

Movements of Juvenile Common Ravens in an Arid Landscape

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ABSTRACT Movement patterns of juvenile birds are poorly understood, yet critically important ecological phenomena, especially for species with a prolonged juvenile period. We evaluated postfledging movements of juvenile common ravens (*Corvus corax*) in a western Mojave Desert landscape composed of a mosaic of natural and anthropogenic elements. Generally, ravens do not begin breeding until after their fourth year. We marked 2 annual cohorts of juvenile ravens and followed them from dispersal from their natal territory for up to 33 months. Movements of juvenile common ravens were similar for males and females. Conspecifics and confined livestock feeding operations represented important resources for juvenile ravens, and juveniles were rarely located in open desert. However, initial movements from the natal territory to the nearest communal point subsidy rather than the closest anthropogenic resource suggested juvenile dispersal was influenced by the combination of conspecifics and anthropogenic resources, rather than the distribution of those resources. Land managers concerned with growing raven populations should reduce access to concentrated anthropogenic resources such as landfills and dairies, which serve as important resources for juveniles. Because juvenile ravens rarely venture into open desert, reducing their numbers by lethal removal or other means is unlikely to lessen raven predation of desert tortoises (*Gopherus agassizii*). (JOURNAL OF WILDLIFE MANAGEMENT 73(1):72–81; 2009)

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Juvenile dispersal is the spatiotemporal process that occurs during emigration from an animal's natal site through subsequent transient stages prior to the first breeding attempt (Vega Rivera et al. 1998, Lang et al. 2002) and is a subset of the related process of natal dispersal, which occurs between birth and first breeding (Greenwood 1980). As juveniles leave the natal territory, spatial patterns in movement behavior provide information regarding resources important for juvenile survival, which may differ from those of adult members of the population (Westcott and Graham 2000, White et al. 2005). Movements during the juvenile phase may be especially important for species with delayed maturation, for whom this period may occupy a significant fraction of their lifespan. However, the lengthy subadult period of long-lived birds is difficult to study and, therefore, juvenile movement is one of the least understood features of avian life history (Vega Rivera et al. 1998, Zollner and Lima 1999, Kershner et al. 2004).

Ravens are long lived (up to 13 yr in wild birds; Boarman and Heinrich 1999), often with an extended juvenile or subadult period and delayed reproduction. The age of first breeding for common ravens in North America is not documented in the published literature (Boarman and Heinrich 1999), but the combined median age of first breeding based on 2 ravens in Great Britain (Ratcliffe 1997) and on 9 records from western North America (W. C.

Webb, University of Washington, unpublished data) is the fourth year.

Groups of ravens composed mainly of juveniles and subadults congregate at concentrated food resources such as animal carcasses (Heinrich 1988, Restani et al. 2001). As human activities usurp natural processes, ravens increasingly exploit anthropogenic sources of food and water, including agricultural activities (Engel and Young 1992a, Roth et al. 2004), urbanization (Knight and Kawashima 1993), roadkill (Kristan et al. 2004), and landfills (Boarman et al. 2006). Anthropogenic sites such as landfills and waste treatment facilities in the western Mojave Desert provide super-abundant and constantly replenished sources of food and water in an otherwise resource-poor arid landscape. As a consequence, the abundance of ravens in the western Mojave has increased by several orders of magnitude since the 1960s (Boarman and Berry 1995, Sauer et al. 2004), and demographic studies have shown increased nest productivity and juvenile survival for nests located closer to these readily identifiable sources of anthropogenic point subsidies (Webb et al. 2004, Kristan and Boarman 2007).

Increased abundance of ravens in the western Mojave and elsewhere, potentially enabled by their exploitation of anthropogenic resources, represents a substantial conservation concern because ravens are predators of sensitive species, including the federally threatened desert tortoise (*Gopherus agassizii*; Boarman 2003). Raven predation has been identified as a primary threat to the desert tortoise in the Desert Tortoise Recovery Plan (U.S. Fish and Wildlife Service [USFWS] 1994) and the Desert Tortoise Recovery Plan Assessment (Tracy et al. 2004). The final raven management environmental assessment directs the USFWS

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Table 1. Categories and spatial extent of land use, land cover, and resources within the study site (20-km buffer around all juv dispersal locations) and within utilization distributions (UDs) for 42 juvenile common ravens with >10 dispersal locations in the western Mojave Desert, May 1999–Mar 2002. The UD quantifies an animal's probability of occurrence at each point in space as determined by kernel analysis. We chose land-use and land-cover categories we thought most important to juvenile ravens and only included them in models of resource utilization. Numbers 1–9 identify resources included in the a priori set of candidate models included in the resource utilization function analysis.

