td>
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<td>0.07</td>
<td>119.85</td>
<td>4.7</td>
<td>0.06</td>
</tr>
<tr>
<td>Close ravens*roads +</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>close ravens*successful nest +</td>
<td>7</td>
<td>0.07</td>
<td>120.03</td>
<td>4.8</td>
<td>0.05</td>
</tr>
<tr>
<td>roads*successful nest</td>
<td></td>
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<tr>
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<td>120.78</td>
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<td>0.04</td>
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<tr>
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<td>121.83</td>
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<td>0.02</td>
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<td>AIC</td>
<td>Parameter</td>
<td>AIC</td>
<td>Parameter</td>
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<tr>
<td>Close ravens<em>subsidies</em>initiated nests</td>
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<td>0.18</td>
<td>127.68</td>
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\textsuperscript{a} Akaike's Information Criterion

\textsuperscript{b} The difference between the model AIC and the smallest AIC in the set under consideration

\textsuperscript{c} Akaike weights
Table 4. Predicted numbers of years occupied and years successful out of five at two distances to point subsidies and two distances to roads. Numbers in table cells are predictions (s.e.).

<table>
<thead>
<tr>
<th>Distance to roads (km)</th>
<th>Distance to point subsidies (km)</th>
<th>Territory predictions ± 1 SE</th>
<th>No. years occupied</th>
<th>No. years successful *</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>3.92 ± 0.29</td>
<td>1.89 ± 0.23</td>
<td></td>
</tr>
<tr>
<td>10.5</td>
<td>0</td>
<td>2.99 ± 0.63</td>
<td>0.42 ± 0.18</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>14</td>
<td>3.14 ± 0.80</td>
<td>0.28 ± 0.14</td>
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<tr>
<td>10.5</td>
<td>14</td>
<td>2.40 ± 0.58</td>
<td>0.06 ± 0.03</td>
<td></td>
</tr>
</tbody>
</table>

* Years successful were significantly associated with both distance to roads and distance to point subsidies.
Figure 1. Study area map. The gray 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 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 predation (i.e. attack by a raven on a styrofoam tortoise model).
Figure 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 (A-C) on predation risk.
Figure 4. Interpolated raven numbers, based on ravens observed within 200 m of sampling points. Pixel values range from 0 (black) to 8 (white). Locations of successful nests are marked with diamonds.
Figure 5. Estimated predation risk, based on the number of ravens at each pixel (interpolated from point-count data) and distance from the nearest successful nest. Successful nests are marked with diamonds. Probability of attack ranges from 0 (black) to 1 (white). The dry lake (uniformly light gray area) is unsuitable habitat for ravens or tortoises.
Figure 6. Estimated predation risk, based on the number of ravens at each pixel (interpolated from point-count data), distance from the nearest successful nest, and distance from the nearest point subsidy. Successful nests are marked with diamonds. Probability of attack ranges from 0 (black) to 1 (white). The dry lake (uniformly light gray area) is unsuitable habitat for ravens or tortoises.
Chapter 7: Recommendations for Management of Ravens at Edwards Air Force Base*

William I. Boarman, USGS-BRD, Western Ecological Research Center, San Diego, CA 92123

EXECUTIVE SUMMARY OF CHAPTER

Human communities often are an inadvertent source of food, water, and other resources to native species of wildlife. Because these resources are more stable and predictable than those in a natural environment, animals that subsist on them are able to increase in numbers and expand their range, much to the detriment of their competitors and species they prey upon. In the Mojave Desert, common ravens (*Corvus corax*) have benefited from human-provided resources to increase in population size precipitously in recent years. This trend has caused concern because ravens prey on juvenile desert tortoises (*Gopherus agassizii*), a federally threatened species. Active management may be necessary to overcome the imbalance that favors ravens at the expense of native prey, especially the desert tortoise.

In this chapter, I discuss management strategies to reduce raven predation on desert tortoises in and around EAFB. These suggestions are based on my own ongoing research into the raven problem in the Mojave Desert as well as a thorough literature search. The resulting recommendations fall into three categories. The first recommendation is to manage raven populations by reducing access to anthropogenic resources. Our research suggests that landfills are the most important anthropogenic resource for ravens; therefore, we recommend that changes in landfill operating procedures implemented during the study be continued and perhaps applied more rigorously. Furthermore, they should be employed at other landfills in the region. Other important anthropogenic sources of food and water for ravens that also need to be restricted include sewage ponds, dairy farms, and dumpsters behind restaurants. Because of ravens wide-ranging movements, it is essential that raven management occur at a regional level; changes implanted at EAFB are not likely to have a lasting effect if they are not also implemented beyond the base’s boundaries. Thus, EAFB should attempt to work with agencies responsible for managing neighboring lands to reduce their facilitation of raven populations.

