Diet composition of common ravens across the urban-wildland interface of the West Mojave Desert

William B. Kristan III, William I. Boarman, and John J. Crayon

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

Key words common raven, *Corvus corax*, diet, Mojave Desert, urban–wildland interface, wildlife

Common ravens (*Corvus corax*) are native to the West Mojave Desert but have increased in number concomitantly with increases in human populations (Knight et al. 1993, Boarman and Berry 1995). Ravens are generalists in foraging ecology and diet and are capable of exploiting a variety of anthropogenic resources. The importance of human-provided resources to raven population growth is supported by the observation that proximity to human developments, such as housing, landfills, sewage treatment ponds, and roads, augments raven reproductive success (Kristan 2001, Webb 2001). Increases in availability of adequate nesting sites have led to raven population increases in other

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areas (White and Tanner-White 1988, Steenhof et al. 1993, Knight et al. 1995), but this was unlikely to explain increases in the West Mojave, because natural nest sites in Joshua trees (*Yucca brevifolia*) were abundant and were used by the majority of ravens in this part of the West Mojave (Kristan 2001). Taken together, these observations suggest that anthropogenic developments augment raven population growth in the West Mojave primarily through direct food subsidies to ravens. The rapid increase in raven populations has become a management concern because large raven populations may harm species such as the threatened desert tortoise (*Gopherus agassizii,* Boarman 2003). Threats from ravens may be particularly severe because predators are more likely to cause extinctions in prey when food subsidies allow their populations to remain high as prey populations decline (Andrén 1992, Sinclair et al. 1998, Courchamp et al. 2000). Based on the large but largely circumstantial body of evidence that human-provided food resources promote raven population growth, removal of food resources has been proposed as a nonlethal method of raven population control in the West Mojave (Boarman 2003).

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

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

Study area

The primary study area was within the western half of Edwards Air Force Base (EAFB) and on lands immediately surrounding the base in the West Mojave Desert of California (Figure 1). The study area covered approximately 770 km^2. The small number of point sources of resource subsidies (features that could be represented by a point on a map, such as towns, artificial water bodies, and landfills) were distributed throughout the area, surrounded by undeveloped shrublands. Vegetation in undeveloped areas was composed of creosote bush (*Larrea tridentata*) and saltbush (*Atriplex* spp.) scrub, often forming a woodland in association with Joshua trees.

Two artificial, permanent water bodies represented sources of water, food, and riparian vegetation (Figure 1). The larger body (Piute Ponds) was an artificial wetland within EAFB that contained well-developed riparian vegetation, including willows (*Salix* sp.), cattails (*Typha* sp.), and rushes (*Juncus* sp.). Piute Ponds supported breeding populations of waterfowl, waders, and shorebirds as well as amphibians such as the African clawed frog (*Xenopus laevis*), which were potential raven prey. A small park with a permanent pond was located in the southeast corner of the study area. Open sewage-treatment facilities also were present near towns in the study area, Mojave (population 3,763) and Rosamond (population 7,430).

Lands included in our study area within the EAFB boundary were used by the Air Force primarily for recreation rather than military exercises, and the vegetation was not heavily disturbed. Undeveloped lands outside the EAFB boundary were used for a variety of purposes, including recreation and sheep grazing. The housing area within EAFB (population

