

SPATIAL PATTERN OF RISK OF COMMON RAVEN PREDATION ON DESERT TORTOISES

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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native species are only consistently found at anthropogenic sites in the Mojave (Knight et al. 1993; W. I. Boarman, unpublished data), and raven numbers have increased 1500% over the last several decades, concomitant with urban growth in the region (Boarman 1993, Sauer et al. 2000).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, USFWS 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 deplete 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

Manuscript received 24 July 2002; accepted 14 November 2002; final version received 21 January 2003. Corresponding Editor: B. Sinervo.

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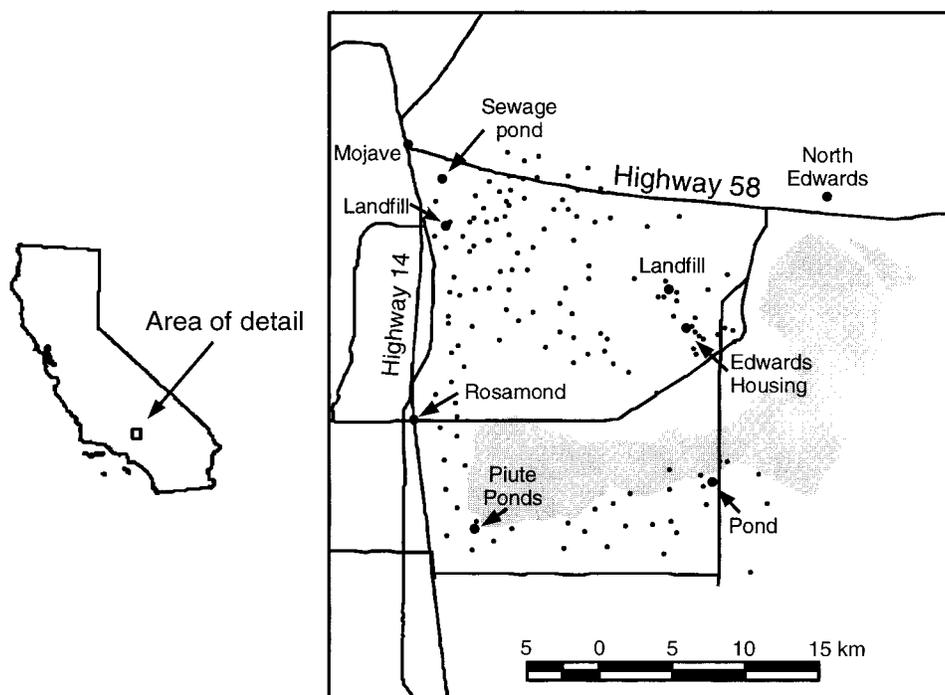


FIG. 1. Study area map. The gray area is a dry lake bed, which is non-habitat for both ravens and desert tortoises. The small solid circles are the locations of sampling points.

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 creosotebush (*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).

Lands within the EAFB boundary were used by the U.S. Air Force primarily for recreation rather than military exercises, and the vegetation was not heavily disturbed. 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 concomittant 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 wished to measure in a standardized way the 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, 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_i (Burnham and Anderson 1998). Akaike weights estimate the relative frequency with which a model would be best supported out of a set of alternatives if the experiment were repeated a large number of times (Burnham and Anderson 1998). A model with $w_i > 0.9$ 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_i are considered plausible explanations for the data, and worth further consideration. Lack of a model with $w_i > 0.9$ 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, suc-

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.