The second recommendation is the limited use of lethal removal of offending ravens or birds in
specially-targeted tortoise management zones. Such practices can be very controversial and their long-term effectiveness is questionable; therefore, we recommend limited use of lethal removal. It may be a valuable tool when a given pair of ravens is a “known offender” based on finding tortoise shells beneath their nests or perches. In addition, lethal removal may be warranted in areas designated as critical habitat for tortoise recovery. Lethal removal may not be warranted at EAFB until active evidence of predation is found. However managers may want to remove ravens from the immediate vicinity of the tortoise nurseries to prevent predation on any tortoises larger than 110 mm MCL that are released to the wild.

The third recommendation is for continuing research and monitoring of raven ecology, raven behavior, and methods of reducing raven predation on tortoises. Research will fill in holes in our understanding of raven predation on tortoises while monitoring is necessary to assess the effectiveness of existing management practices. Each of these is critical to developing an adaptive management approach in which management efforts are employed as scientific experiments—with replicates and controls—to yield an unbiased assessment of their effectiveness. Finally, to be successful, these strategies should be implemented in concert with actions that reduce other causes of desert tortoise mortality to aid the long-term recovery of their populations.

INTRODUCTION

Humans have the unique ability to modify landscapes and alter the distribution of habitats and resources. The effects of landscape changes become more widespread and pronounced as humans increasingly populate natural areas. Such changes often are detrimental to native species, but can be beneficial to generalists that not only make use of disturbed habitats but also may subsist on anthropogenic resources. Such species—termed “abundant vertebrates” by Goodrich and Buskirk
(1995)—can create problems for habitat specialists through predation, competition, disease transmission, and hybridization. The effect is not limited to the disturbed areas. “Spillover predation” (Kristan & Boarman 2003; Schneider 2001) occurs when vertebrate predators (i.e., subsidized predators; Soulé et al. 1988), subsisting on human-provided food bonanzas, move into adjacent native habitats and prey on species that may already be rare. Similarly, “hyperpredation” (Smith & Quin 1996) occurs when predator populations are maintained by some abundant, often introduced, prey, but depredate rare native prey when they come across them in the same habitat. We have shown that Common Ravens likely prey on desert tortoises under both of these circumstances at Edwards Air Force Base (EAFB) and that their predatory patterns are likely facilitated by anthropogenic resources provided at the EAFB landfill and other sites throughout the region. Active management may be necessary to overcome the imbalance that favors ravens at the expense of native prey, such as the Desert Tortoise (*Gopherus agassizii*).

At EAFB, common ravens are a classic subsidized predator. They have a varied diet, including grains and scavenged carcasses, as well as live prey (Boarman & Heinrich 1999; Webb et al. 2004)—a versatility that allows them to benefit from garbage at landfills and dumpsters. They are able to travel long distances to take advantage of anthropogenic food and water sources, and they make use of power towers, billboards, and other structures as nest substrate (Boarman 1993a; Kristan & Boarman 2004, In review). Their reproductive success and fledging survival are enhanced by proximity to resources (Kristan & Boarman 2001; Webb 2001). As a result of these factors, local raven populations have increased by more than 1000% during a recent 25-year period (Boarman & Berry 1995). Raven abundance is a concern to resource managers because they are known to prey on juvenile desert tortoises (*Gopherus agassizii*), a Federally- and state-listed threatened species (Boarman 1993b), in the vicinity of EAFB. In this chapter, I detail a comprehensive, long-term program to reduce the effect of raven
predation on desert tortoise populations by (1) managing raven populations and their habitats, and (2) conducting research and monitoring to improve our understanding of the ecology and behavior of ravens, especially with regard to their predation on tortoises. In addition, I make a case for using an adaptive management approach in which the effectiveness of management efforts is assessed through experiments that have proper controls and replicates. In other words, I advocate that developing an effective management plan for ravens and tortoises be viewed as a science-based, evolving process. Several recommendations are specific to EAFB, but they should be implemented in a more regional context because the ravens at EAFB are an integral part of a much larger population inhabiting the western portion of the west Mojave and the southern part of the Central Valley (Boarman et al. In review). More details and supporting data for these and other management recommendations can be found in Boarman (2002; 2003).