Land cover or land use	Resource	No.	Area (km ²)	Occurring within UDs		
				Area (km ²)	SD	UDs
Commercial, residential areas	Urban	1	184.83	17.66	37.01	31
Isolated commercial services	Commercial		101.45	3.66	10.41	21
Roads	Roads	7	731.96	29.38	63.80	42
Vacant cleared land	Disturbed	5	295.74	22.65	44.37	42
Low density housing	Exurban	6	25.66	2.77	4.17	31
Crops and pasture	Crops, pasture	2	110.64	12.48	14.39	22
Water	Water		1.74	1.17	0.16	6
Landfills and sewage ponds	Waste facility	9	3.87	0.92	1.06	25
Dairies, stables, and hobby farms	Feeding operations	3	0.79	0.17	0.17	30
Light industry and mines	Industry		39.67	2.88	5.60	35
Parks, campgrounds	Recreation		1.43	0.38	0.35	15
Wetlands	Wetlands		0.68	0.64	0.07	5
UD juv with <10 locations	Conspecifics	1	980.83	116.50	359.39	42
Creosote scrub	Desert	4	1,775.01	68.17	141.83	30
Saltbush scrub	Desert	4	915.19	69.89	124.25	38
California annual grassland	Desert	4	298.87	23.30	35.00	6
Woody scrub	Desert	4	358.45	11.39	20.09	15
Blackbush scrub (<i>Coleogyne ramosissima</i>)	Desert	4	19.35	0.00	0.00	1
Singleleaf pinyon (<i>Pinus monophylla</i>) and juniper (<i>Juniperus</i> spp.) woodland	Desert	4	146.32	15.69	14.11	5
Semidesert chaparral	Desert	4	196.45	29.13	30.03	5
Alkali playa	Desert	4	229.47	19.92	28.01	9
Desert native grassland	Desert	4	3.69	3.69	0.00	1
Rabbitbrush scrub (<i>Chrysothamnus albidus</i>)	Desert	4	11.69	3.62	2.07	3
Chamise chaparral (<i>Adenostoma fasciculatum</i>)	Desert	4	1.66	0.00	0.00	0
Mojave riparian forest	Desert	4	2.98	2.82	0.23	2
Total desert			3,959.13			
Total anthropogenic land use			1,200.30			
Total study site			6,438.42			

to reduce raven predation on the desert tortoise and other reptiles and mammals throughout the deserts of southern California, USA, by shooting, poisoning, and trapping ravens (USFWS 2008).

Our objectives were to increase understanding of 1) postfledging juvenile dispersal behavior, 2) raven spatial ecology and resource use, and 3) the relationship between anthropogenic subsidies and growing raven populations. We assumed that spatial patterns in the direction, distance, and degree of clustering of raven juvenile locations would provide insight into the mechanisms driving the early stages of raven juvenile dispersal. We also assumed that movements of raven juveniles and subsequent variation in space use within the home range (third-order scale: Johnson 1980) reflected the quality and abundance of resources necessary for juvenile survival.

STUDY AREA

We conducted our study at Edwards Air Force Base (34°38'N, 118°6'W) and in the surrounding human communities and native land-cover types of the western Mojave Desert, which lies within the Mojave Desert Floristic Province (Hickman 1993). The extent of the study site was defined as the area within a 20-km buffer of all raven location data (see below) and encompassed 5,460 km².

Land cover in the study site consisted of a mixture of natural and anthropogenic types (California Natural Diversity Database 1999; Table 1). Mean annual precipitation was 112 mm and fell mainly as rain between November and March (MacMahon 2000). Mean annual temperature was 18.1° C, with hot summers (mean monthly max. temp 25–30° C, Jun, Jul, and Aug) and cool winters (mean max. temp 10–15° C, Dec, Jan, Feb; MacMahon 2000). Native vegetation communities included Mojave Creosote Bush (*Larrea tridentata*) Scrub and Desert Saltbush (*Atriplex* spp.) Scrub. Common anthropogenic land-use types included urban, exurban (low-density residential housing), agriculture, ranching, light industry, and military flight-support operations.

