EFFECTS OF ANTHROPOGENIC DEVELOPMENTS ON COMMON RAVEN
NESTING BIOLOGY IN THE WEST MOJAVE DESERT

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Abstract. Subsidized predators may affect prey abundance, distribution, and demography. Common Ravens (Corvus corax) are anthropogenically subsidized throughout their range and, in the Mojave Desert, have increased in number dramatically over the last 3–4 decades. Human-provided food resources are thought to be important drivers of raven population growth, but human developments add other features as well, such as nesting platforms. From 1996 to 2000, we examined the nesting ecology of ravens in the Mojave Desert, relative to anthropogenic development. Ravens nested disproportionately near point sources of food and water subsidies (such as towns, landfills, and ponds) but not near roads (sources of road-killed carrion), even though both sources of subsidy enhanced fledging success. Initiation of breeding activity was more likely when a nest from the previous year was present at the start of a breeding season but was not affected by access to food. The relative effect of environmental modifications on fledging success varied from year to year, but the effect of access to human-provided resources was comparatively consistent, suggesting that humans provide consistently high-quality breeding habitat for ravens. Anthropogenic land cover types in the desert are expected to promote raven population growth and to allow ravens to occupy parts of the desert that otherwise would not support them. Predatory impacts of ravens in the Mojave Desert can therefore be considered indirect effects of anthropogenic development.

Key words: anthropogenic resources; Common Raven; Corvus corax; land cover types; Mojave Desert, California; nest site choice; nesting success; subsidized predator.

INTRODUCTION

Predators are important components of ecosystems and can regulate prey populations and enhance biological diversity (e.g., Crooks and Soule 1999). Anthropogenic development can alter ecosystem function through effects on predators, either by removing them (Crooks and Soule 1999) or by augmenting them (Polis et al. 1997). Generalist scavengers and predators, such as birds of the family Corvidae, may benefit from anthropogenic changes to the environment, leading to increased predation (Andrén 1992, Kristan and Boorman 2003, Marzluff and Neatherlin 2006). These “subsidized predators” (Soule et al. 1988) have the potential to be particularly dangerous to prey species, because anthropogenic resources protect them from food shortages due to prey population declines (Sinclair et al. 1998). Corvids, such as the Common Raven (Corvus corax), that live in close association with people may often become subsidized predators (Boorman 1993).

Although ravens are commonly associated with people throughout their range (Marzluff and Angell 2005), they may be particularly dependent on anthropogenic resources in extreme environments, such as the arctic (Restani et al. 2001) and the desert (Boorman et al. 2006). Ravens have been implicated as contributors to declines of several threatened or endangered species (Liebezeit and George 2002), such as the Marbled Murrelet (Brachyramphus marmoratus), California Least Tern (Sterna antillarum browni), Snowy Plover (Charadrius alexandrinus), San Clemente Loggerhead Shrike (Lanius ludovicianus mearnsi), Sandhill Crane (Grus canadensis), and desert tortoise (Gopherus agassizii; Morafka et al. 1997). In challenging environments, anthropogenic subsidies support ravens, allowing them to use otherwise unsuitable environments (Restani et al. 2001) and to become predators of species that were otherwise safe from raven predation (Truett et al. 1997). Although other corvids may be more effective nest predators in some areas (Marzluff and Neatherlin 2006), in the West Mojave Desert ravens have been the focus of concern due to their predation on desert tortoises; presence of ravens is associated with elevated risk of tortoise predation (Kristan and Boorman 2003). These predatory effects increase the importance of understanding the contributions of anthropogenic resources to the spread and persistence of Common Ravens.
Anthropogenic developments make multiple, simultaneous changes in the landscape to which ravens could respond. Food and/or water are provided as side effects of refuse disposal and irrigation, and ravens can achieve large population sizes at resource bonanzas (Boarman and Heinrich 1999, Restani et al. 2001, Boarman et al. 2006, White 2006). Foods provided by campgrounds in temperate rain forests of Washington State affect the reproductive success and spatial distribution of ravens (Marzluff et al. 2006). In addition to food and water subsidies, development provides nest and roost sites in the form of trees, poles, buildings, and other nonnatural features, which in some environments may have greater effects than food and water. For example, ravens in sagebrush steppe habitats are able to use power towers as nesting substrates and, consequently, have increased in abundance in areas that have had power towers added without a concomitant change in anthropogenic food and water subsidies (Steenhof et al. 1993).