The loss of juvenile tortoises lowers recruitment of new individuals into the breeding population, which affects the ability of the population to recover from other threats (United States Fish and Wildlife Service 1994). Many human activities result in adverse impacts on adult components of tortoise populations; efforts to reduce these threats will be fruitless if tortoise populations cannot recruit young (Congdon et al. 1993; United States Fish and Wildlife Service 1994). Conversely, if little or nothing is done to reduce adult mortality, improve reproduction, and reverse declining health of adult tortoises, raven management will have little impact on long-term tortoise recovery (Doak et al. 1994; Frazer 1993).

In the Mojave desert in general, and EAFB specifically, ravens are known to capture or scavenge many food items including lizards, rodents, invertebrates, grains, seeds, birds, snakes, and tortoises (Camp et al. 1993; Kristan et al. 2004; Sherman 1993). Evidence that ravens prey on juvenile desert tortoises [<100-mm midline carapace length MCL] comes from a handful of direct observations and
strong circumstantial evidence (Boarman 1993b; Boarman & Hamilton In prep.; Bureau of Land Management 1990; Morafka et al. 1997). Circumstantial evidence is mostly in the form of tortoise shells found beneath active raven nests and shells that bear evidence of raven predation found lying on the desert floor beneath likely perch sites (Berry 1985; Boarman & Hamilton In prep.; Bureau of Land Management 1990; Campbell 1983; Rado 1990). We did not find remains of juvenile tortoises beneath any raven nests at EAFB, but found several nearby. The lack of juvenile tortoise shells found may reflect the low density of tortoises on the Base rather than the lack of active predation. As the tortoise population recovers on the Base, predation is likely to increase if the current density of ravens remains or increases.

Because raven populations are supported by abundant anthropogenic resources, they are able to decimate tortoise populations without being affected by the loss of tortoises as food (Smith & Quin 1996). Raven predation may result in reduced numbers of juvenile tortoises in the hatchling to eight-year old age classes, and reduced recruitment of tortoises into the larger and older size-age classes (e.g., tortoises from 9 to 20 years of age; Bureau of Land Management 1990). The best way to determine the effect raven predation has on tortoise populations is to evaluate data from actual tortoise populations. However, these data have limitations because juvenile tortoises are often difficult to detect and are consequently underrepresented in samples. In addition, the method employed for determining tortoise density is imprecise (Corn 1994; Tracy et al. 2004), yielding unreliable estimates of age class structure which do not support strong inferences. Nonetheless, these data represent the only available information that can be used to determine long-term trends in tortoise demography.

Data from permanent tortoise study plots provide a glimpse at the levels of raven predation that are occurring on juvenile desert tortoises in the California deserts (Berry 1990; Bureau of Land Management 1990) and its affects on tortoise populations. The data show apparent gaps in
representation among juvenile and immature size classes in some populations, particularly in those where predation pressure from ravens is presumably high (e.g., West Mojave). However, the gaps may also be from reduced natality or increased mortality from other causes.

The next best way to evaluate the likely impact ravens have on tortoise populations is through modeling. Four such models have been presented in the literature. The model presented by Congdon et al. (1993) shows that, to remain stable, a desert tortoise population may require juvenile survivorship of approximately 75% per year. However, in declining populations in which adult survival is depressed, annual juvenile survivorship must be about 95 to 97% for the population to recover. Thus, in populations where raven predation is high, a sufficient number of juvenile tortoises are probably not surviving to reach the larger size and older age categories. A Fish and Wildlife Service (1994) model also concluded that juvenile survivorship becomes increasingly important in populations suffering increased adult mortality. In another model, Ray et al. (1993) concluded that ravens are not likely to be a major problem for tortoise populations. Because their model was based on a healthy, increasing population, it has limited applicability to the EAFB tortoise population, which is declining due to increased adult and juvenile mortality. In a third model, Doak et al. (1994) concluded that conservation actions should focus on adult females rather than just juvenile tortoises. They questioned the value of raven control, but stated that "programs to reduce raven predation of small tortoises…are unlikely to significantly change current population trends unless combined with other, more effective, measures" (p. 458, Doak et al. 1994). Therefore, there is little actual conflict between the models by Congdon et al. (1993) and Doak et al. (1994). A critical evaluation of the three competing models using current data is needed. However, it is clear that reduction of raven predation will probably not work if efforts to increase adult survival are not also implemented successfully.
RECOMMENDED MANAGEMENT ACTIONS

