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Ecology of a population of subsidized predators: Common ravens in the central Mojave Desert, California

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Abstract

Human subsidies have resulted in the rapid growth of populations of common ravens (*Corvus corax*) in the Mojave Desert. This is a management concern because ravens prey on threatened desert tortoises (*Gopherus agassizii*). We conducted weekly counts for 29 months at 10 sites on the US Army's National Training Center, Fort Irwin, California to evaluate factors affecting the distribution of ravens. Raven abundance varied seasonally, diurnally, and with human abundance. It was greatest near resource subsidies, specifically the landfill and sewage ponds. Although other studies have documented heavy use of landfills by ravens, the use of sewage ponds had not been previously reported in the published literature. We suggest that raven management should focus on reducing access to anthropogenic resources.

Keywords: Anthropogenic resource; Corvid; *Corvus corax*; Invasive species; Military; Subsidized predator

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1. Introduction

Commensal predators such as the common raven (*Corvus corax*) benefit from a myriad of resource subsidies provided by human activities. These resource subsidies can include food (e.g. organic garbage), water (e.g. reservoirs), nesting substrates (e.g. telephone poles), and safety from inclement weather or predators (e.g. abandoned buildings). Subsidies facilitate population persistence and may increase population size and range. Concentrated human resources may increase predator densities, affecting prey populations in adjacent habitat through spillover predation (Chapman et al., 1996; Holt, 1984; Schneider, 2001). Subsidized predators can drastically impact native populations because subsidies insulate subsidized populations of predators from the effects of declines in prey populations (Sinclair et al., 1998). Predation may be a major concern for the conservation of endangered and threatened species. It is important to understand the factors that affect the predator's population size during the development of management strategies designed to reduce the predators' effect on native prey populations.

In the Mojave Desert of California, *C. corax* is a subsidized predator (Boarman, 2003; Soulé, 1988). It benefits from anthropogenic resources such as food, particularly in the form of garbage and agricultural wastes, water from sewage ponds and municipal areas, and nesting substrate in the form of billboards, power towers, bridges, and buildings. Ravens that nest in close proximity to anthropogenic resources have improved probabilities of their fledglings surviving to at least 2 year old (Webb et al., 2004). Human subsidies appear to be responsible for recent increases ($>1000\%$ over 24 years) in raven populations in the Mojave Desert (Boarman and Berry, 1995). Populations of animals preyed on by ravens face greater predation pressure near human developments due to artificially high raven densities (Kristan and Boarman, 2003). One prey species, the desert tortoise (*Gopherus agassizii*), is of particular concern to conservation biologists. Ravens in the Mojave Desert prey on neonate and juvenile desert tortoises, and the ravens may be partially responsible for the tortoises' status as Threatened (Boarman, 1993, 2003; US Fish and Wildlife Service [USFWS], 1994).

To better manage populations of ravens, it is necessary to characterize the birds' spatial and temporal distributions with respect to important anthropogenic resources and activities. We report on populations of the common raven from in and around the National Training Center of the US Army at Fort Irwin, California, hereafter referred to as the "Base". We ask several questions: (1) Does the raven's abundance at the Base's landfill vary by age? (2) Do ravens move from site to site within the Base or are numbers of ravens at individual sites independent of each other? (3) Does the raven's use of specific sites vary with abundance of human-provided resources? (4) Does the raven's abundance vary by time of day and season? (5) Is the number of ravens directly affected by foot and vehicle activity? (6) Does the raven's abundance correlate with changes in human abundance? (7) Is the raven's abundance associated with that of the coyote (*Canis latrans*), another human commensal that may be either competitors or help ravens access buried garbage?

2. Materials and methods

2.1. Study area

The Mojave Desert encompasses 140 000 km^2 of Nevada, Utah, and California (Jaeger, 1957). Topology consists of mountain ranges and bajadas interspersed with basins.

Elevations range from below sea level to approximately 2400 m. Climate is seasonal: 39.1 °C mean high in the summer to −0.4 °C mean low in the winter, with an annual mean temperature of 17.7 °C (Rowlands, 1995a). Average rainfall is 108.5 mm, with nearly 80% falling in winter. The flora is dominated by short, widely spaced shrubs in the allscale-alkali scrub and creosote bush scrub vegetation complexes (Rowlands, 1995b).