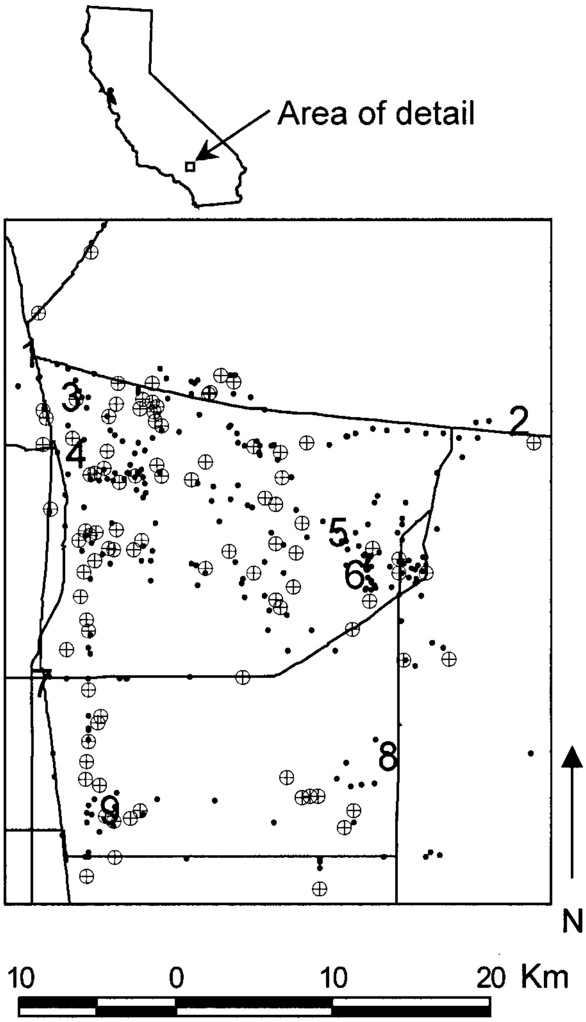

Figure 1. Map of raven nests observed in the West Mojave Desert, spring 1999 and 2000. Lines represent major roads, numbers are sources of human food subsidies, small dots are the locations of raven nests, and crossed circles are nests from which pellets were collected. 1 = Mojave, 2 = North Edwards, 3 = Mojave sewage pond, 4 = Mojave landfill, 5 = Edwards Air Force Base landfill, 6 = Edwards Air Force Base housing, 7 = Rosamond, 8 = Pond, 9 = Piute Ponds wetland.

7,423) and the towns of Rosamond and Mojave all consisted of single-family homes, apartment complexes, and commercial developments (e.g., restaurants, grocery stores, etc.). Solid-waste disposal sites (landfills) were present near EAFB housing and southeast of Mojave.

Methods

Pellet collection and analysis

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

Statistical analysis

We expressed diet contents as percent of pellets that contained each food item (100 × [number of pellets with the item]/[total number of pellets in collection]), and as percent of nests that had the food item in $\geq$1 pellets (100 × [number of nests with the food item]/[total number of nests]).

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

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

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

Results

Raven pellets contained a variety of food items reflecting their opportunistic, generalist diet (Table 1). We found mammals in 76.5% of pellets and at

Table 1. Contents of pellets collected from common raven nests in the West Mojave Desert, during spring 1999 and 2000.

Class	Order	Contents	Num. pellets[a]	% of pellets	Num. nests[b]	% of nests
Amphibia			11[c]	2.0	6	6.1
	Anura	Unknown	2	0.4	2	2.0
		Xenopus laevis	9	1.6	5	5.1
Insecta[d]			210	37.4	80	81.6
	Hymenoptera	Ants	9	1.6	8	8.2
	Coleoptera	Unknown	5	0.9	5	5.1
	Mantodae	Mantis ootheca	9	1.6	7	7.1
	Orthoptera	Unknown	3	0.5	3	3.1
	Unknown	Unknown	193	34.3	79	80.6
Malacostraca[d]			1	0.2	1	1.0
	Isopoda	Sow bug	1	0.2	1	1.0
Aves			123	21.9	57	58.2
	Columbiformes	*Columba livia*	1	0.2	1	1.0
		Zenaida sp.	4	0.7	4	4.1
	Gruiformes	*Fulica americana*	1	0.2	1	1.0
	Unknown	Eggshell	44	7.8	31	31.6
		Unknown	80	14.2	46	46.9

(*Continued*)

[a] The number of pellets that contained one or more of the item.
[b] The number of nests that contained one or more of the item.
[c] Italics represent the broadest categories that could be consistently identified. Bold denotes categories used for ordination analyses.
[d] Insects and isopods were classified as "arthropods" for ordination analyses.

Table 1 (*continued*). Contents of pellets collected from common raven nests in the West Mojave Desert, during spring 1999 and 2000.