There is strong circumstantial evidence that ravens have achieved large population sizes in the Mojave Desert of California because of anthropogenic development. Although they are native, resident species in the west Mojave Desert of California, ravens are not desert specialists and have historically existed at low population densities there (Boarman and Berry 1995, Camp et al. 1995). Over the last several decades, ravens have increased in number throughout southern California (Sauer et al. 2000), by a factor of 15 in parts of the Mojave Desert (Boarman and Berry 1995, Camp et al. 1995). Increases in raven numbers are concomitant with ongoing anthropogenic development in the region, and this correlation suggests that human subsidies are contributors to raven population increases (Boarman 1993). Breeding populations in the Mojave Desert are largest in the western 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). Additionally, we know that breeding ravens in the west Mojave Desert with diets including anthropogenic foods, such as trash and road-killed carrion, have enhanced fledging success. This suggests that development affects raven populations via supplemental food (Kristan et al. 2004). However, sites that provide access to anthropogenic foods in the Mojave will also usually allow ravens to use artificial structures such as power towers, buildings, and ornamental trees for nest sites, such that the apparent effects of diet composition on fledging may only be correlated with beneficial effects of using anthropogenic nest sites. Consequently, it is not known whether food and water, anthropogenic alterations of the desert environment, or a combination of these correlated effects of development have been responsible for the increase.

In this study we addressed the effects of a variety of aspects of anthropogenic development in the west Mojave Desert on variation in raven reproductive success, in a lightly developed area with a large raven population. We used a variance partitioning approach to evaluate how much of the effect of development on raven reproductive success could be attributed to access to food subsidies compared with other changes to the desert environment. Finally, we evaluated the spatial distribution of raven nests relative to conspicuous sources of food and water to determine whether ravens disproportionately used sites that were near resource subsidies.

**Methods**

**Study area**

The primary study area was within the western half of Edward Air Force Base (EAFB), and in lands immediately surrounding the base, in the west Mojave Desert, California, USA. Several permanent water bodies were present on the study area, which contributed water, food, and riparian vegetation 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 raven prey, including waterfowl, waders, and shorebirds, as well as amphibians such as the African clawed frog (Xenopus laevis; Kristan et al. 2004). Open sewage treatment facilities were also present near two towns in the study area, Mojave (population 3763) and Rosamond (population 7430).

Vegetation on the study area consisted primarily of creosotebush (Larrea tridentata) and saltbush (Atriplex spp.) scrub, both of which often contained Joshua tree (Yucca brevifolia). Creosotebush is a large shrub, standing 1.5–3 m in height, and individual plants were generally widely spaced. Saltbushes were short, standing 1 m or less, and individuals were more densely spaced than creosotebush. Joshua tree is a yucca with the growth form of a tree, growing up to 10 m or more, and is used extensively as nest sites by ravens and other bird species on the study area.

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

**Data collection**

*Nest searching and breeding measures.—*Nest searching and reproductive monitoring were conducted each
year from 1996 to 2000. Ravens build large (~0.5–1 m 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 were visible from several hundred meters. We attempted to find all raven nests in the study area by scanning visible, suitable platforms for nests while driving throughout the area. Most of the area had extensive networks of primitive roads and trails, and it was possible to travel within 0.5–1 km of all points within the study area in which potential raven nest platforms were present. When nests were found, they were assigned unique identifiers and their positions were recorded to within 10 m using global positioning system (GPS) units. New nests were discovered each year, and thus the number of nests under observation increased with time. In 1999 and 2000, we increased our search effort in areas that were far from our typical travel routes, and by 2000 we had found a sufficient number of nests to be confident that (1) we had found a majority of the nests on the study area (we believe ≥90%, based on the distribution of nests, nesting habitat, and the territorial spacing of ravens), and that (2) we had not undersampled any portion of the study area.

Once nests were found, we returned weekly to record breeding activity. We made several reproductive measures from each nest, representing different aspects of breeding biology: nest site occupancy, initiation of breeding, clutch initiation date, clutch size, and number of chicks fledged. Not all nests were equally accessible and not all variables could be recorded for each nest. Occupancy (presence of a pair of ravens within a territory during the breeding season), initiation (including any breeding activity from nest construction or repair on), and fledging success (number of chicks fledged from a nest) could be observed from the ground without access to the nests themselves. Clutch size was only recorded from nests that could be observed using a mirror attached to a telescoping pole, or from higher nest sites that could be climbed.