The primary purpose of a raven management program is to enhance juvenile tortoise survival, thereby facilitating recruitment of young tortoises into the reproductive population. For the long term, I recommend habitat alterations coupled with monitoring and research to develop management strategies based on a better understanding of the ecology of ravens with regard to raven predation. For the short-term, I recommend limited lethal removal of ravens as a means of lowering the predation pressure of ravens on desert tortoises. This includes removing known offenders, ravens that are almost certainly killing tortoises, as well as reducing the overall raven population in certain areas with the assumption that doing so will reduce the number of birds potentially depredating tortoises. Lethal actions may not be necessary at EAFB until evidence appears that ravens are actively preying on tortoises or as a prophylactic measure if juveniles are released before they reach 110 mm MCL. The long-term actions should be implemented at the same time as the short-term ones, but must be continued until tortoise populations recover. In the sections below, these recommendations are discussed in detail, with the hope that this document may guide land managers and researchers in their immediate and long-term efforts to reduce raven predation on desert tortoises.

Reduce Raven Access to Anthropogenic Food and Water Resources

Given the rapid growth in the raven population in and around EAFB, the immediate concern of Base resource managers should be to reduce raven numbers by limiting access to anthropogenic resources. Of these resources, solid wastes at the sanitary landfill should be a primary focus, as they provide an important source of food year round for ravens (Boarman et al. 1995; Engel & Young 1992; Kristan & Boarman 2003). This food subsidy is particularly important during times of normally low natural food availability and helps to increase survivorship of ravens resulting in an increased
population. Landfills provide food for nestlings and breeding adults in the spring, thereby facilitating greater survival and reproductive success (Kristan & Boarman 2001; Webb 2001). Ravens are known to fly up to 65 km in a day (Engel & Young 1992; Boarman unpublished data), and range over several hundred kilometers throughout the year (Heinrich et al. 1994; Stiehl 1978). Hence, any given landfill could influence raven populations over a broad area (Boarman 2002). Because ravens move about seasonally, and individuals eat a varied diet, birds from landfills may forage in tortoise habitat many kilometers away and may feed on juvenile tortoises. Furthermore, water is a critical resource for ravens in the desert. Any water source close to a landfill will be heavily used by ravens and make that landfill highly attractive to ravens (Boarman et al. 1995; Boarman unpublished data).

Because of the heavy use of landfills by ravens, intense efforts must be placed on reducing raven access to organic wastes and standing water at landfills. EAFB is already doing much of what is necessary to reduce raven use of the landfill, but more can be done. For example, on several occasions we observed garbage protruding through torn tarps: tarps need to be checked and repaired regularly and replaced when repairs are not possible. Ravens often access grubs and insects from the compost heap: this area needs to be kept cleaner and compost needs to be covered better. Using the EAFB landfill as a model, EAFB should work with officials at Lancaster, Boron, and Mojave landfills to help them transition to cleaner garbage containment practices. In addition, garbage is accessed by ravens within the residential area at EAFB during garbage pickup day, a problem that can be prevented by using self-closing garbage cans rather than plastic bags. Dumpsters behind stores, restaurants, and commons should also be self-closing to keep ravens from eating from them.

Public education can also help to reduce food subsidies, as citizens who purposely feed ravens or who inadvertently do so by leaving pet food out, may not realize the effect of their actions. Specifically, pet food is a problem at the three dog kennels immediately west of the Base boundary near Silver Bell
Ranch. Perhaps the Base can encourage county or Humane Society officials to work with the kennel owners to find ways to feed the dogs without also feeding large numbers of ravens. Finally, the dairy farms in the Antelope Valley area are important sources of food for ravens. Retrofitting dairy farm equipment or changing practices to reduce raven access can be expensive, but the cost can be partially recovered because less food will be lost to ravens. In Point Reyes National Seashore, dairy farmers have been successful at nearly eliminating raven access to cattle food by feeding their cows in large feeding barns with covered sides (pers. obs.). Perhaps erecting small canopy covers over feeding troughs would be similarly effective. EAFB could elicit the assistance of County Agriculture Extension agents or USDA Wildlife Services to help the dairy farmers find a cost-effective solution.