Our study was focused mostly in the central Mojave Desert within the cantonment of the Base in San Bernardino Co., California (Fig. 1). The Base encompasses 642 km^2 and occurs north of I-15 and Barstow, California. The operational headquarters and living area are confined to the cantonment in the south-central portion of the Base. The cantonment, which covers slightly less than 10 km^2, contains the military landfill, sewage treatment plant (with evaporation ponds), parks, trees, residential housing for approximately 10 000 military personnel and their families, support buildings, and other structures (e.g. shade awnings, wash racks, and storage areas). Desert areas surrounding the cantonment are used for military training and lack abundant, permanent anthropogenic resources.

2.2. Surveys

Ravens were trapped at the landfill with a rocket net on 31 May 1996 and 21 May 1997 to individually identify and track their movements among sites. We baited the trap site with meat scraps for approximately 3 weeks prior to trapping. All captured birds were

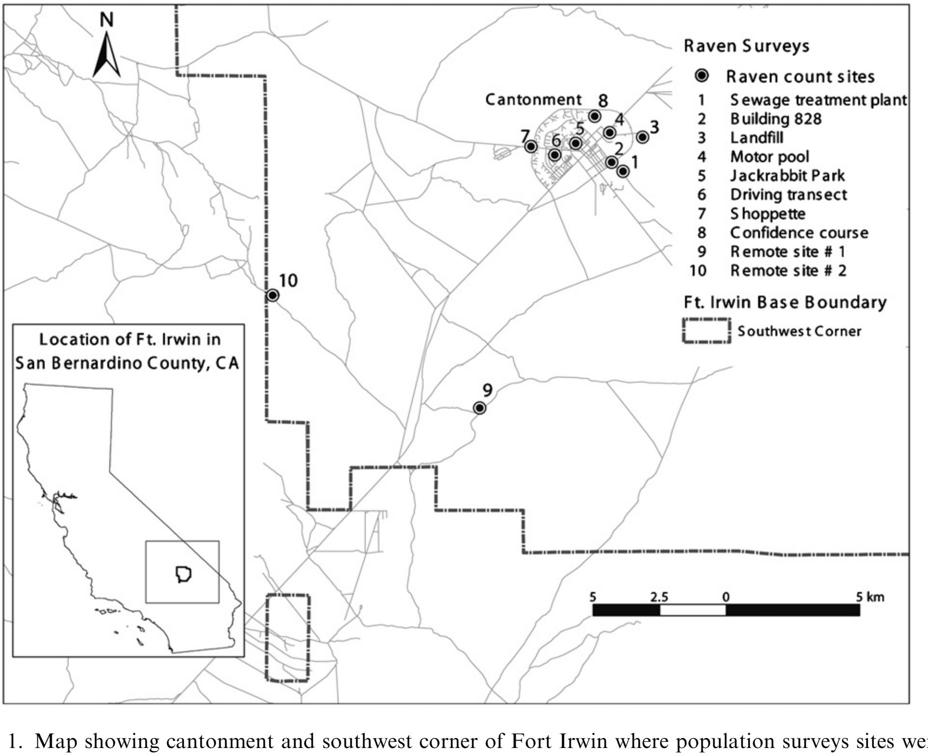


Fig. 1. Map showing cantonment and southwest corner of Fort Irwin where population surveys sites were.

aged (Heinrich, 1994; Kerttu, 1973), weighed, and measured (wing cord, culmen length and depth, and tarsus length and width).

Ravens were surveyed weekly during April 1995–August 1997. We selected eight sites within the cantonment that were used by ravens: sewage treatment pond, a tall vehicle shade awning, solid waste landfill, motor pool at the Operations Group Maintenance Area, Jackrabbit Park, a 1.6 km road transect that meandered through residential and light commercial areas, convenience store, and exercise course (Fig. 1). We also selected two remote desert reference sites located in areas devoid of anthropogenic resources, and rarely used for troop movement or training. Desert Reference 1 was located 1 km from the nearest paved road or other attraction site (116° 48′ 53.9″ N, 35° 12′ 46.0″ W) for ravens and Desert Reference 2 was 2 km from the nearest paved road or other attraction site (116° 43′ 47.7″ N, 35° 10′ 28.8″ W). Each site was visited three times each day: morning, midday, and afternoon. Visits were conducted in the same order with a random start site chosen at the beginning of the survey day. At each site, all ravens were counted for 10 min. At all sites except the road transect, the counts included all birds that were within a 100 m radius of the site at the time of arrival, and all birds that passed through the area during the count. The road transect was surveyed by driving slowly along a 1.6 km section of roads and counting all ravens observed within 100 m of either side of the transect.