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

Known nests at which no breeding activity was observed were checked weekly until it became too late for a pair to initiate a successful brood (mid-May). Nest sites without a breeding pair by mid-May were checked once more in early June to confirm that no late nesting attempts were made. Nest sites of pairs that initiated breeding were checked weekly until the fate of the breeding attempt was known.

*Nest sites and land cover variables.*—We measured several potential predictors of raven reproductive activity. Because we were interested in whether alteration of the desert environment had effects in excess of their associated changes in access to food and water, variables were defined in a way that would indicate anthropogenic alteration to the desert environment. For example, the discrete variable “nest substrate” consisted of both natural and anthropogenic categories, with the expectation that anthropogenic nest substrates may be better for breeding ravens, and may help to explain anthropogenic effects on population growth. Generally, raven nests are placed in elevated structures, although we have found ravens in the Mojave Desert nesting close to the ground outside of this study area. Of the collection of substrates observed, we operationally defined nest substrates as Joshua tree, cliff, building (including human-occupied, under construction, and abandoned), pole (including transmission lines, telephone poles, abandoned observation tower, and billboards), and tree (planted, primarily ornamental trees in developed areas). The anthropogenic categories for this variable were cliff, building, pole, and tree. Similarly, the variable “shrub cover” consisted of anthropogenic and natural categories. For shrub cover, we recorded the species of the dominant shrub (creosotebush, saltbush, both species, or neither) in the immediate vicinity of the nest, with the expectation that a lack of native shrub cover would be strongly associated with anthropogenic development. Substrate and shrub cover were unchanged during the duration of the study for each nest, and were recorded once. In 1999 and 2000, we began visiting known nest sites and searching for new sites early enough to record whether the previous year’s nest was present at the beginning of the breeding season. In 2000, unusually heavy spring rains left standing water in pools throughout much of the south end of the study area, which was near a dry lakebed. During 2000, we therefore recorded the presence of standing water within sight of the nest at the time when chicks fledged.

We measured the distance from each nest to the nearest point source of resource subsidies (“point subsidies,” including landfills, towns, artificial wetlands, and sewage ponds), and to the nearest road using a GIS (ArcView 3.3). Point subsidies were large, permanent sources of food or water that could be represented by a single point (such as a landfill or pond) or polygon (such as housing areas) on a map. Point subsidies were sources of food and water, but also typically altered the vegetation and introduced artificial nest substrates. Similarly, roads were expected to directly affect raven reproduction by contributing edible refuse or road-killed carrion (Austin 1971, Knight and Kawashima 1993). Ravens nesting near roads had a high incidence of small mammals in their diets, consistent with consumption of road-killed animals (Kristan et al. 2004). We confined our analysis to highways and high-speed, high-traffic-volume paved roads, such as the roads ringing the core.
study area, but we excluded the lightly used dirt roads used during nest searching. These distance-based measurements of access to sources of food and water were augmented at each nest site with a field assessment of the degree of anthropogenic development at the nest (the variable “development”). Nests could be “developed” (if the nest was located within a developed area, such as a town), “undeveloped” (if the nest was located in the desert, >400 m from a development), or “mixed” (if the nest was located in the desert, but <400 m from a development).

Statistical analyses

Strategy for dealing with collinear predictors.—An important problem for biologists studying effects of multiple variables in the field is that predictor variables are frequently correlated in their distributions (multicollinearity; Graham 2003). Although the ideal design would be based on uncorrelated predictors, landscapes rarely provide orthogonal gradients, and the subset of sites used by ravens could have correlated predictors even if the landscape as a whole did not. Common treatments for multicollinearity include eliminating all but one of a set of highly correlated predictors, or deriving “latent variables” that are multivariate representations of sets of intercorrelated predictors (e.g., using principal components to represent sets of correlated environmental variables in a regression, or using structural equation modeling; Malaeib et al. 2000). These methods work particularly well when collinearity is strong, but may omit important information when collinearity is weak.