Effect	Coefficient	1 SE	z	P	AIC†	Δ AIC‡	w_i §
Model 1					434.2	7.2	0.02
Occupied nests	-3.64×10^{-4}	1.69×10^{-4}	-2.16	0.031			
Point subsidies	-3.15×10^{-4}	4.36×10^{-5}	-7.23	<0.001			
Roads	4.92×10^{-5}	4.40×10^{-5}	1.12	0.264			
Model 2					430.7	3.7	0.13
Initiated nests	-2.53×10^{-4}	1.14×10^{-4}	-2.22	0.026			
Point subsidies	-2.91×10^{-4}	4.75×10^{-5}	-6.12	0.000			
Roads	4.99×10^{-5}	4.36×10^{-5}	1.15	0.252			
Model 3					434.7	7.6	0.02
Successful nests	-8.99×10^{-5}	8.27×10^{-5}	-1.09	0.277			
Point subsidies	-3.34×10^{-4}	4.30×10^{-5}	-7.77	<0.001			
Roads	5.73×10^{-5}	4.59×10^{-5}	1.25	0.212			
Model 4					433.9	6.8	0.03
Point subsidies	-3.45×10^{-4}	4.19×10^{-5}	-8.24	<0.001			
Roads	4.08×10^{-5}	4.37×10^{-5}	0.93	0.351			
Model 5					427.0	0.0	0.81
Number fledged	-2.26×10^{-1}	7.72×10^{-2}	-2.92	0.003			
Point subsidies	-3.48×10^{-4}	4.11×10^{-5}	-8.46	<0.001			
Roads	8.19×10^{-6}	4.50×10^{-5}	0.18	0.856			

† Akaike's Information Criterion.

‡ The difference between the model AIC and the smallest AIC in the set under consideration.

§ Akaike weights.

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 point-count 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 ± 3.55 individuals (mean \pm 1 SD) and the number within 200 m of the sampling point was 0.55 ± 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 Δ AIC was within four units of the best model, and the w_i 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

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.

Effect	Coefficient	1 SE	<i>z</i>	<i>P</i>	AIC†	ΔAIC‡	<i>w</i> _i §
Model 1					211.4	1.6	0.28
Occupied nests	-8.49	4.26 × 10 ⁻⁴	-1.99	0.046			
Point subsidies	-2.76 × 10 ⁻⁴	9.34 × 10 ⁻⁵	-2.96	0.003			
Roads	-5.96 × 10 ⁻⁵	1.01 × 10 ⁻⁴	-0.59	0.554			
Model 2					209.8	0.0	0.61
Initiated nests	-7.01 × 10 ⁻⁴	2.74 × 10 ⁻⁴	-2.55	0.011			
Point subsidies	-2.03 × 10 ⁻⁴	9.92 × 10 ⁻⁵	-2.05	0.041			
Roads	-3.08 × 10 ⁻⁵	9.91 × 10 ⁻⁵	-0.31	0.756			
Model 3					214.8	5.0	0.05
Successful nests	-2.96 × 10 ⁻⁴	1.89 × 10 ⁻⁴	-1.56	0.118			
Point subsidies	-3.08 × 10 ⁻⁴	9.07 × 10 ⁻⁵	-3.40	0.001			
Roads	-1.68 × 10 ⁻⁵	1.05 × 10 ⁻⁴	-0.16	0.873			
Model 4					215.4	5.5	0.04
Point subsidies	-3.42 × 10 ⁻⁴	9.00 × 10 ⁻⁵	-3.81	<0.001			
Roads	-7.42 × 10 ⁻⁵	1.01 × 10 ⁻⁴	-0.74	0.462			
Model 5					216.2	6.4	0.02
Number fledged	1.65 × 10 ⁻¹	1.54 × 10 ⁻¹	1.07	0.287			
Point subsidies	-3.38 × 10 ⁻⁴	9.12 × 10 ⁻⁵	-3.71	<0.001			
Roads	-5.05 × 10 ⁻⁵	1.03 × 10 ⁻⁴	-0.49	0.625			

† Akaike's Information Criterion.

‡ The difference between the model AIC and the smallest AIC in the set under consideration.

§ Akaike weights.

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 ($\chi^2 = 3.85$, *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 ΔAIC 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

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 date of the predation risk trial as a nuisance covariate.