We defined resources as the suite of physical and biological components in the environment that lead to occupancy of a particular place by individuals. This definition includes, but is not restricted to habitat (local physical characteristics; Block and Brennan 1993, Jones 2001). Anthropogenic land-use types that provide food and water for ravens (hereafter, point subsidies) in the region (e.g., sewage ponds, landfills) form readily identifiable, distinct point sources of rich, artificial resources set within an otherwise resource-poor arid landscape. Adult ravens defend resources within their territories (Marzluff and Heinrich 1991) but are unable to

exclude conspecifics from rich resources such as landfills that become communal point subsidies and frequently attract dozens or hundreds of ravens. This heterogeneous spatial distribution of native land cover, anthropogenic land use, and anthropogenic point subsidies is propitious for evaluating the relative importance of these resources on juvenile dispersal.

METHODS

Trapping and Tracking

During spring of 1999 and 2000, we located 98 raven nests and marked 240 nestlings at approximately 4.5 weeks of age, just prior to fledging, which typically occurs during the fifth week in this area. We tagged all nestlings with individually coded patagial tags marked with alphanumeric or numeric-alpha writing that was visible from a distance. We applied wing tags to both wings, using either plastic clips or pop rivets. A subset ($n = 102$) of marked juveniles received radiotransmitters (Advanced Telemetry Systems, Isanti, MN, and Holohil Systems Ltd., Carp, ON, Canada) attached with a backpack-styled harness (Buehler et al. 1995). Transmitters weighed 22 g and were approximately 3% of the average fledgling's body mass. All capture and experimental techniques strictly followed guidelines described in Gaunt and Oring (1997), and we obtained approval from the Chancellor's Committee on Laboratory Animal Care of the University of California, Riverside (Animal Use Protocol A-S 9907013-1). Because male and female ravens are morphologically indistinguishable, we used molecular techniques to identify sex of individuals. During visits to the nests, we sampled 2 small growing feathers from each nestling and determined sex using a polymerase chain reaction that amplifies homologous chromobox-helicase-DNA-binding gene fragments on the W and Z chromosomes (Griffiths et al. 1998).

We monitored marked juveniles by returning to the vicinity of their natal territories 1–3 times per week. Because adult ravens vigorously defend active nesting territories against intruders, we defined natal territories as the area centered on the nest and defended by the nesting adults. Based upon observations of territorial behavior of breeding adult pairs, this area usually extended 0.5 km to 1.0 km from the nest. We returned to each natal territory until we found juveniles dead or we relocated them ≥ 3 km outside the natal territory.

We relocated juveniles that survived emigration from their natal territory by radiotracking and by visually searching throughout the study area. We tracked ravens from May 1999 to March 2002 (33 months). Thus, we followed juveniles from the 1999 cohort into their fourth year and birds from the 2000 cohort into their third year. We searched the entire study area on a monthly basis to maintain a uniform search effort throughout the study. We visually confirmed all locations of radiotagged birds because of the relative ease of obtaining visual confirmation in the open desert environment and to avoid potential for error from triangulating signals (White and Garrot 1990, Engle

and Young 1992). We minimized spatial and temporal correlation between sequential observations for the same individuals by obtaining locations ≥ 24 hours apart, a period more than sufficient for a raven to traverse the diameter of the study site. We relocated radiotagged juveniles mainly by motorized vehicle. We detected signals using dual 3-element Yagi antennas attached to vehicle rooftops by 1-m-high swiveling masts, in tandem with an ATS R2000 portable scanning radio receiver (Advanced Telemetry Systems). We also used handheld portable 3-element and 2-element Yagi antennas to search on foot for radiotagged juveniles. On 3 occasions, we flew a Cessna 185 equipped with dual wing-mounted, 3-element Yagi antennas to conduct an aerial search for missing transmitter signals up to 300 km from the perimeter of the study site. Detectability of transmitter signals ranged from 1 km to 50 km, depending upon the search mode (vehicle, foot, or aircraft), topography, and behavior of the individual birds. We employed vehicle-based radio receiving equipment 4 times annually (once in spring, summer, fall, and winter) to search extensively outside the study site by driving up to 200 km from the perimeter of the study site.

We recorded locations of juveniles in Universal Transverse Mercator coordinates using handheld Global Positioning System (GPS) units (Magellan GPS 300, accuracy ± 10 m; Rockwell Precision Lightweight GPS Receiver, ± 15 m). We plotted locations of juveniles on a study site map constructed using Geographic Information System (GIS). When we located marked juveniles, we counted the number of conspecifics within circular radii of 100 m of each marked juvenile.

Analyses

We measured several indices of juvenile dispersal including median, initial, and mean distance moved between locations, and the maximum distance we located individuals from their nests. We checked for normality of all variables using the Kolmogorov–Smirnov goodness-of-fit test and then tested for sex-related differences in movement indices using t -tests.