Rather than choosing one of these common methods, our approach was to first characterize the partial effects of sets of predictor variables on raven reproductive parameters using generalized linear models (GLM), and then to subdivide the effects of these predictors using a variance partitioning approach (Legendre and Legendre 1998). This approach had the advantage that we could treat sets of variables that all indicated a type of subsidy (such as food and water, or alteration of the desert environment) as a group. We could thereby assess the relative proportion of the effects of the group of “access to food” variables that were independent of the group of “altered environment” variables, as well as the proportion that was shared between the two. This approach allowed us to use sets of predictors as though they were latent variables, but without needing to throw out variation explained by single variables.

Spatial distribution of nests.—We compared the spatial distribution of raven nests with randomly located points placed in raven nesting habitat within the study area. We generated 5000 random points within the study area and then omitted points that fell in areas without nesting habitat, such as dry lakebeds. This procedure resulted in 4345 points with a random distribution relative to roads and point subsidies. Distances to roads and point subsidies from raven nests and random points were calculated from GIS maps, and the densities of nests and random points as a function of distance from roads or point subsidies were estimated using fixed-kernel density estimation (Bowman and Azzalini 1997). Differences between the kernel estimates for nests and random points were assessed with a randomization test (Bowman and Azzalini 1997). This procedure produces both an overall test of the differences between the two curves and a reference band to which the curves can be compared. Distances at which nest and random probability densities fall outside of the reference band are significantly different.

**Effects of predictor variables on breeding measures.**—We analyzed territory occupancy, breeding initiation, clutch size, and fledging success separately, so that influences on different aspects of breeding ecology could be compared. The effects of all predictor variables on breeding variables were analyzed with generalized linear models (logistic regression for binary dependent variables such as occupancy and breeding initiation, Poisson regression for counts). Occupancy could not be reliably scored until the second year of the study (1997), when known territories could be revisited. Evaluating initiation of breeding required frequent visits to known territories early in the season so that early, failed breeding attempts could be detected (e.g., repair of old nests, new nest linings, clutches of eggs that were depredated before a clutch was completed). In 1999, we increased our visitations early in the season to improve our ability to detect initiation, and thus only analyzed initiation for 1999 and 2000. Clutch size and fledging success were analyzed for all five years of the study, but analysis of laying date effects on fledging were confined to 1999 and 2000.

Consistent use of territories over time is frequently correlated with consistent reproductive success, and territory occupancy over time has been proposed as a measure of territory quality (Sergio and Newton 2003). We used the number of years of occupancy, of initiation, or of successful fledging (i.e., number of fledglings >0) as measures of the consistency in reproductive activity over time. However, these variables were strongly influenced by the number of years a territory was under observation. We thus analyzed effects of the full set of predictor variables on consistency of use or success over time by comparing a model that included all of the predictor variables as well as the number of years of observation against a model with only the number of years of observation. We used a likelihood ratio test as a means of statistically controlling the effects of sampling duration. Significant reductions in model fit when predictor variables were removed indicated a significant effect of the full set of predictors on the breeding variable. The tests of effects of each predictor were taken from the model that included all of the predictors and the numbers of years of observation.

Relative effects of access to food and habitat alteration on fledging.—Models from our test for partial effects of
predictor variables were subjected to variance partitioning (Legendre and Legendre 1998) so that the relative effects on fledging success of a group of variables representing access to permanent, persistent sources of food, and a group representing habitat alteration could be compared. Variation in access to food was represented by distance to roads, distance to point subsidies, and local development. Habitat alteration was represented by the rest of the predictor variables (nest substrate, shrub cover, presence of the previous year’s nest, presence of water at fledging), because each of these either included anthropogenic categories (nest substrate and shrub cover) or was expected to be influenced by anthropogenic development (e.g., the probability of presence of the previous year’s nest could increase in stable, protected anthropogenic nest substrates, and surface water was consistently available at construction sites, housing developments, or artificial water bodies). We used this analysis, in effect, to partition each model’s \( R^2 \) into components that were attributable to just one group of variables, or were shared by both. Because this analysis subdivided the total variance explained for each model (i.e., each year), all predictor variables were included whether they had significant partial effects or not. The size of the “shared” component depends both on the amount of intercorrelation between the sets of independent variables and on the amount of variation in fledging success that is explained by the correlated parts of these variables. Because values from this analysis are analogous to \( R^2 \), they do not have standard errors or tests of significance associated with them; rather, we used this analysis as a descriptive tool to help explain patterns of effects of sets of intercorrelated predictor variables.