Class	Order	Contents	Num. pellets	% of pellets	Num. nests	% of nests
Mammalia			430	76.5	91	92.9
	Carnivora	Unknown	1	0.2	1	1.0
		Unknown Felidae	1	0.2	1	1.0
	Lagomorpha	*Lepus* sp.	19	3.4	18	18.4
		Sylvilagus sp.	33	5.9	26	26.5
		Unknown	6	1.1	6	6.1
	Rodentia	*Ammospermophilus* sp.	12	2.1	9	9.2
		Dipodomys sp.	282	50.2	83	84.7
		Microtus sp.	2	0.4	2	2.0
		Mus sp.	3	0.5	3	3.1
		Neotoma sp.	10	1.8	8	8.2
		Ondatra zibethica	1	0.2	1	1.0
		Peromyscus sp.	6	1.1	6	6.1
		Thomomys sp.	6	1.1	5	5.1
		Unknown	117	20.8	59	60.2
	Unknown	Unknown	56	10.0	37	37.8
Plant			102	18.1	46	46.9
	Plant	Miscellaneous	31	5.5	24	24.5
		Seeds	68	12.1	38	38.8
		Seeds, cultivated	5	0.9	5	5.1
Reptilia			72	12.8	43	43.9
	Sauria	*Cnemidophorus* sp.	10	1.8	9	9.2
		Dipsosaurus dorsalis	1	0.2	1	1.0
		Sceloporus sp.	1	0.2	1	1.0
		Unknown	19	3.4	13	13.3
	Serpentes	*Crotalus* sp.	1	0.2	1	1.0
		Unknown	38	6.8	29	29.6
	Unknown	Unknown	3	0.5	3	3.1
Substrate			63	11.2	40	40.8
Trash			136	24.2	56	57.1
	Trash	Aluminum foil	18	3.2	14	14.3
		Cellophane	11	2.0	9	9.2
		Fabric	6	1.1	6	6.1
		Glass	8	1.4	7	7.1
		Miscellaneous	15	2.7	8	8.2
		Paper	59	10.5	38	38.8
		Plastic	82	14.6	43	43.9
		Styrofoam	3	0.5	2	2.0
		Wood	1	0.2	1	1.0
Unknown Vertebrata			67	11.9	46	46.9
	Total		560		98	

[a] The number of pellets that contained one or more of the item.

[b] The number of nests that contained one or more of the item.

[c] Italics represent the broadest categories that could be consistently identified. Bold denotes categories used for ordination analyses.

[d] Insects and isopods were classified as "arthropods" for ordination analyses.

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

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

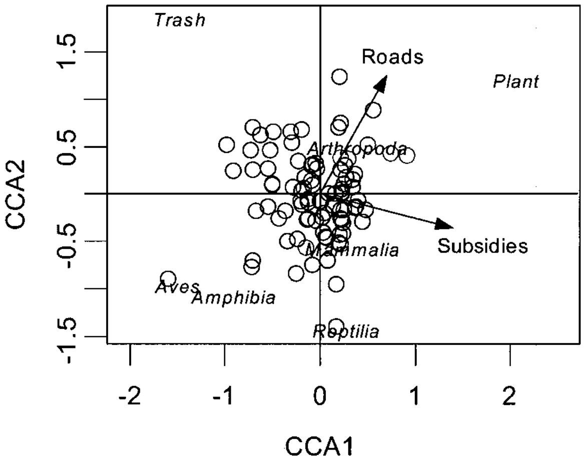

Figure 2. Partial canonical correspondence analysis biplot that positions nests (open circles) relative to axes of change in diet (CCA 1 and CCA2), controlling for the number of pellets from each nest. Food items are positioned near the nests in which they were most common. The variables that constrain the ordination are represented by vectors from the origin of the plot. The length of the vector is proportional to the magnitude of the effect of that variable on the CCA axes, and the direction of the vector indicates the direction of the relationship between the variable and the CCA scores. Data are from raven nests observed in the West Mojave Desert, spring 1999 and 2000.

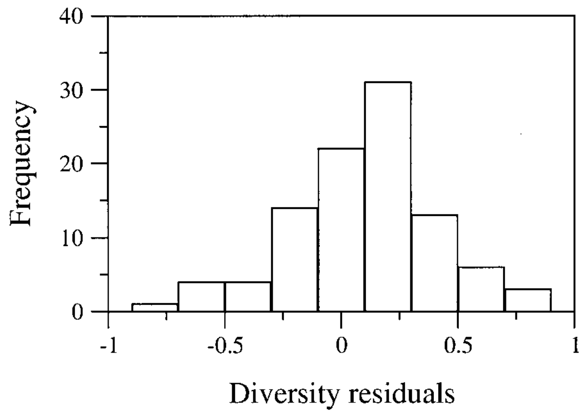

Figure 3. Histogram of the Shannon diversity index residuals for collections of pellets at each raven nest, corrected for differences in the number of pellets among nests. Collections are from raven nests in the West Mojave Desert, spring 1999 and 2000.