Model	<i>df</i>	<i>P</i>	AIC†	ΔAIC‡	<i>w</i> _i §
Close ravens × successful nest	4	0.01	115.19	0.0	0.57
Close ravens × subsidies + close ravens × successful nest + subsidies × successful nest	7	0.02	118.59	3.4	0.11
Close ravens × subsidies × successful nest	8	0.03	119.82	4.6	0.06
Close ravens × roads × successful nest	8	0.07	119.85	4.7	0.06
Close ravens × roads + close ravens × successful nest + roads × successful nest	7	0.07	120.03	4.8	0.05
Close ravens × roads × initiated nests	8	0.08	120.78	5.6	0.04
Successful nest	2	0.48	121.69	6.5	0.02
Subsidies	2	0.08	121.83	6.6	0.02
Close ravens × subsidies × fledged	8	0.03	121.94	6.8	0.02
Subsidies × successful nest	4	0.10	122.52	7.3	0.01
Close ravens	2	0.85	122.96	7.8	0.01
Close ravens + successful nest	3	0.59	123.12	7.9	0.01
Close ravens × subsidies × initiated nests	8	0.09	123.61	8.4	0.01
Close ravens × subsidies	4	0.15	123.67	8.5	0.01
Close ravens × roads × occupied nests	8	0.21	125.78	10.6	<0.01
Close ravens × subsidies × occupied nests	8	0.18	127.68	12.5	<0.01

† Akaike's Information Criterion.

‡ The difference between the model AIC and the smallest AIC in the set under consideration.

§ Akaike weights.

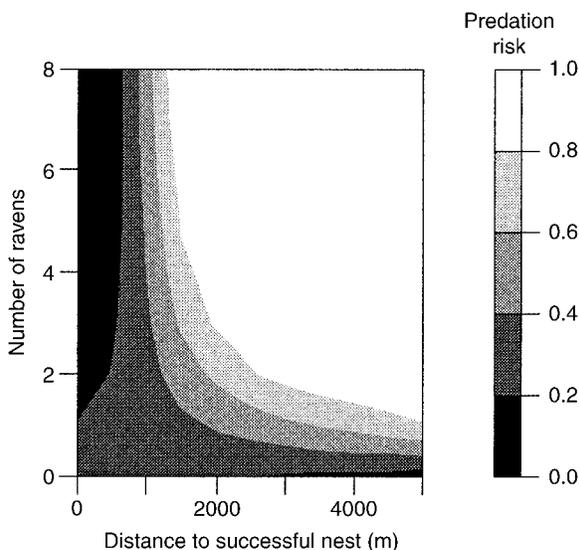


FIG. 2. The effects of distance to the nearest successful raven nest and number of ravens observed within 200 m of the sampling point on risk of predation (i.e., attack by a raven on a styrofoam tortoise model).

(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 0.442. 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