If, over time, some areas are consistently more attractive for juvenile ravens, then dispersal locations should be spatially clustered. We inspected the degree of clustering in location data using a refined nearest-neighbor analysis that employs a Monte Carlo simulation (Diggle 1981). This approach compares the observed mean distance between locations with the estimated expected mean distance based upon 100 simulations of random point patterns with the same sample size and area as the original data (Diggle 1981). We evaluated clustering of location data individually for all birds with >10 locations outside the natal territory and for the population as a whole using one randomly selected location from all birds with >5 locations outside the natal territory (Biotas, version 1.03; Ecological Software Solutions, Urnäsch, Switzerland).

We expected distribution of anthropogenic resources to influence initial dispersal behavior because other studies in this region identified a close relationship between demographic parameters and nest proximity to anthropogenic

sources of food and water (Webb et al. 2004, Kristan and Boarman 2007). We used GIS to quantify the distance between each nest and the nearest anthropogenic source of food or water, distinguishing between larger communal point subsidies that consistently attracted many ravens from smaller point subsidies more easily defended by adult territory holders. We used linear regression to compare the initial departure distance and the nest distance from the nearest point subsidy and the nearest communal point subsidy.

Direction of dispersal would be nonrandom if juvenile ravens tended to disperse in a particular cardinal direction. We tested for nonrandom direction of dispersal using Rayleigh's z -test in ArcView 3.3 using the Animal Movements extension (Hooge et al. 2000). For a sample of angles, the Rayleigh test calculates a mean angle and a mean angular deviation, then tests the null hypothesis that the angular data are randomly distributed with respect to the mean angle.

The pattern of dispersal might resemble a random walk if juvenile ravens moved randomly in search of food, water, and other resources. We used the Animal Movements site-fidelity test (Hooge et al. 2000) to determine if the pattern of juvenile dispersal resembled a random walk. The site-fidelity test uses a Monte Carlo simulation of random angles with distances between existing sequential points from the original data to determine walk points. Each simulation calculates a new center of activity and generates a value for the mean squared distance (MSD values) of dispersal points from the center of activity. We started the simulation from the first location outside the natal territory and used 100 simulations for each individual with >10 locations outside the natal territory. We used the simulated distribution of MSD values for each individual to evaluate the significance of the observed individual dispersal patterns. We considered observed distribution patterns nonrandom if the MSD values of observed patterns occurred within the upper 2.5% (dispersed dispersal pattern) or lower 2.5% (clumped dispersal pattern) of the tails of their respective simulated distributions. Otherwise, we considered observed dispersal patterns random if the MSD values of the observed patterns occurred between the upper and lower 2.5% of the tails of their respective simulated distributions. We compared male and female site fidelity using a Pearson chi-square test (SPSS Inc., Chicago, IL).

To describe the degree of sociality among juvenile ravens, we quantified the amount of space sharing among juvenile ravens by calculating the volume of home range overlap between all pairs of juveniles with >10 postdispersal locations. We quantified home ranges in ArcView 3.3 using the Animal Movements extension (Hooge et al. 2000) by implementing a 99% fixed-kernel estimator (Seaman et al. 1999). Kernel analysis quantifies an animal's probability of occurrence at each point in space, or its utilization distribution (UD). We defined home range as the 99% fixed-kernel UD for juvenile ravens with ≥ 10 dispersal locations outside the natal territory. We chose a fixed-kernel

estimator because this technique frees the UD estimate from parametric assumptions, provides a means of smoothing location data (Worton 1989), and produces estimates with small variance and bias (Bowman 1985). We chose the smoothing parameter objectively using least squares cross-validation (Seaman et al. 1999). We established that our minimum of 10 dispersal locations was an appropriate level of sampling in our study to quantify relative differences in space use (Garton et al. 2001) by determining that there was no correlation between number of dispersal locations per individual and home range size for individuals with >10 postdispersal locations ($r^2 = 0.01$, $P = 0.49$).