**RESULTS**

*Nest substrates and distribution*

Ravens used a diverse set of nest substrates, and nests were nonrandomly distributed within the study area. Raven nests were found in Joshua trees \( (n = 196) \), poles \( (n = 93) \), trees \( (n = 46) \), cliffs \( (n = 4) \), and buildings \( (n = 4) \). Nests were less commonly found near point subsidies (e.g., 38% were within 2 km of a points subsidy) than near roads (e.g., 59% were within 2 km of a road; Fig. 1), and nests declined in abundance with increasing distance from either. However, the distributions of random points show that there was a smaller land area near point subsidies than near roads, and ravens nests were found proportionately more than expected within 1 km of point subsidies, and were found proportionately less than expected at >4.5 km from point subsidies (Fig. 1). In contrast, raven nest sites were found proportionately less than expected within 0.5–1 km of roads, and proportionately more than expected at >5 km from roads (Fig. 1).

*Reproductive performance*

Fledging success varied annually and responded to development at nest sites. Mean fledging success ranged from 0.36 chicks per occupied territory in 1996 to 1.69 chicks per occupied territory in 1999 (Table 1). Mean number of chicks fledged from successful nests (i.e., nests with at least one chick fledged) ranged from 2.0 chicks per nest in 1998 to 2.57 chicks per nest in 1999. Fledging success declined from the most developed to the least developed areas (for developed areas, 1.72 ± 0.24 fledglings (mean ± SE), \( n = 33 \) nests; for mixed areas, 1.18 ± 0.21, \( n = 20 \) nests; for undeveloped areas, 0.92 ± 0.07, \( n = 226 \) nests).

With the exception of clutch size, reproductive variables were correlated with at least one environmental predictor variable every year. The predictor variables associated with fledging success differed among years (Table 2), with close proximity to roads most frequently associated with high fledging success. Nest site occupancy was significantly associated with environmental variables in three years (1996, 1997, and 2000, but not 1999; Table 3). Unlike their effects on fledging success, roads were only significantly associated with occupancy rate in one year (1997). Initiation of breeding within occupied nests was correlated with environmental
variables in both years that it was assessed (Table 4). Proximity to roads, point subsidies, or presence of local development were not significant in any model, but the presence of a nest at the beginning of the breeding season was associated with increased initiation rates in both years and with the number of years of initiation.

Variables that measured direct access to food resources (distance to roads, distance to point subsidies, and degree of urbanization at the nest) accounted for a relatively large and consistent percentage of the effect of the environment on fledging success (Table 5). Effects of access to food accounted for between 33.7% and 57.7% of the total effect of environmental variables within a year. Access to food also accounted for 63.0% of the total effects of environmental variables on the number of successful years of reproduction. In contrast, habitat alteration accounted for a typically lower and more variable proportion of the total effect of environmental variables within a year. Access to food was highly variable within a year (completed clutches ranged from 1 to 7 eggs), but was not strongly correlated with environmental variables in any year (range of $P$ values 0.13–0.86). Mean clutch size was 4.42 eggs in 1999 and 4.54 in 2000 (low clutch sizes not strongly correlated with environmental variables in either year). Laying date was associated with fledging success in both years analyzed. Fledging success decreased with later laying in 1999 (deviance = 26.45, $df = 1$, $P < 0.0001$) and 2000 (deviance = 31.42, $df = 1$, $P < 0.0001$; Fig. 2).

Chick survival is highly variable within a year (completed clutches ranged from 1 to 7 eggs), but was not strongly correlated with environmental variables in any year (range of $P$ values 0.13–0.86). Mean clutch size was 4.42 eggs in 1999 and 4.54 in 2000 (low clutch sizes not strongly correlated with environmental variables in either year). Laying date was associated with fledging success in both years analyzed. Fledging success decreased with later laying in 1999 (deviance = 26.45, $df = 1$, $P < 0.0001$) and 2000 (deviance = 31.42, $df = 1$, $P < 0.0001$; Fig. 2).