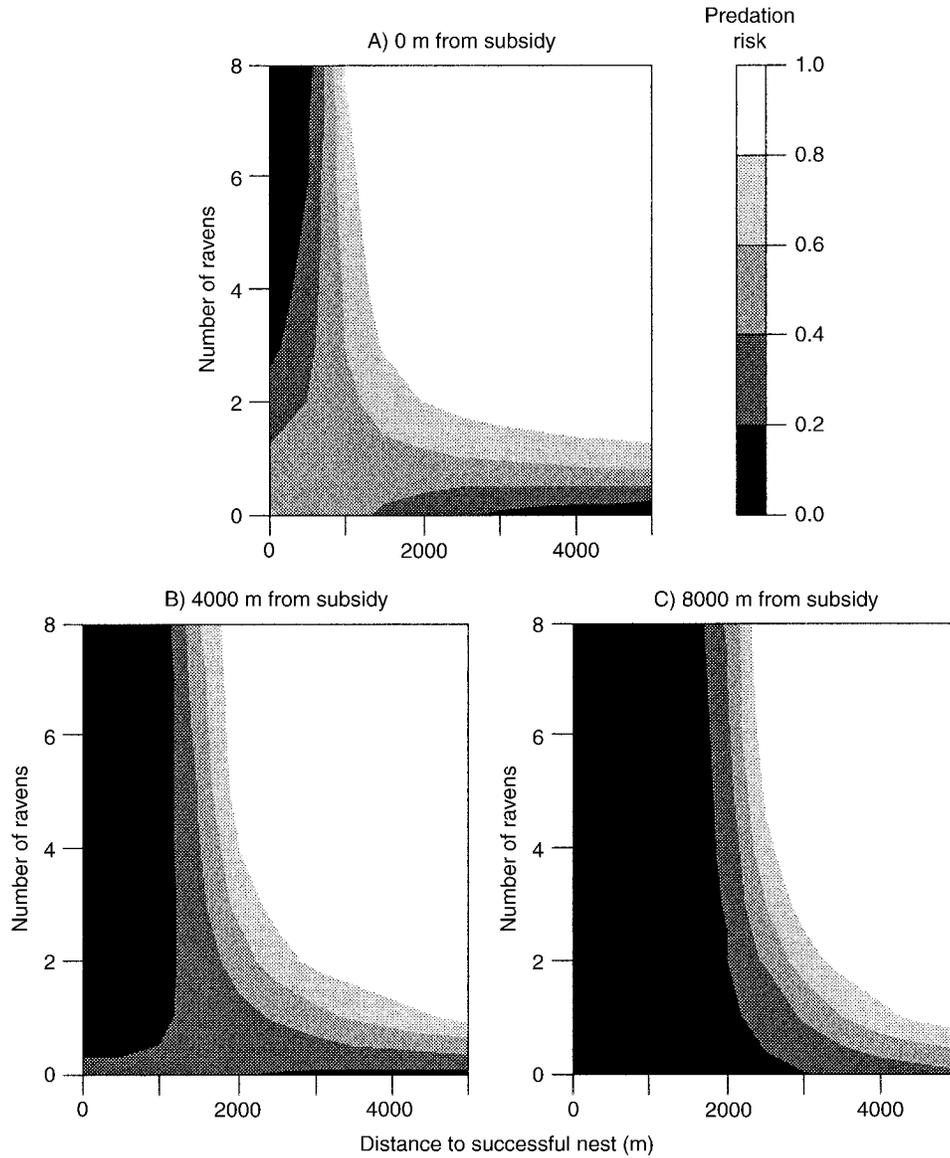


FIG. 3. The effects of distance to the nearest successful raven nest, number of ravens observed within 200 m of the sampling point, and distance from anthropogenic point subsidies (A–C) on predation risk.

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 oc-

cupied 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

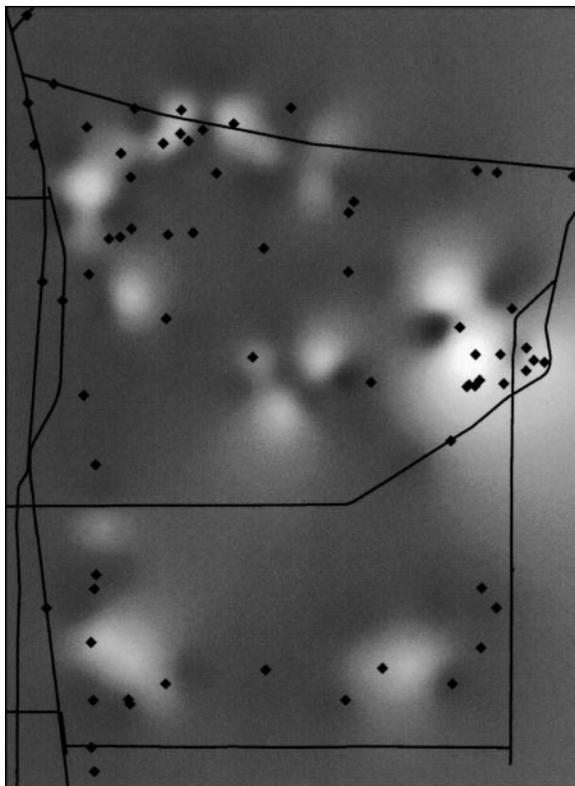


FIG. 4. Interpolated raven numbers, based on ravens observed within 200 m of sampling points. Pixel values range from 0 (black) to 8 (white). Locations of successful nests are marked with diamonds.

(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.