To characterize resource use by juvenile ravens, we constructed GIS layers combining land cover (natural vegetation types) and land use (anthropogenic landscape elements) using data from the California Gap Analysis Project (GAP; Davis et al. 1998) as an initial template. The California GAP data classify vegetative land cover according to plant communities recognized by the California Natural Diversity Database (1999), and land use following Anderson et al. (1976). We refined GAP land-use categories based on our personal knowledge of the region. We used United States Geological Survey (USGS) 7.5-minute digital orthophoto quarter quadrangles to digitize the entire study site according to land-use and land-cover categories to an accuracy of 25 m. Our efforts were simplified because the spatial extent of land use and land cover are mutually exclusive. In contrast to more mesic areas where land use may co-occur with native land cover, the native desert vegetation in this arid region is virtually eliminated by imposed land uses. In addition to the preexisting GAP land-cover and land-use designations, we introduced additional anthropogenic land-use categories that we considered prominent features of the landscape, including disturbed (areas denuded of native vegetation), exurban (low density housing), crops and pasture, waste facilities (sewage ponds and landfills), and confined livestock feeding operations (dairies, stables, and hobby farms). Our introduced low-density housing class (exurban) was distinguishable from the native GAP residential class primarily because it was highly interspersed with other land classes, whereas the residential land class is highly contiguous and has low interspersation with other land classes. Previous studies in arid regions have shown low abundance of ravens in native plant communities (Engel and Young 1992, Knight and Kawashima 1993, Kristan and Boarman 2003), so we parsimoniously combined 12 native plant communities into one *desert* category (Table 1). We then combined this data layer with a USGS roads layer (USGS Mojave Desert Ecosystem Program, Barstow, CA) because previous studies have shown that ravens respond to road-killed carrion and other foraging opportunities presented by roads (Knight and Kawashima 1993, Kristan et al. 2004).

To determine resource use, we compared land-use and land-cover types to raven distribution patterns. In Animal Movements, we converted 99% fixed-kernel UDs to raster format with 25×25 -m cell sizes, and then used the

Table 2. Resources, models (and resources included in each model), and model selection frequency from the a priori set of candidate models compared using Akaike's Information Criterion in the resource utilization function analysis for 42 juvenile common ravens with >10 dispersal locations in the western Mojave Desert, May 1999–March 2002.

Resources	Models	Resources in models	Frequency
1) Utilization distribution from all juv <10 locations	A) Global—all resources	1–9	0.976
2) Distance to crops and pasture	B) Anthropogenic	2, 3, 6, 7, 8, 9	0.015
3) Distance to confined feeding operations	C) Conspecifics only	1	0.007
4) Distance to desert	D) Desert only	4	0.002
5) Distance to disturbed	E) Conspecifics and anthropogenic	1, 2, 3, 6, 7, 8, 9	0.132
6) Distance to exurban	F) Point subsidies	2, 3, 6, 8, 9	0.000
7) Distance to roads	G) Roads	7	0.000
8) Distance to urban	H) Urban and exurban	6, 8	0.007
9) Distance to waste facilities	I) Communal point subsidies, urban, and exurban	3, 6, 8, 9	0.007
	J) Communal point subsidies, and conspecifics	1, 3, 9	0.009
	K) Urban, exurban, conspecifics, and communal point subsidies	1, 3, 6, 8, 9	0.007
	L) Urban, exurban, and conspecifics	1, 6, 8	0.068

ArcView 3.3 extension FocalPatch (Marzluff et al. 2004) to generate point themes from the UD in which each cell contained a value between 0 and 99 for the height of the UD, where 0 represented highest use. We restricted our subsequent analyses of resource use to the top 50% (values between 0 and 49) of individual UD. We required a cutoff value because of the computational demands of the subsequent analyses of resource use and justified values between 0 and 49 because the frequency distribution of postdispersal locations and 99% UD suggested that UD values >49 represented areas where we rarely located juvenile ravens. Although such areas may be important to determining resource selection patterns, they are not pertinent to our study.

For each land-use and land-cover category, we created a separate GIS layer where each cell contained the distance of that point to the nearest other cell containing that category (cell values = 1 for identity). In addition to land-cover and land-use surfaces, we also generated a 99% UD using pooled postdispersal locations of individual birds with <10 postdispersal locations. This UD represented an independent resource base of conspecifics. Variation in the density of conspecifics along with continuous surfaces of land cover and land use represented the complete set of resources to which we compared variation in the height of UD for juvenile ravens with >10 dispersal locations.

We used the resource utilization function (RUF; Marzluff et al. 2004) to quantify resource use of juvenile ravens with >10 dispersal locations at the third-order, or within home range, scale (Johnson 1980). This approach assumes that space use relates to resource use and relates variation in the height of the UD to spatially defined resources using multiple linear regression, while accounting for spatial autocorrelation in location data introduced by kernel analyses. The RUF uses a model from the Matérn class where the correlation is a function of the distance between locations with the range set by the bandwidth from individual kernel density estimates (Marzluff et al. 2004). The RUF determines the resources at each grid cell in the UD and relates height of the UD to resource values at each

cell to produce coefficients of relative resource use. Coefficients in the RUF indicate the relative importance of each resource to each juvenile raven. Advantages of the RUF include reducing impact of location error, treating the animal or group as the unit of observation, and using a response variable that is a continuous and probabilistic measure of space use (Marzluff et al. 2004).