2.3. Analyses

2.3.1. Factors affecting abundance of ravens

We tested for patterns in temporal and spatial abundance, and distribution of ravens within the cantonment. Was it possible that raven numbers across the entire cantonment were fairly constant, that is, was it a relatively closed population? If so, totals at the landfill should be negatively associated with totals summed across the remainder of the sites. Alternatively, large numbers of birds may leave the base at more or less the same time, resulting in a positive association among sites. These predictions were examined using simple linear regression analysis on mean totals by month ($n = 29$). Tables of Pearson correlation coefficients were constructed to further examine potential temporal associations (positive or negative) in numbers of ravens among sites. Correlations were calculated for mean monthly totals ($n = 29$), maximum monthly totals ($n = 29$), and daily totals $97 \leqslant n \leqslant 101$. A Dunn-Sidák multiple comparisons correction (Sokal and Rohlf, 1995) was used to adjust the experimentwise error rate (level at 0.05).

Using data from point count surveys, numbers of ravens at the 10 sites at the Base ($n = 10$) were compared using a nested repeated measures ANOVA, with month nested within season and survey nested within month, and with blocking factors of time of day and month in which the survey was completed. Post hoc contrasts on the main effects were achieved with a Tukey's HSD (Zar, 1996).

We generated an a priori hypothesis with ordered expectations based on results from a similar study we conducted at Edwards Air Force Base, California. Our null hypothesis, H_0, was $m_1 = m_2 = m_3$, where m_1 was the mean number of ravens at heavy human resource sites (the landfill and sewage ponds), m_2 was the mean at light human resource sites (all other human-modified sites at the Base), and m_3 was the mean in natural desert habitat. The alternative hypothesis, H_A, was $m_1 > m_2 > m_3$. The ordered expectation was tested using isotonic regression, a powerful one-tailed ANOVA/linear regression technique (Barlow et al., 1972; Gaines and Rice, 1990). The isotonic regression statistic, E^2, is the ratio of the between groups sums of squares and the total sums of squares and can be calculated from the *F*-statistic obtained from a standard ANOVA (Barlow et al., 1972). The groups ($k = 3$) had unequal sample sizes ($n_1 = 58$, $n_2 = 174$, $n_3 = 56$). Thus, we transformed E^2 into an *S* statistic (Robertson et al., 1988), where $S = \mathrm{d}E^2/(1-E^2)$ with *d* being the degrees of freedom ($n - k = 288-3 = 285$). Tabled critical values of *S* were used to determine statistical significance. To avoid pseudoreplication, monthly means for each site were entered into the analysis.

Variation in raven numbers over 29 months was examined graphically through cross-correlation, analysis of variance, and Rayleigh's test for circular uniformity. Cross correlation compared the total number of ravens per month across the 29 months of surveys. A nested repeated measures ANOVA used blocking factors of season, month (nested within season), and survey time (nested within month). Because raven numbers were uncorrelated across sites, each site was treated as an independent measure of raven abundance. Thus, repeated measures were surveys with differing time of day, month, and season at the same site. Season was classified as winter (December, January, February), spring (March, April, May), summer (June, July, August), and autumn (September, October, November). Survey time was classified as morning (0630–1030), midday (1100–1430), and afternoon (1500–2000). Post hoc contrasts between means were determined using Tukey's HSD technique. Rayleigh's test for circular uniformity (Zar, 1996) identifies concentrations of data occurring in a cyclical series (e.g. time, direction). Rayleigh's test generates two parameters, *R*, a measure of departure from a uniform distribution with a probability of *p*, and θ, a measure the angle or direction of the peak in distribution.

The effect of actual, direct human activity was tested using nested repeated measures ANOVA for time effects with activity being treated as the dichotomous (present or absent) main effect. Separate analyses were conducted for overall activity, vehicle traffic, and foot traffic. Post hoc contrasts were examined to determine the pattern of effects, both main and nested.

We used predictable fluctuation in human population within the cantonment to further test the association between human and raven abundance. We performed an isotonic regression to compare human abundance classes against an a priori ordered expectation that raven abundance would be correlated positively with human abundance. The number of people on the Base varied in a regular 28-day cycle following the rotation of troops through the training program. An advance party arrived for the first 2 days, during which time the number of people in the cantonment was at intermediate levels. For the next 7 days, large numbers of troops arrived at the cantonment and prepared for exercises. Troops were several kilometers away from the cantonment during the following 14-day training period and numbers of people in the cantonment were intermediate again. Finally, numbers of people again rose when the troops returned to the cantonment for 5 days. Subsequently, the cycle began again. Twice a year, in winter and summer, many people permanently housed on the Base left for 2 weeks. At this time the human population was unusually low.