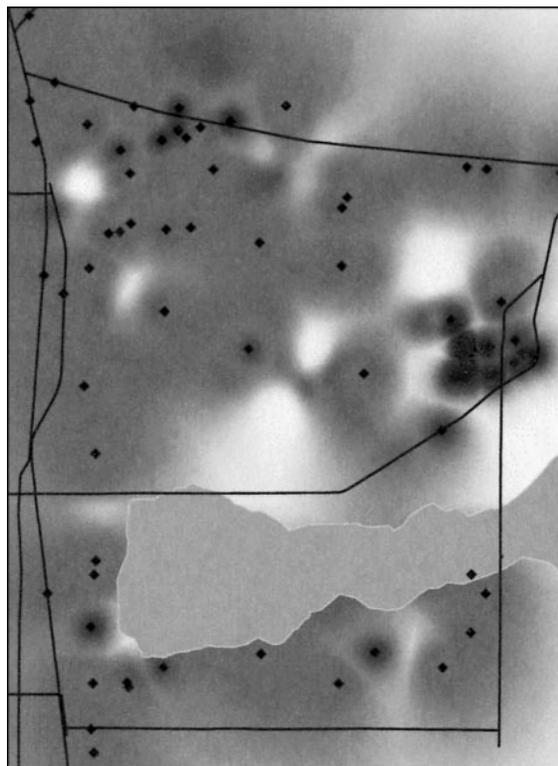


FIG. 5. Estimated predation risk, based on the number of ravens at each pixel (interpolated from point-count data) and distance from the nearest successful nest. Successful nests are marked with diamonds. Probability of attack ranges from 0 (black) to 1 (white). The dry lake (uniformly light gray area) is unsuitable habitat for ravens or tortoises.

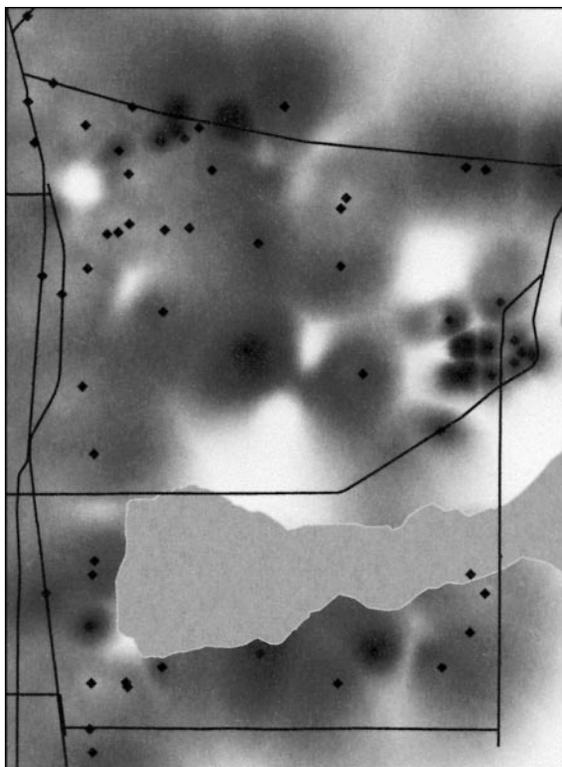


FIG. 6. Estimated predation risk, based on the number of ravens at each pixel (interpolated from point-count data), distance from the nearest successful nest, and distance from the nearest point subsidy. Successful nests are marked with diamonds. Probability of attack ranges from 0 (black) to 1 (white). The dry lake (uniformly light gray area) is unsuitable habitat for ravens or tortoises.

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

TABLE 4. Predicted occupation and success of territories (numbers of years out of five years) at two distances to point subsidies and two distances to roads.

Distance to roads (km)	Distance to point subsidies (km)	Territory predictions (mean \pm 1 SE)	
		No. occupied	No. years successful [†]
0	0	3.92 \pm 0.29	1.89 \pm 0.23
10.5	0	2.99 \pm 0.63	0.42 \pm 0.18
0	14	3.14 \pm 0.80	0.28 \pm 0.14
10.5	14	2.40 \pm 0.58	0.06 \pm 0.03

[†] The number of years successful was significantly associated with both distance to roads and distance to point subsidies.

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. Hagen, W. Deal, G. Goodlett, and T. Okamoto provided invaluable logistical and field support.

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