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

Table 2. The relationship between numbers of chicks fledged from a nest and the diet composition estimated from pellets found at the nest, based on a Poisson regression of number of chicks fledged; West Mojave Desert, spring 1999 and 2000.

	Estimate	Std. Error	*z*-value	*P*
Intercept	–1.04	0.28	–3.76	<0.01
CCA1[a]	–0.04	0.04	–1.17	0.24
CCA2[a]	0.05	0.02	2.53	0.01
Years observed[b]	1.12	0.17	6.54	<0.01

[a] The scores from the first two axes of a canonical correspondence analysis of diet composition, which are numerical representations of variation in diet.

[b] The number of years (one or two) that a nest was used in this study.

Although there was substantial variation in diet diversity among nests (Figure 3), diet diversity was not related to distance to roads (r^2=0.008, df=1,96, f=0.81, P=0.37) or to point subsidies (r^2=0.029, df =1,96, f=2.92, P=0.09; Figure 4 *a, b*).

Discussion

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

Because ravens are opportunistic, we interpreted patterns of variation in diet composition in the EAFB ravens as patterns of variation in food availability. This type of inference is limited by the known biases in pellet-based diet studies (Marti 1987, Redpath et al. 2001). Since pellets contain indigestible components of food such as bone, feather, and fur, the highly digestible foods such as muscle tissue are underestimated by pellet analysis

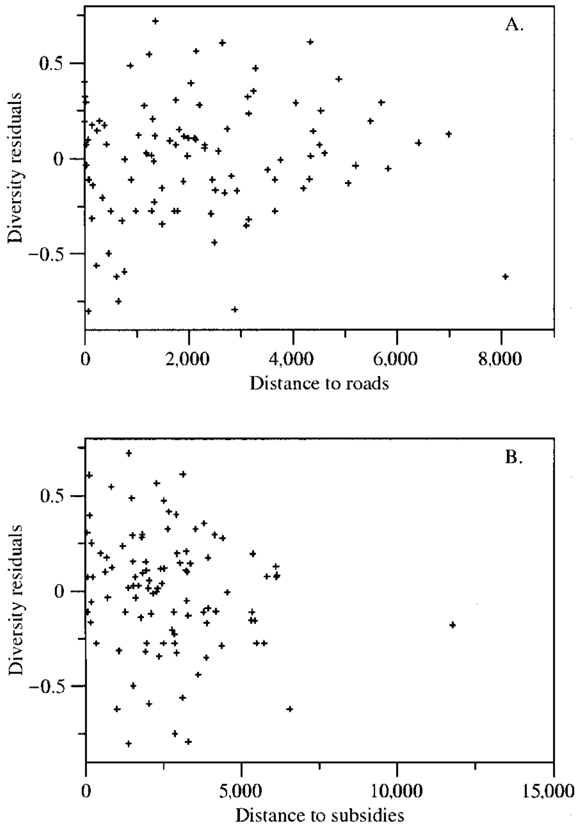

Figure 4. Shannon diversity index residuals relative to distance (m) from roads (a) and distance (m) to point sources of resource subsidies (b). Data are from pellet collections made at common raven nests in the West Mojave Desert, spring 1999 and 2000.

(Marti 1987). Additionally, small mammals tend to be overestimated and birds underestimated in pellets relative to direct observation of foraging predatory birds (Redpath et al. 2001). We lacked alternative methods for comparison, but we did not find evidence in our pellets of scavenging on large animals, even though we have observed this behavior in this population. However, the set of foods detected in the pellets included a variety of vertebrate taxa, trash, and plant materials, a range sufficiently broad to reflect effects of human developments. Thus, even in light of suspected biases in pellet analyses, we considered it appropriate to use our data to evaluate the effects of human developments on the relative composition of food items that can be detected in raven pellets.

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

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

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

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

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

Management implications

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

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