We examined whether ravens may be commensals on coyotes or not by calculating a Pearson correlation coefficient between numbers of coyotes and numbers of ravens when the former was noted during a census ($n = 54$ surveys). Then, human activity was entered as a covariate to investigate whether the disruption by humans upset the interspecies association.

2.3.2. Analyses of age

Chi-square goodness of fit test was used to determine if presence at the landfill varied by age. The expected frequencies were based on the assumption that proportions by age class (hatch year, second year, and adult) were equal. We calculated simple correlation coefficients between age class and number of days each bird was detected at those locations for all sightings of wing- and radio-tagged birds at the landfill and the sewage pond.

3. Results

3.1. Factors affecting abundance of ravens

Tallies at the landfill and those summed across the remainder of the Base were not correlated (Fig. 2; $r^2 = 0.0002$). Four significant correlations (3 positive, 1 negative) were found between motor pool and other sites (vehicle shade awning, Jackrabbit Park, exercise course, and desert reference 2, respectively; Table 1). The motor pool may have drawn ravens during the day because it was the site of a night roost.

Number of ravens differed significantly across the ten survey sites (Table 2; $F_{9,110} = 142.06$, $P<0.0001$). These differences were due to higher numbers of ravens at the landfill than at every other site (Fig. 3), and to higher numbers at the sewage treatment plant than at all sites but the landfill (Tukey's HSD). Numbers at the other eight sites did not significantly differ from each other. Both time of day ($F_{240,2419} = 3.50$, $P<0.0001$) and survey month ($F_{110,240} = 1.34$, $P<0.05$) contributed to the variation in numbers of ravens across sites and, thus, on the entire Base (Table 3). Together, month, time of day, and site accounted for 75% (i.e. $r^2 = 0.75$) of the variation in numbers of ravens at the Base. The highest numbers were present between summer and winter, during the afternoon, and at the landfill and sewage treatment plant. Coefficients of variation calculated for mean abundance of ravens at different seasons and times of day showed little difference.

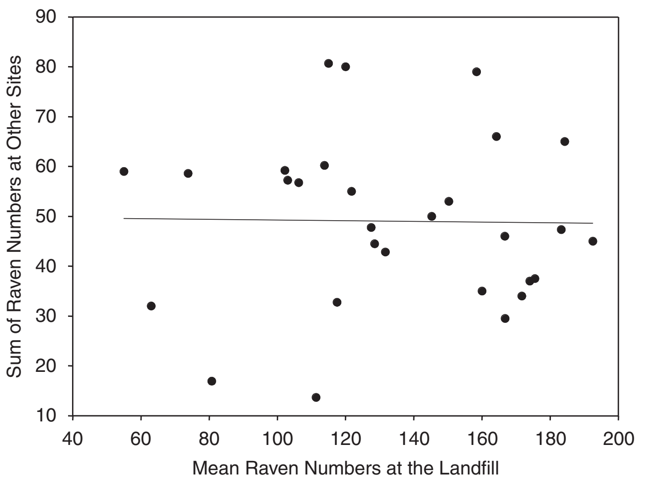


Fig. 2. Mean numbers by month of common ravens at the landfill vs. means summed across the other nine sites surveyed.

Table 1
Pearson correlation coefficients, r, and probability, P, of Type I error under the null hypothesis of no correlation of common raven numbers among sites based on individual survey totals