The kernel analysis resulted in a wide range of kernel sizes ranging from 300 to >1 million sample cells (median 16,832, SD 178,511). The RUF analysis package processes a maximum of 1,000 sample cells from a UD at a time while running on a desktop personal computer. Given the large number of sample points within UD and the RUF computational limitation, we subsampled UD with >1,000 sample points until we used all the points within the UD or created 20 subsamples (median 17.5, range 1–20). We assembled subsamples for RUF analysis by randomly selecting 250 points from each quartile of the UD for UD values between 0 and 49 (quartile 1 [UD values 0–12], quartile 2 [UD values 13–24], quartile 3 [UD values 25–36], and quartile 4 [UD values 37–49], where the values represent the native grid UD values where 0 is highest and 49 is the lowest use). We then recombined the randomly selected quartile data to produce subsamples totaling 1,000 points from the UD.

We then generated and compared several models of resource use. We developed 12 a priori models, each representing a different hypothesis of resource use. Each model contained different combinations of resources to relate to variation in height of UD of juvenile ravens (Table 2), and we used Akaike's Information Criterion (AIC) to select the best models within each subsample. Not all resources occurred within every UD (Table 1), so we omitted resources from the candidate models for individual birds if the resource did not occur within the UD for that individual. Within each subsample, we derived model-weighted resource coefficients and standard errors from the model with the lowest AIC value and all other models in the subsample with ΔAIC values <10 (Burnham and Anderson 2002). We equally weighted final estimates of resource

Table 3. Juvenile dispersal metrics for 42 juvenile common ravens with >10 dispersal locations in the western Mojave Desert, May 1999–June 2002. All values are means except for dispersal distance, where medians are reported.

Dispersal measurement	M (<i>n</i> = 25)		F (<i>n</i> = 17)		<i>t</i>	<i>P</i>
	\bar{x}	SE	\bar{x}	SE		
Home range (km ²)	142	71	188	10	0.38	0.70
Home range diam (m)	8,890	2,106	10,380	3,073	0.41	0.68
Dispersal distance (m)	7,913	1,568	7,901	1,878	≤0.09	0.99
Max. dispersal distance (m)	17,828	2,320	18,362	3,627	0.13	0.90
Initial dispersal distance (m)	5,778	1,387	5,984	1,908	0.09	0.93
Distance between locations (m)	2,897	518	4,100	1,256	0.89	0.39

coefficients and standard errors across subsamples for UD_s with multiple subsamples.

RESULTS

The mean fledging date for the 1999 cohort was 6 June (SD 7 days) and 4 June for the 2000 cohort (SD 7 days). Combining both years, 38% (90 individuals, 32 with transmitters) survived emigration from their natal territories. Juveniles with transmitters and wing-tagged-only birds had similar survival rates, but those that fledged earlier and those fledging from nests closer to point subsidies had higher survival rates to dispersal and higher survival rates up to 9 months later (Webb et al. 2004). We obtained 2,451 locations by tracking raven juveniles from May 1999 until February 2002. Mean date when we first observed birds outside the natal territory was 14 July and 16 July for the 1999 and 2000 cohorts, respectively, on average 46 days after the estimated fledging date for each individual (SD 19 days). We located juveniles 1,626 times outside their natal territories, including 200 locations of birds that we sighted <10 times. The number of individuals and the frequency of sightings outside the natal territory were 28 individuals (1–4 locations), 20 individuals (5–9 locations), 11 individuals (10–19 locations), 19 individuals (20–39 locations), 12 individuals (40+ locations). There were 42 individuals with >10 postdispersal locations; of these 22 carried transmitters.

The length of time that we followed individuals after initial dispersal from the natal territory ranged between 57 days and 981 days (\bar{x} = 503, SD 266). Survival of juvenile ravens that survived emigration from their natal territories was 47% for hatch-year, 88% for second-year, and 88% for third-year birds (Webb et al. 2004). As is typical of mark-recapture studies, for a few (5) individuals we were unable to distinguish with certainty among mortality, permanent emigration, or radio failure. Of 32 birds with transmitters that survived natal dispersal, 2 had failed transmitters, we found 13 dead, 12 were still alive at the end of study, and 5 were missing at the completion of the study. It is likely that ≥4 of these missing birds died and their transmitters were destroyed. We saw one of the missing birds with a transmitter just once outside natal territory, and it is likely that its transmitter was destroyed by a mammalian predator or scavenger (Webb et al. 2004). We observed the other 4 missing birds between 6 and 184 times over 5–18 months.