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towns (Kristan et al. 2004, Boarman et al. 2006). Additionally, the benefits of fledging from nests near these food sources extend to at least nine months post-departure from natal territories (Webb et al. 2004). The benefit of proximity to roads is not surprising, because roads are a source of carrion, particularly when they run through undeveloped habitat (Austin 1971, Camp et al. 1993). Roads also allow ravens to scavenge food that they would otherwise need to hunt, and make available prey that would otherwise be too big for them to kill and open (Boarman and Heinrich 1999). Although proximity to roads was the most consistent predictor of fledging success (Table 2), it is likely that the multiple changes that occur in developed areas provide diverse benefits to ravens (Knight et al. 1995). To illustrate, based on our model of numbers of years of reproductive success (Table 2), nests predicted to be the most consistent producers of fledglings were clustered near roads and near sources of anthropogenic resources (Fig. 3). In general, towns, landfills, and other point subsidies are not located far from roads, but roads can run far from anthropogenic developments in a lightly developed landscape; this is certainly true of our study area (Fig. 3). Consequently, distance to roads is somewhat independent of proximity to towns, which allowed us to detect their independent statistical effects. However, towns were always close to roads, which frequently masked any direct, independent effect of point subsidies. The positive effects of food subsidies on raven population size and/or reproductive success seen elsewhere (Marzluff and Neatherlin 2006, White 2006), along with the increased use of anthropogenic foods near point subsidies (Kristan et al. 2004), support the conclusion that access to food is an important factor affecting raven reproductive success at both roads and point subsidies. In contrast, because Joshua trees were abundant (57% and nest substrate had no consistent effect on fledging, artificial nest substrates were not as important as food or water supplements for ravens in the West Mojave. Water at nest sites may be important independent of food (Table 2), because ravens will fly to water sources when water is lacking at nest sites (Sherman 1993). Water at nest sites would make this unnecessary. Variables representing access to food and habitat alteration were intercorrelated on our study area, but access to food had more consistent positive effects than the other kinds of changes to the desert environment. For example, ravens nesting in developed areas would be close to roads, close to food subsidies, would have no native shrub cover, and would be more likely to nest in trees or buildings than in Joshua trees. These intercorrelations accounted for the sometimes substantial

<table>
<thead>
<tr>
<th>Year</th>
<th>Total dev.</th>
<th>Total df</th>
<th>Model dev.</th>
<th>Model df</th>
<th>$P$ for overall model</th>
<th>Significant variables</th>
<th>Nonsignificant variables</th>
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<td>1997</td>
<td>107.8</td>
<td>128</td>
<td>24.5</td>
<td>11</td>
<td>0.010</td>
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<td>202.0</td>
<td>145</td>
<td>46.3</td>
<td>11</td>
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<td>235.0</td>
<td>229</td>
<td>17.3</td>
<td>12</td>
<td>0.130</td>
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<tr>
<td>2000</td>
<td>387.3</td>
<td>324</td>
<td>66.3</td>
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<td>&lt;0.001</td>
<td>nest***</td>
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<tr>
<td>No. yr</td>
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<td>330</td>
<td>7.2</td>
<td>11</td>
<td>0.780</td>
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</tbody>
</table>

Note: Nonsignificant variables were included in the model but did not have significant partial effects.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. 

Table 3. Effects of distance to roads, distance to point subsidies, development at the nest, nest substrate, shrub cover, presence of a nest at initiation, and presence of water at fledging on nest site occupancy (for years 1997–2000) and number of years of occupancy (No. yr).

<table>
<thead>
<tr>
<th>Year</th>
<th>Total dev.</th>
<th>Total df</th>
<th>Model dev.</th>
<th>Model df</th>
<th>$P$ for overall model</th>
<th>Significant variables</th>
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<td>2000</td>
<td>460.2</td>
<td>331</td>
<td>124.4</td>
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<td>shrub*, nest***</td>
<td>roads, development, shrub</td>
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<tr>
<td>No. yr</td>
<td>132.3</td>
<td>229</td>
<td>20.4</td>
<td>12</td>
<td>&lt;0.001</td>
<td>nest***</td>
<td>roads, development, shrub</td>
</tr>
</tbody>
</table>

Note: Nonsignificant variables were included in the model but did not have significant partial effects.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. 