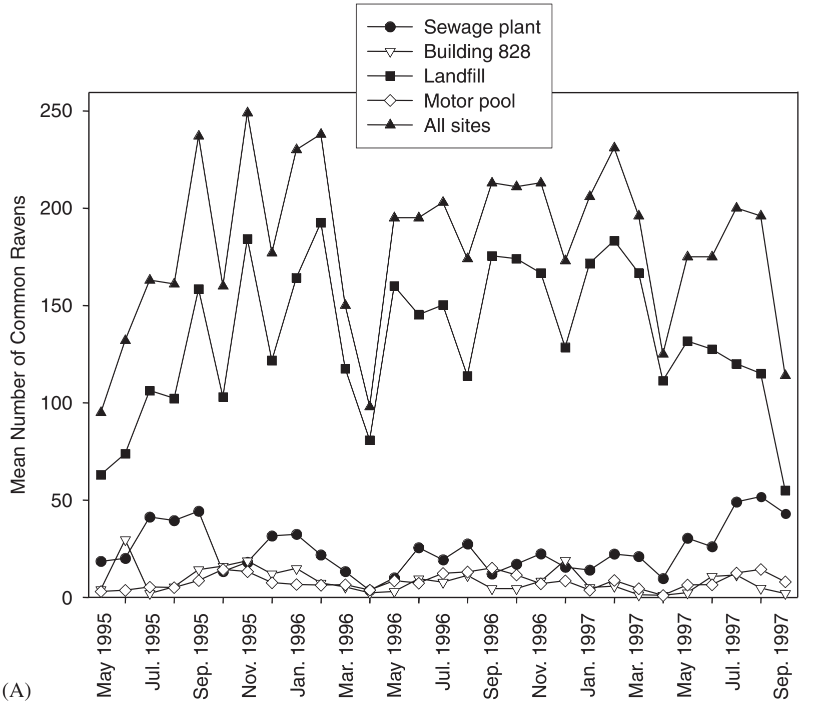
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9
Site 2	0.05 ns								
Site 3	0.01 ns	−0.07 ns							
Site 4	0.17 *	0.2 **	0.14 ns						
Site 5	0.18 *	0.09 ns	0.08 ns	0.2 **					
Site 6	−0.03 ns	0.02 ns	0.09 ns	−0.02 ns	0.14 ns				
Site 7	0.16 ns	0.1 ns	0.12 ns	0.18 *	0.17 *	0.06 ns			
Site 8	0.14 ns	0.12 ns	−0.02 ns	0.21 **	0.05 ns	−0.06 ns	−0.06 ns		
Site 9	−0.18 *	−0.12 ns	−0.01 ns	−0.07 ns	−0.06 ns	0.08 ns	0 ns	−0.08 ns	
Site 10	−0.11 ns	−0.02 ns	−0.11 ns	−0.25 ***	−0.01 ns	−0.08 ns	0.14 ns	−0.15 ns	0.02 ns

These totals are the least conservative because of the larger sample compared to monthly means or maxima and given that they ignore monthly and daily fluctuations. Raven numbers are not correlated among sites under the Dunn-Sidák experimentwise a' of $1-(1-0.05)^{1/45} = 0.001$. Site 1 = sewage treatment pond, Site 2 = vehicle shade awning, Site 3 = landfill, Site 4 = motor pool, Site 5 = Jackrabbit Park, Site 6 = residential, Site 7 = convenience store, Site 8 = exercise course, Site 9 = desert reference 1, and Site 10 = desert reference 2. For levels of significance, *** represents $P \leqslant 0.01$, ** represents $P \leqslant 0.05$, * represents $P \leqslant 0.10$, and "ns" represents $P > 0.10$.

Table 2
Mean number of common ravens observed at each of the ten survey points

Site	Mean	S.E.	n	Total number of ravens detected
Landfill	134.3	5.5	101	13564
Sewage treatment plant	24.9	1.8	101	2514
Vehicle shade awning	9.2	1.4	101	929
Motor pool	7.8	0.6	101	791
Jackrabbit Park	2.7	0.3	101	274
Exercise course	1.9	0.3	101	191
Residential	1.9	0.2	101	188
Convenience store	1.3	0.2	100	127
Desert reference 2 east	0.3	0.1	97	31
Desert reference 1 west	0.3	0.1	97	30

Fig. 3. Fluctuations in mean numbers by month of common ravens at Base. (A) Numbers at the landfill drive most of the pattern for the entire Base. The next three most heavily used sites and all sites combined are also presented. Note the sharp decrease in both springs. (B) The six sites with the fewest ravens are presented. *Note*: Remote Site = Desert Reference.


Sewage plant
Building 828
Landfill
Motor pool
All sites
Mean Number of Common Ravens
0
50
100
150
200
250
May 1995
Jul. 1995
Sep. 1995
Nov. 1995
Jan. 1996
Mar. 1996
May 1996
Jul. 1996
Sep. 1996
Nov. 1996
Jan. 1997
Mar. 1997
May 1997
Jul. 1997
Sep. 1997
(A)