We last saw 3 of these missing birds at a dairy where other ravens had been shot or poisoned. Raven carcasses at the dairy were often unrecoverable because of burial by manure or burial in large pits with deceased dairy cows. We last located one of the missing birds in a small town at the periphery of the study site, and this individual was the best candidate for possible emigration from the study site.

Indices of juvenile dispersal were normally distributed and did not differ between sexes. Median dispersal distance from the nest was 7.9 km (range 1–27 km; Table 3). Dispersal distances, mean distance moved between locations, and home range size did not differ by sex (Table 3). No individuals were known to have left the study site, based upon extensive aerial and vehicle-based efforts searching up to 300 km outside the study site.

Juvenile dispersal occurred abruptly for 69 juveniles never observed again inside the natal territory. However, dispersal from the natal territory occurred more gradually for 21 individuals later relocated back in their natal territory. For individuals with gradual dispersal, time between the first dispersal location and the final location inside the natal territory sometimes lasted several weeks (\bar{x} = 21 days, SD = 16 days, range 1–58 days). We later found 4 juveniles that we sighted at least once outside the natal territory dead inside the natal territory. In one case, a dispersing brood of juveniles moved to an adjacent territory 600 m away from their natal nest. The adjacent territory was also home to 4 resident juveniles. The 3 visiting juveniles remained in the adjacent territory for 15 days before we relocated them at a communal point subsidy 7.6 km from their nest.

There was no relationship between initial departure distance and nest proximity to the nearest point subsidy (n = 28, r^2 < 0.01, P > 0.99) but was between the initial departure distance and nest proximity to the nearest communal point subsidy (n = 28, r^2 = 0.60, P < 0.01). Mean and standard error of ravens visually estimated within a 100-m radius of each relocated juvenile were 75 ± 68 birds. In 69% (62 of 90 survivors) of all cases, the first dispersal location occurred at a communal point subsidy. Most dispersal locations (77%; 1,253/1,626) occurred within 200 m of communal point subsidies. The proportion of locations obtained at communal point subsidies for juveniles with >10 postdispersal locations did not differ (t = 0.99, P = 0.096) between radiotagged (78%) and wing-tagged individuals (69%). From these data, we identified 8 communal point subsidies that consistently attracted large flocks of ravens (ranging from a dozen to several hundred ravens at a time), including members of our marked sample of juveniles. All but 2 juveniles with >10 dispersal locations used ≥1 of these 8 communal point subsidies at least once (mode = 2, SD = 1, range 0–4). Communal point subsidies and the number of locations at each included a dairy (377), an exurban neighborhood in Rosamond containing a dense collection of hobby farms and stables (277), a shopping mall in Mojave (212), the Edwards Air Force Base landfill (121), an urban hobby farm in Rosamond (115), the Lancaster