Table 4. Effects of distance to roads, distance to point subsidies, development at the nest, nest substrate, shrub cover, and presence of a nest at the beginning of the breeding season on initiation of breeding (for years 1999–2000) and number of years of initiation of breeding (No. yr).
percentage of explainable variation in fledging success that was shared by access to food and habitat alteration (Table 5). However, access to food had more consistent effects on fledging success over time compared with effects of habitat alteration (Table 5). In both years that habitat alteration variables were significant, shrub cover was an important effect, with nest substrate also contributing to the number of chicks fledged in 1997 (Table 2). We had expected that if our shrub cover variable was important to raven reproduction, it would be because areas without native shrubs were associated with anthropogenic development. However, this was not the reason for the importance of shrub cover as an independent effect in 1997 and 2000. In both of these years, the independent effect of shrub cover was instead due to differences in fledging success between nests in creosotebush- and saltbush-dominated vegetation. Nests in creosotebush scrub areas did poorly, fledging 0.57 and 0.42 chicks in 1997 and 2000, respectively, whereas nests in saltbush scrub did better, fledging 1.17 and 1.12 chicks, respectively. In other years, nests in these cover types were lower and more similar to each other. This effect of native shrub cover type was not correlated with distance from roads or point subsidies, and represents an independent, but temporally variable, effect of habitat. The fledging success in 1997 and 2000 for nests in saltbush scrub suggests that the West Mojave Desert is occasionally able to support relatively high reproductive success, but success in native cover types is annually variable, and is still lower than the overall mean for developed nests of 1.72 chicks per occupied territory. Thus, human-provided resources create consistently high-quality habitat in what would otherwise be highly variable, frequently poor-quality habitat for ravens in the Mojave Desert.

Interestingly, variables that predicted fledging success did not always predict other aspects of raven breeding biology. Ravens disproportionately placed territories near point subsidies, but did not disproportionately use areas near roads, in spite of the reproductive benefit of access to road-killed carrion. This may have been because road-killed carrion is ephemeral over short time periods. Table 5. Relative magnitude of effect of access to anthropogenic food subsidies and habitat alteration on fledging success within a year and for the numbers of years of success over time.

<table>
<thead>
<tr>
<th>Variable</th>
<th>All included</th>
<th>Access to food</th>
<th>Habitat alteration</th>
<th>Both</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>No. yr†</td>
<td>34.6</td>
<td>21.8 (0.630)</td>
<td>9.3 (0.269)</td>
<td>3.6  (0.104)</td>
</tr>
</tbody>
</table>

Notes: Access to subsidies includes distance to roads, distance to point subsidies, and development at nest sites. Habitat alteration includes nest substrate and shrub cover (for all years); presence of previous year’s nest (for 1999 and 2000); and presence of water at fledging (for 2000). “Both” represents the shared variation between access to food and habitat alteration.

† Values are the deviance explained, with the proportion of model deviance explained given in parentheses.

‡ The number of years of successful nests. Habitat alteration variables used were nest substrate and shrub cover.

Fig. 2. Initiation dates for nests that successfully fledged at least one chick (gray shaded bars) and those in which breeding was initiated but no chicks fledged (hatched bars). Julian day 1 is 1 January.
periods compared with the constantly replenished supply of refuse at landfills. Studies of distributions of ravens in the Mojave have found a greater abundance of ravens in urban areas (Knight and Kawashima 1993; W. I. Boarman, W. B. Kristan III, G. Goodlett, T. Bailey, M. Hagan, and W. Deal, unpublished data) and near roads (Knight et al. 1993), but these patterns are dominated by large, conspicuous aggregations of non-breeding adults and juveniles found at anthropogenic “attraction sites” such as landfills and towns. The distribution of breeding ravens in our study area was quite different than the distribution of non-breeders (Kristan and Boarman 2003), and the decisions underlying distributions of breeders and non-breeders may also differ. A majority of ravens nested >2 km from point subsidies (Fig. 1), a distance beyond which large aggregations of ravens are not usually found (Kristan and Boarman 2003). Developments in our study area covered a relatively small total area and raven populations within them were dense, such that available territories may have been limited, forcing individuals to nest in poor habitats. The lack of attraction to roads and their associated power lines by ravens in our study contrasts with the behavior of ravens 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). This difference may be due, in part, to the large proportion of nests in our study that were found in a natural nest substrate (Joshua trees) that was absent from these other study areas.