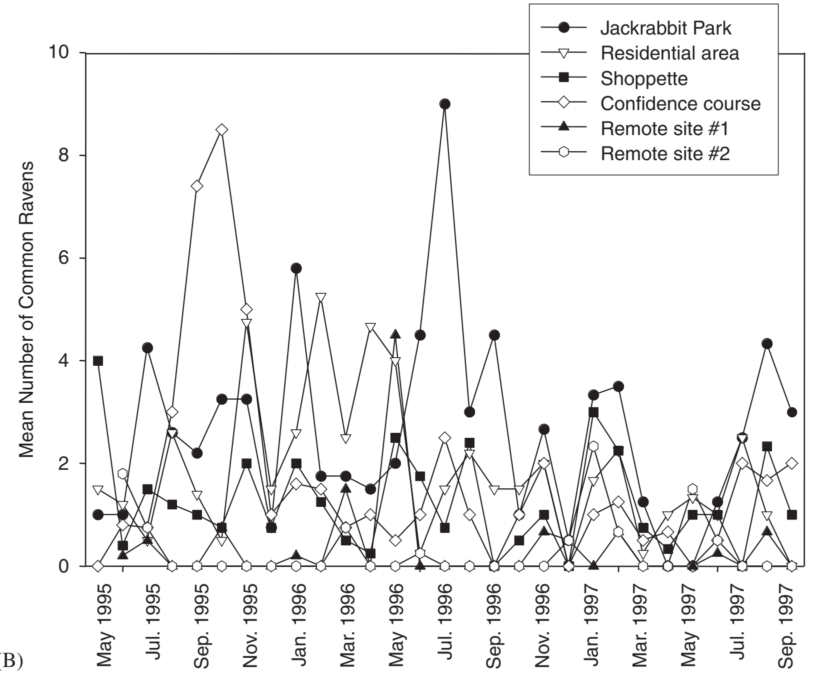

Jackrabbit Park
Residential area
Shoppette
Confidence course
Remote site #1
Remote site #2
Mean Number of Common Ravens
0
2
4
6
8
10
May 1995
Jul. 1995
Sep. 1995
Nov. 1995
Jan. 1996
Mar. 1996
May 1996
Jul. 1996
Sep. 1996
Nov. 1996
Jan. 1997
Mar. 1997
May 1997
Jul. 1997
Sep. 1997
(B)

Table 3
Mean number of common ravens observed across all sites at each of the four seasons and three times of day

	Mean	S.E.	Total number of ravens detected	C.V.
Season				
Winter	14.80	1.60	675	2.81
Spring	9.04	1.01	706	2.97
Summer	11.69	1.01	862	2.54
Autumn	11.87	1.46	536	2.85
Time of the day				
Morning	8.96	0.81	951	2.79
Midday	10.52	0.98	952	2.87
Afternoon	16.30	1.43	876	2.60

Ravens were much more common (mean = 78.9, S.E. = 8.08) at sites with heavy relative to light (mean = 4.0, S.E. = 0.34) human resources. The ravens were also more common in light human resources relative to no human resources (mean = 0.4, S.E. = 0.10). The ordered expectation of higher raven numbers at sites with heavy human resources > light human resources > no human resources was significant ($E^2 = 0.55$, $P \ll 0.01$). Numbers at the landfill were particularly high: 18 times the mean number at light resource sites and 225 times that at open desert sites. Regardless of whether monthly means, monthly maxima, or individual survey numbers were used, we failed to detect correlations in counts of ravens among most sites once we adjusted for the experimentwise error rate for the appropriate number of multiple comparisons made (Table 1).

Numbers of ravens on the Base showed an oscillatory pattern across months with a 3 month cycle (Fig. 3; $r = -0.76$, $P < 0.001$). Season showed a significant effect on abundance of ravens across the Base ($F_{3,8} = 4.88$, $P < 0.05$), with numbers decreasing from winter to spring, but remaining the same at other seasons, as per Tukey's HSD. Month nested within season neither showed a separate effect ($F_{8,24} = 0.57$, $P > 0.50$), nor did the time of day during which the survey was conducted ($F_{24,2743} = 1.24$, $P > 0.10$). Rayleigh's test revealed a significant departure from uniformity with a peak in raven abundance in October and a trough in March (Fig. 4; Rayleigh's $R = 0.084$, $\theta = 277.4$, $P < 0.001$, d.f. = 2221).

Significantly higher numbers of ravens were tallied during times of no human presence at the survey points ($F_{1,22} = 5.77$, $P < 0.05$), regardless of the month of the survey ($F_{22,48} = 0.72$, $P > 0.50$). Within a given period, time of day affected activity ($F_{48,2707} = 1.98$, $P = 0.0001$). Human activity was highest during morning and midday periods and lowest during the afternoon, and the numbers of ravens were highest during afternoon. The strong association between abundance of humans, time of day, and numbers of ravens is present whether the presence of humans comes from vehicle traffic ($F_{48,2704} = 1.92$, $P < 0.001$) or foot traffic ($F_{48,2705} = 1.84$, $P < 0.001$). When landfill surveys were removed from the analysis, abundance of humans had no effect on numbers of ravens ($F_{1,22} = 2.98$, $P > 0.25$).