A third source of food for ravens associated with humans is the carcasses of road-killed animals along highways (Boarman & Heinrich 1999). Road kills are an abundant resource along highways in the desert (Boarman & Sazaki 1996; Rosen & Lowe 1994) and are likely to make up a substantial proportion of the diet of birds nesting near highways. Road kills may help increase nesting success where there otherwise would not be adequate food to support a raven family (Knight & Kawashima 1993; Kristan & Boarman 2001). Reducing the incidence of road kills using barrier fences (3- to 6-mm-mesh hardware cloth; Boarman & Sazaki 1996) along major roads and highways would remove a steady source of food for ravens. Boarman and Sazaki (1996) found that 13-mm-mesh barrier fence reduced vertebrate mortality by 90%; they recommended fences be used in concert with culverts to allow animal movement and prevent fragmentation of tortoise and other animal populations. As road kills are probably a relatively minor source of food for the overall population, this recommendation should be viewed as a lower priority than some of the other ones.

Sources of free or standing water are yet another resource—the importance of which cannot be underestimated in an arid environment—that must be controlled to reduce raven populations. In the
eastern Mojave Desert, Sherman (Sherman 1993) found that breeding ravens left their territories every day to drink water several kilometers away. Year-around sources of standing water at EAFB include sewage ponds, runoff from excess lawn watering, over-irrigation of ornamental trees (e.g., at Building 4795), golf course ponds, and puddles beneath leaking faucets. The presence of these unnatural sources of water may facilitate a higher raven population by providing water during periods of low availability, while allowing ravens to expand their range into parts of the desert isolated from natural sources of water. In addition, because ravens are able to travel long distances on both a daily and a seasonal basis, human-provided water sources may affect raven populations over a broad area. Reducing availability to ravens of anthropogenic sources of water could be accomplished by modifying sewage and septage containment practices in four possible ways: (i) covering the water, (ii) altering the edge of the pond with vertical walls, (iii) placing monofilament line or screening over the entire pond, or (iv) adding methyl anthranilate, or other harmless taste aversive chemicals to standing water sources. Availability of other sources of water could also be reduced. Emphasis should be placed on reducing availability of water during the spring, when ravens are nesting, and summer, when water demands for ravens are high but natural sources are low. The need to reduce raven populations must be balanced against the need to provide water for other forms of wildlife that depend on anthropogenic sources of water (e.g., migratory birds), so a multispecies evaluation should be made before implementing this action (e.g., Knight et al. 1998).

Agricultural practices also make food and water available to ravens (Engel & Young 1992, personal observation). Grains at cattle feed lots and dairies, rodents and insects in alfalfa fields, and nuts and fruits in orchards and row crop fields all are eaten by ravens (Boarman & Heinrich 1999). Water is accessible on farms and dairies at irrigation ditches, ponds, puddles, and sprinklers (G. C. Goodlett, personal communication; W. Webb personal communication; personal observation). Nearly half of our
171 wing-tagged ravens spent some portion of their time at agricultural sites, which were a minimum of 20 km from where the birds were initially trapped (Boarman et al. In review). Controlling raven access to subsidies in an agricultural setting presents a challenge, as food and water are ubiquitous; however, doing so is an important step in reducing the abundance of ravens. Education will play a critical role, as extension agents can encourage agricultural professionals to cover unused grain containers, bury or render carcasses immediately, and dispose of other wastes and byproducts in secure containers. Although this task is not within the purview of EAFB, we recommend EAFB resource managers work closely with appropriate entities to effect similar changes (particularly with regard to landfills and dairy farms) in surrounding areas.

Water availability can be further reduced by modifying landscape irrigation practices. Watering of lawns at parks and residences in EAFB can be done more efficiently to reduce runoff into the gutters. Pooled irrigation water would evaporate by morning if watering were done sometime after sunset during the spring and summer. Drip irrigation of shrubs and trees, if employed correctly, would also help reduce pooling in some areas. Most of these practices are consistent with standard water conservation practices, so may need little or no investigation, training, and policy changes to effect, only more aggressive implementation and enforcement.

**Discourage Nesting Behavior**

Efforts to discourage ravens from nesting also may help reduce raven populations and local raven predation on tortoises. The majority of raven predation on tortoises probably occurs in the spring (April and May) when tortoises are most active and ravens are feeding young (Boarman & Hamilton In prep.; Boarman & Heinrich 1999). Parent ravens spend most of their time foraging within approximately 0.4 km of their nest (Sherman 1993); hence, this is probably the zone of greatest impact.
on the tortoise population (Kristan & Boarman 2003). Removing raven nests with eggs in them would probably have the greatest benefit because birds are less likely to renest at that stage, and if they do, they are less likely to be successful (Kristan & Boarman 2001; Marzluff et al. 1995; Webb 2001). In addition, it is best to remove nests before chicks have hatched, as the pressure to feed 3 to 7 hatchlings is likely to increase the frequency of tortoise predation. Another alternative is to coat the eggs in corn oil, which prevents hatching and causes the parents to continue incubating rather than renesting that year (Wildlife Services 2001). Although labor intensive, this will reduce reproduction and brood-related foraging. Recent evidence from EAFB indicates that fledging success is significantly reduced in late broods. Thus, if destroying nests or oiling eggs causes initiation of clutches to be delayed sufficiently, then these reproduction efforts would probably fail. However, adults would still be present and may prey on tortoises.