Occupancy and initiation of breeding were not affected by access to anthropogenic food resources, but were more commonly affected by other alterations to the desert environment (Table 3). There was no evidence that females nesting far from food sources had difficulty completing a clutch, because clutch size was not related with any of our predictor variables. Lack of a consistent effect of anthropogenic resources on occupancy, in spite of consistent effects on reproductive

Fig. 3. Distribution of raven nests relative to major point sources of anthropogenic food and water subsidies, and to major paved roads. Sizes of nest symbols are proportionate to the predicted number of years of successful breeding, having controlled for the number of years of observation of nests. Identifications of point subsidies are: 1, Edwards Air Force Base; 2, North Edwards; 3, Edwards landfill; 4, Branch Park; 5, Piute Ponds; 6, Rosamond; 7, Mojave landfill; 8, Mojave sewage ponds; 9, Mojave.
success, suggests that occupancy does not reflect habitat quality for this population (Sergio and Newton 2003). Initiation of breeding was also affected by variables associated with changes in the desert environment in both years analyzed (1999 and 2000), but not by access to food. The best predictor of initiation in both years was the presence of the previous year’s nest at the beginning of the breeding season, a pattern that has been noted before for ravens (Steenhof et al. 1993). We hypothesize that either the nest may act as a cue that stimulates breeding behavior, or the presence of a nest may reduce the amount of energy or time required for a pair to prepare for egg-laying. Alternatively, it is possible that territories in which nests were reused will more often be occupied by experienced breeders. This alternative, however, does not explain why reuse of a nest predicted breeding initiation but not fledging success, given that experienced breeders are often more successful than novices in avian populations (Martin 1995).

Another possible benefit of nesting in developed areas is early initiation of breeding (Fig. 2). Early breeding has been linked to reproductive success in ravens breeding in undeveloped habitats in Grand Teton National Park, Wyoming, USA (Dunk et al. 1997). Dunk et al. (1997) attributed the effect to mild winters that improved the breeding condition of ravens or increased the availability of food. In our population, nests near roads or subsidies initiated earliest and had the greatest fledging success. Ravens nesting in developed areas laid eggs 13 days earlier, on average, than in undeveloped areas in 2000 and 9 days earlier in 1999. Like Dunk et al. (1997), we detected a benefit of early breeding, but the cause is probably different in the Mojave than in Grand Teton. The earliest clutches in both years were laid in the first or second week of March, and the latest were laid in the last week of May. This wide range of initiation dates means that the earliest chicks fledged before the last eggs were laid; if successful, the fledging dates for the latest clutches would be late July. Average high temperature at EAFB in May is 26.6°C and in July is 36.1°C, so that chicks hatched later in the season would have to endure much warmer temperatures than those hatched earlier. Nestlings may be particularly vulnerable to overheating, because they lack the mobility to move to shade and water sources. A similar effect of heat has been suggested for ravens in Idaho (Steenhof et al. 1993), but increased fledging success from transmission towers was attributed to cooler nest microclimates than in natural cliff nests. Post-fledging, juvenile survival rates decline with date as well on our study area, which appears to be attributable to temperature (Webb et al. 2004).

The fact that high-quality anthropogenic habitat is spatially restricted to areas near roads and human developments does not restrict the distribution of ravens, and we found many occupied, active raven nests far from roads and human developments. It is possible that these were younger, less dominant birds that were excluded from nesting in higher quality habitat. The birds that attempted to breed in these territories would forage primarily in the habitat surrounding the nest (Sherman 1993), and would thereby pose a threat to prey populations near these nests (Kristan and Boarman 2003). Ravens are effective predators as well as opportunistic scavengers, and may impact sensitive vertebrate species within their breeding territories, notably the desert tortoise. To the extent that human developments in the region are promoting the spread and persistence of a large number of Common Ravens in areas that are marginal breeding habitat, human activities can have effects on these sensitive species far from the actual developments that serve as attractants to ravens.

Acknowledgments

Fieldwork between 1996 and 1998 was conducted by G. C. Goodlett, T. Bailey, K. Anderson, and P. Frank. J. Spickler participated in the 1999 field season. W. C. Webb contributed nest locations and nesting data in 1999 and 2000. 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. Yee, K. Phillips, M. Restani, S. Hannon, and an anonymous reviewer.

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