Abundance of ravens correlated positively with overall abundance of humans in the cantonment (low = 173.6, S.E. = 8.12; medium = 183.9, S.E. = 22.64; high = 202.2, S.E. = 10.34). The isotonic regression yielded significant positive results ($S_{2,98} = 4.48$,

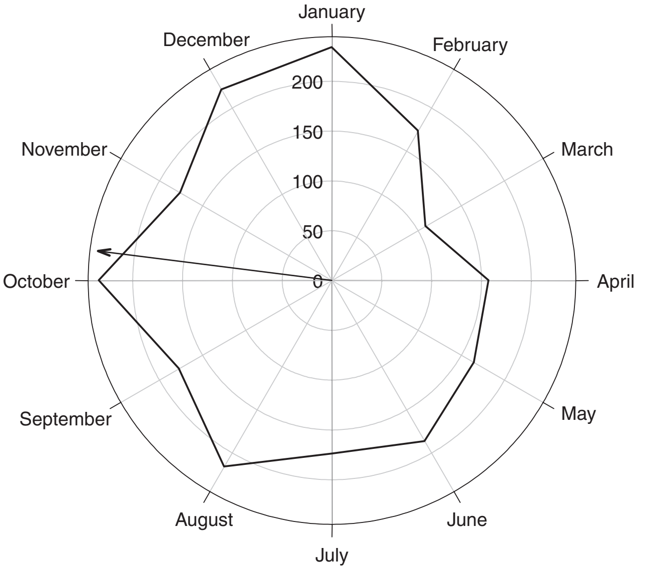


Fig. 4. Mean monthly abundance of common ravens at Ft. Irwin, 1995–1997. The arrow signifies peak abundance, on average ca. the first week of October. The dip in numbers in spring February–April is significant Rayleigh's test: $r = 0.084$, d.f. $= 2221$, $P < 0.001$.

$P \ll 0.05$). Abundance of ravens followed the patterns in abundance of humans associated with cycling of the troop-training schedule.

Numbers of coyotes did not depress numbers of ravens. Instead, their abundances were strongly positively associated ($r_s = 0.58$, $P = 0.0001$). This correction was also seen when human activity is used as a covariate ($r = 0.38$, $P < 0.01$, covariate $r = 0.06$).

3.2. Age

An average of 18.6 (S.D. = 43.83) ravens were counted at all sites per survey, but not all ravens on the Base were counted. Having no a priori knowledge of the population's demographic structure, our H_0 was that an equal number of each age class would be represented. Fewer hatch year (HY) birds were trapped than expected by chance ($X^2 = 33.272$, $p < 0.0001$, d.f. $= 2$). HY birds were only trapped on 31 May 1996, not a year later on 21 May 1997. Tagged birds in their second summer (i.e. 1 year olds) were far more common at the landfill than adults (mean immatures = 11.4, S.E. = 2.55, $n = 14$ vs. mean adults = 4.0, S.E. = 1.40, $n = 10$; $r = -0.44$, $P < 0.05$).

4. Discussion

4.1. Factors affecting abundance of ravens

Given the large number of ravens usually present at the landfill, we probably characterized a significant proportion of the ravens on the Base. Although sites most heavily used during the day were surveyed, we did not survey other locations that contained low numbers of ravens. However, we regularly found radio transmittered birds at low-density sites. Additionally, the night roost at the Rotational Unit Facility Maintenance Area had an average of 446 (S.D. = 173.1) ravens (Boarman, unpubl. data). On one winter evening, this roost contained over 1000 birds. They arrived after sunset and departed before sunrise. Given that only an average of 18.6 ravens were found on daytime surveys, the majority of roosting birds probably left the Base during the day. Thus, conclusions about raven abundance are tempered by the large variation among locations, times of day, and seasons.

We expected numbers of ravens at the landfill to be negatively correlated with numbers at other sites. When not at the landfill, the ravens were expected to be using other parts of the cantonment, and vice versa. However, our expectation was not realized. Ravens at the landfill apparently were not moving as a group to other specific sites surveyed on the Base. Instead, they were probably dispersing individually or in small groups to multiple sites on, and perhaps off, the Base. Many ravens apparently left the Base during the day, resulting in low numbers at the landfill (e.g. morning). These regular movements off the Base indicated an important connection between the Base and the Barstow area. Ravens took frequent advantage of resources in both areas, and neither can be viewed separately when considering Base or regional populations of ravens.