Removing nests outside of the breeding season probably would not affect raven populations or their predation on tortoises if they readily rebuild at the beginning of the next nesting season. However, evidence from EAFB suggests that ravens without a nest in their territory at the beginning of the breeding season were less likely to commence nesting than were those that already had an intact nest (Chapt. 3 and Kristan & Boarman 2004, in review). Further experiments may be necessary to show that actively removing nests outside of the breeding season results in lower reproductive output by ravens. Also, before nests are removed, caution should be taken so as not to greatly impact other bird populations (e.g., great horned owls and red tail hawks) because these raptors often nest in raven nests (and vice versa).

In addition, the construction of new structures that could potentially provide ravens with nesting substrate (e.g., power towers, telephone poles, billboards, etc) should be avoided in tortoise habitat, and, if possible, existing nesting structures should be removed in areas where natural substrates are lacking.
Structures that facilitate nesting in areas ravens otherwise could not nest in may pose a danger to nearby tortoise populations particularly if they are well away from other anthropogenic attractants. At EAFB, a significant number of ravens nested on myriad anthropogenic structures (e.g., radar towers, high-tension power poles, telephone poles, buildings, etc.; Webb 2001; personal observation). Many of these structures can be modified to prevent raven nesting, but some cannot. Telephone and power towers of solid construction rather than lattice and with diagonal crossbars instead of horizontal ones are harder for ravens to nest on (personal observation). Additional reductions in tortoise losses to ravens can be accomplished by removing unnecessary towers and abandoned buildings and vehicles, which may serve as nesting substrates near or within tortoise management areas, especially if natural nesting substrates are not found in abundance. Because ravens hunt primarily from the wing and will readily perch on small shrubs and the ground, there is little value in modifying structures to prevent perching.

Lethal Actions against Individual Ravens

There is no evidence that lethal removal will have a long-lasting effect on raven population levels, raven foraging behavior, or survival of juvenile tortoises. In Iceland, a large-scale raven removal program found that there was no measurable reduction in numbers of breeding pairs following nine years of removal (Skarphédinsson et al. 1990). There is a strong regional influence on the raven population at EAFB with a connection to the Central Valley, 80 km to the west, which may serve as a source population for ravens living in the west Mojave Desert. Still, a relaxation from predation pressure in specific areas for several years may help tortoise recruitment. The US BLM conducted two short-term, multi-agency projects that involved lethal removal of ravens for the benefit of tortoise populations. In 1989, a pilot program poisoned and shot 106-120 birds at the Desert Tortoise Natural Area, (Kern County, California) and at the landfill at the US Marine Corps Air Ground Combat Center in
Twentynine Palms (San Bernardino County) (Rado 1993). Little effort was made to monitor adequately the effectiveness of this aborted program on tortoise populations (Boarman 1993b). Some success at taking this approach was demonstrated in 1993 and 1994 in an experimental program in which 49 ravens were shot (Boarman, unpublished data). Again, little effort was made to monitor the effect this limited program had on either tortoise populations or territorial replacement by other ravens. I recommend that lethal actions should only be implemented as a short-term solution in an effort to give the local tortoise population a small window of time with minimal predation. Lethal actions should be accompanied by non-lethal, long-term raven management measures for there to be a reasonable probability of success at reducing raven predation (Schneider 2001).

One case in which lethal removal may be particularly effective at reducing juvenile tortoise mortality involves ravens that are known to prey on tortoises. Evidence suggests that some ravens may be responsible for taking relatively large numbers of tortoises (Boarman & Hamilton In prep.; Bureau of Land Management 1990). These individuals can be identified by the presence of juvenile tortoise shells beneath their nests, which are generally used year after year by the same individual breeding ravens (Boarman & Heinrich 1999). By removing those birds known to prey on tortoises, survival of juvenile tortoises may increase locally. However, it is very difficult to identify an offending bird with absolute certainty. Furthermore, it is even harder to find tortoises killed by a raven, because the shells may be spread over a broad area. Territorial ravens should be selectively removed in areas managed for tortoise recovery if they are found with at least one tortoise shell bearing evidence of raven predation within 1.6 km of their nest, a reasonable estimate of the radius of their territories in the California desert (based on Sherman 1993). Under this recommendation, targeted ravens would be shot by rifle or shotgun, or trapped and humanely killed where shooting is not possible (e.g., on power lines or in residential areas) or is not successful. Young ravens found in nests of removed adults should be euthanized humanely if
they can be captured. Poisoning with DRC-1339, or other appropriate agents, could be used against targeted birds in these limited areas if it is shown to be safe for other animals. Poisoned carcasses should be removed when feasible.

Lethal removal of ravens also may be a useful tool in situations where critical tortoise populations face threats from several sources, including raven predation. In this case, ravens would be removed from specific areas (e.g., experimental captive release and translocation areas if young tortoise will be released before they are large enough to avoid predation by ravens) with historically high tortoise mortality and raven predation, particularly where demographic analyses indicate that juvenile survivorship has been unusually low. Areas near anthropogenic resources (e.g., landfills and towns) that meet these criteria could be targeted because they are likely to facilitate a high level of spillover predation, that is predation by ravens that move (“spillover”) from areas with abundant anthropogenic resources, but no tortoises, into tortoise-occupied areas with low levels of anthropogenic resources (Kristan & Boarman 2003). It must be noted that evidence from ravens preying on least terns (*Sterna abtillarum*) at Camp Pendleton, California, indicated that territorial ravens may actually keep other ravens from accessing food within the former individuals’ territorial. Using taste aversive chemicals, Knittle et al. (1992) trained territorial ravens to not eat tern eggs while at the same time keeping other ravens from hunting in the tern colony. I do not believe this is a viable option for ravens preying on widely tortoises in the desert, but this hypothesis should be tested empirically.

**RESEARCH AND MONITORING**

Research and monitoring are important components of management. New research will provide needed information about raven predation on tortoises, while monitoring of raven populations will provide feedback on the effectiveness of current management efforts. Taken together, research and
monitoring will yield information necessary to develop and modify future phases of a comprehensive raven management program.

The first objective of research efforts should be to determine behavior and ecology of ravens as they pertain to predation on tortoises. Information on the ecology and behavior of ravens in the California deserts is necessary to design and modify effective long-term management actions. Over the past 10 years, data have been collected in the western Mojave Desert, mostly at EAFB, on several aspects of raven ecology. Most of that research focused on populations in moderately to heavily human-dominated landscapes, so information is sparse on raven ecology and behavior in settings that are more natural. To provide a clearer picture of raven ecology in the deserts, some future research should focus on birds in more natural landscapes (e.g., Joshua Tree National Park and Mojave National Preserve), particularly where predation on tortoises is occurring, as well as in areas dominated by agriculture. In addition, basic ecological research is necessary to better understand raven demography and life history. Such studies may provide insight into the raven’s great population increase, as well as identifying where the population is most vulnerable to management efforts.

There are several specific objectives that still need to be met to fully understand and manage raven predation on desert tortoises: (1) discover how and where ravens forage on tortoises by studying individuals or pairs that are known to prey on tortoises; (2) identify the preferred food items and foraging methods employed by ravens in different parts of the desert and determine if forage choice is learned in the nest, developed after fledging, or is simply an opportunistic behavior; (3) identify the important sources of water for ravens in the Mojave; (4) determine the extent of predation by ravens on tortoises and other animals and its effect on prey populations; (5) investigate how raven territoriality affects raven populations and their predation rates on tortoises and how this relationship is altered by removal of the territorial individuals; (6) evaluate how concentrated anthropogenic food and water
sources influence raven populations and behavior in tortoise habitat; (7) characterize the nesting and foraging ecology of ravens living near highways to determine the relative importance of road kills to those birds; and (8) determine if alterations to the habitat (e.g., from livestock grazing) change tortoise vulnerability to raven predation.

In addition, regional surveys should be conducted in the California deserts to locate and map ravens and their nests and communal roosts. Information on the densities and distributions of ravens and their nest, perch, and roost sites is necessary to understand the causes of their increases, to direct and modify management efforts, and to monitor the effectiveness of management efforts. Objectives of this effort would be to characterize distribution, behavior, and ecology of raven populations in the California deserts; monitor changes in population levels and distribution of ravens as a result of management changes; and identify potential causative factors for changes in raven population levels and distribution. Inventories should include private and public lands. Project proponents and other interested parties could contribute funds to a coordinated surveying program that would concentrate both on specific sites and on broad regional patterns.