Our results supported the hypothesis that food and water were important anthropogenic resource subsidies for common ravens in the Mojave Desert. Ravens were significantly more abundant at the landfill and sewage pond than at other sites. In general, landfills had important concentrations of ravens (Dorn, 1972; Engel and Young, 1992; Knight et al., 1993; Restani et al., 2001). Knowles et al. (1989, unpublished report) reported large numbers of ravens at sewage ponds (C. Knowles, R. Gumtow, P. Knowles, and P. Houghton; FaunaWest Wildlife Consultants, Boulder, MT. Relative abundance and distribution of the common raven in the deserts of southern California and Nevada during the fall and winter of 1988–1989. Unpublished report to Bureau of Land Management, Riverside, CA).

Low raven abundance was expected at the two remote desert reference sites because the sites provided no resource attraction. Although the mean number of ravens was higher at some other anthropogenic sites (shade awning, motor pool, Jackrabbit Park, road transect, convenience store, and exercise course), they were not significantly greater than the remote desert sites. This lack of difference was surprising given that anthropogenic sites generally provide some resources for ravens. The lack of significance may be an artifact of lack of power in our statistical tests because of the high degree of variance relative to mean at these sites. Camp et al. (1993) also measured very low raven abundance in remote areas of the Mojave Desert and Knight et al. (1993) found significantly fewer ravens in natural areas compared to powerline and highway corridors.

Ravens were significantly more common on the Base in the afternoon. The closure of the landfill at 16:00 probably best explained this discovery. The landfill was surrounded by a chain link fence, which prevented people from disturbing the birds. The negative association obtained between raven abundance and actual human activity supported this hypothesis. Restani et al. (1996) obtained similar results with ravens in Greenland. The higher numbers of ravens in the afternoon, with similar coefficients of variation, suggested that afternoon was a good time to conduct surveys to obtain valid estimates of the raven's population density.

Abundance of ravens on the Base was seasonal, fluctuating widely throughout the year. The density of ravens was significantly lower in the spring than in other seasons. Austin

(1971) and Knight et al. (1999) also obtained a similar pattern of lower raven numbers in the Mojave Desert in spring. The low point was probably due to a combination of accumulated mortality, particularly in fledglings, over the year, and partly due to dispersion over a broader area for breeding. The autumn's significant peak in raven abundance was surprising. We believe the numbers were higher than expected in the winter because ravens were concentrated at human-provided food sites during a time of year when non-human food sources are rare (Restani et al., 2001).

Number of ravens in the cantonment varied in concordance with a regular 4-week cycle of troop rotation schedules. As abundance of humans peaked in the cantonment, so did raven abundance. When troops abandoned the cantonment for training exercises in remote desert locations, raven abundance dipped significantly. Many ravens may have followed the troops into the desert, but others may have left the base altogether. Restani et al. (2001) reported raven abundance roughly tracked reductions in human abundance in southwest Greenland. The observations supported the hypothesis that raven and human populations were closely associated in the Mojave Desert.

Numbers of ravens and coyotes at the landfill were positively correlated with each other. Ravens followed wolves and cougars in order to scavenge on their leftover carcasses (Mech, 1970; Pearse, 1938). Coyotes heavily used the landfill and its superabundance of food probably prevented any competition between ravens and coyotes. The positive correlation between the species remained, even after controlling for human activity levels. This suggested either that there was an attraction between the species (for example, coyotes may help ravens by making food available when they tear open packages, move heavy debris, and dig into dirt cover), or that both species were attracted to the same resources. However, there were also negative interactions: on one occasion, a coyote caught and consumed a raven at the landfill (M. Masser, pers. comm.).

4.2. Age

Young (second year) ravens tended to use the landfill more than adults. Restani et al. (2001) also observed significantly more immatures and juveniles at a landfill in Greenland, particularly in late summer. Our data were consistent with the observation by Heinrich et al. (1994) that non-breeders (hence primarily juveniles) joined feeding flocks or crowds. However, feeding crowds also contained adults.

5. Conclusion

The density of the Ravens on the Base was tied to human activities. Ravens occurred in considerably greater numbers at the landfill and sewage pond than at other anthropogenic and undisturbed sites. Their numbers also fluctuated in response to predictable patterns in the size of the human population at the Base, which varied with the troop training cycle. The resource subsidies provided by human activities were well used by ravens. The ravens at the Base were a regular part of the broader raven population, including neighboring urban and agricultural areas to the south. For the long term, management efforts should focus on reducing the availability of resource subsidies, especially at landfills and sewage ponds. These efforts may have great success, but only when coupled with similar efforts on a broader, region-wide basis (Boarman, 2003).

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