Another research objective is to develop and test specific methods to directly manage raven populations and behavior. Several possibilities exist to reduce raven’s impact on tortoise populations, but few have been tested. Aversive chemicals, anti-perch devices, and noisemakers can keep birds away from specific resource sites that may facilitate increasing raven populations (e.g., landfills). Poisons, shooting, and relocating following live trapping, are all possible ways of removing ravens from specific areas. Removal of nests both during and outside the nesting season may reduce future nesting behavior. Finally, oiling of eggs prevents reproduction (Wildlife Services 2001) and may reduce hunting activity, hence predation pressure. Tests are needed to determine the effectiveness of these and other measures with ravens in the Mojave Desert. However, these are likely to have only minor effects on raven
predation on tortoises and the costs may outweigh the benefits.

Human-provided nest and perch sites in areas where tall natural substrates are lacking may facilitate hunting, roosting, and nesting in areas where tortoises may otherwise not have been subject to raven predation. If the nest and perch sites are removed or made unattractive to or unusable by ravens, then raven predation on nearby tortoises may be reduced. Perch sites are probably less important than nesting sites because ravens do most of their hunting while in flight, and often perch to eat in low bushes or on the ground. If, however, new nesting substrates are introduced to an area previously devoid of adequate nesting sites, then foraging on tortoises may be facilitated. Future research should determine if: (1) raven dependence on human-provided perches and nest sites aids hunting, nesting, and overall survival, and (2) modifying raven perches, roost sites, and nest sites on a localized basis helps reduce raven predation on tortoises.

One of the most effective and humane ways of killing ravens is by injecting the avicide DRC-1339 (Seamans & Belant 1999) into hard-boiled eggs. The method does, however, cause concern because of the potential impact to non-target species. To determine whether DRC-1339 has an impact on non-target species, an experiment should be conducted to determine what other species of animals in the California deserts might eat hard-boiled eggs. Data from the 1989 pilot raven control program (Rado 1993) suggest that animals other than ravens are not likely to eat the hard-boiled eggs. Still, a more comprehensive study is necessary to provide conclusive results.

Lastly, an effort should be made by social scientists to determine how humans use the desert, what practices might be amenable to change, and how best to effect those changes. We need to know what will affect how people live in and use the desert. For example, what can we do to help or convince dairy farmers to change management practices? How can we reduce the number of people who leave food and water (e.g., open garbage cans, pet food, etc.) where ravens can access them? How can we
ADAPTIVE MANAGEMENT APPROACH

I recommend that the management of ravens to reduce predation on desert tortoises should take an adaptive management approach, with feedback on successes and failures guiding a process that is constantly evolving. To work within a true adaptive management framework (Walters 1986), the plan must include a scientifically based method for determining if the program’s goals and objectives are being met. This method includes control and treatment areas to properly evaluate the action's effectiveness (Marzluff & Ewing 2001). If goals are not being met, there should be a coordinating body that can evaluate and make changes to the program.

To assess effectiveness of management techniques at reducing raven predation on tortoises, monitoring of raven status and predation rates on juvenile tortoises should be conducted. Implementation of some of the actions may be ineffective or insufficient to accomplish the plan’s goals. To determine this, tortoise and raven populations must be monitored using a scientifically sound protocol that will yield sufficient power to determine if desired changes occur. Raven monitoring should focus on population abundance, spatial distribution, and reproductive success. Furthermore, management actions should be implemented in a way that will facilitate scientifically-sound monitoring, such as use of treatment and control sites, replications where possible, and development and implementation of specific protocols (Marzluff & Ewing 2001). Tortoise monitoring is problematic and was discussed above. Monitoring results may indicate that modifications to existing or implementation of additional actions may be necessary. Changes to the plan may also be indicated by additional information on raven and tortoise ecology derived from research or from other relevant sources. This action is central to carrying out the proposed management plan because it provides the data necessary to
evaluate and modify the program to determine the nature of future actions.

POSSIBLE FUTURE ACTIONS

Other actions that could be considered in future phases of a raven management program include: poisoning groups of birds at concentration sites; applying conditioned taste aversion methods at landfills and other food and water sources; and researching and implementing other specific control measures (e.g., use of monofilament line at landfills, ponds, etc). If various measures suggested herein fail, it may become necessary to more aggressively employ lethal removal at various important concentration sites (e.g., landfills, dairy farms, and agricultural fields). These actions could be proposed and evaluated as part of subsequent phases of a comprehensive raven management plan for the Base.

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