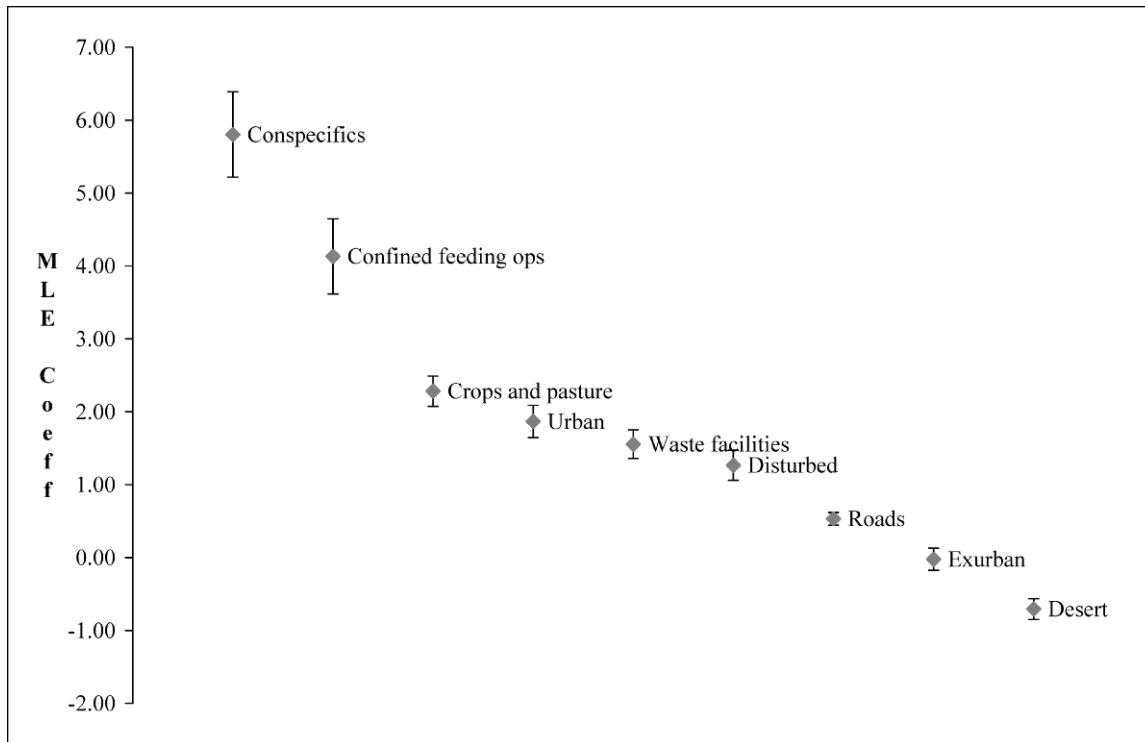


Figure 1. Resource coefficients estimated by maximum likelihood (MLE) by the resource utilization function for dispersing juvenile common ravens in the western Mojave Desert, May 1999–March 2002. Values represent means and 95% confidence intervals for 42 juvenile ravens with >10 dispersal locations. ops = operations.

landfill (80), the Mojave sewage ponds (72), and the Mojave landfill (17).

From 28 nests with ≥ 2 surviving broodmates, there were 123 occasions in which we located ≥ 2 broodmates from 22 nests on the same day outside of the natal territory. Number of nests and the frequency of occasions were 13 (1–3), 4 (4–9), and 5 (10–25). We often located surviving broodmates in close proximity; on 53 of the occasions in which we observed broodmates in the same day, we observed them <1 m apart. On 40 occasions, these observations of close proximity between broodmates occurred at a communal point subsidy, with a large number of conspecifics counted within 100 m of the focal juveniles ($\bar{x} = 65$, $SD = 68$, range 1–300). All locations of broodmates close to each other at communal point subsidies occurred between June and early November during the broodmates' first year.

Most juveniles with >10 dispersal locations had clumped (25 with 95% of the simulations with higher MSD values) rather than random (16 with <95% of the simulations with greater or lower MSD values) or dispersed (one with >95% of the simulations with lower MSD values) locations when compared to a Monte Carlo random walk simulation combining the observed dispersal distances between successive locations with randomly generated angles. The observed pattern of clumped, random, and dispersed locations did not differ between males and females ($\chi^2 = 1.82$, $n = 42$, $P = 0.40$). Most (24) juveniles with >10 postdeparture locations had clustered nearest-neighbor distributions ($Z < -1.96$), 6 had uniform distributions ($Z > 1.96$), and 12 fit a random distribution ($-1.96 < Z < 1.96$). The nearest-neighbor

distribution at the population level that included one randomly chosen location from all juveniles with >5 dispersal locations was clustered ($Z = -11.81$, $P < 0.001$). There was no tendency for the pattern of individual locations to be clustered, uniform, or randomly distributed based upon gender differences ($\chi^2 = 1.45$, $n = 42$, $P = 0.48$). The overall direction of dispersal was no different from random for all individuals, with the exception of 2 males (6° , 83.8° angular deviation, $Z = 3.87$, $P < 0.01$; and 173° , 83.5° angular deviation, $Z = 2.63$, $P < 0.01$).

Including all RUF subsamples, the global model was the most frequently supported model ($\Delta AIC < 10$) from the set of candidate models (model selection frequency 0.976; Table 2). At the population level, conspecifics and confined feeding operations were the resources with the largest positive coefficients, whereas distance to desert and distance to exurban housing were negatively associated with resource utilization (Fig. 1). The resources with largest positive coefficients for individual RUFs were conspecifics (20 individuals), confined feeding operations (10), waste facilities (2), roads (2), exurban (2), urban (2), disturbed (2), and desert (2). All but 7 juveniles shared 100% of their UD with ≥ 1 other juveniles.

DISCUSSION

Although there are sex differences in natal dispersal patterns in most bird species (Greenwood 1980), male and female ravens showed similar patterns of juvenile movement including distances moved, direction of movement, and clustering of dispersal locations. A combination of anthro-

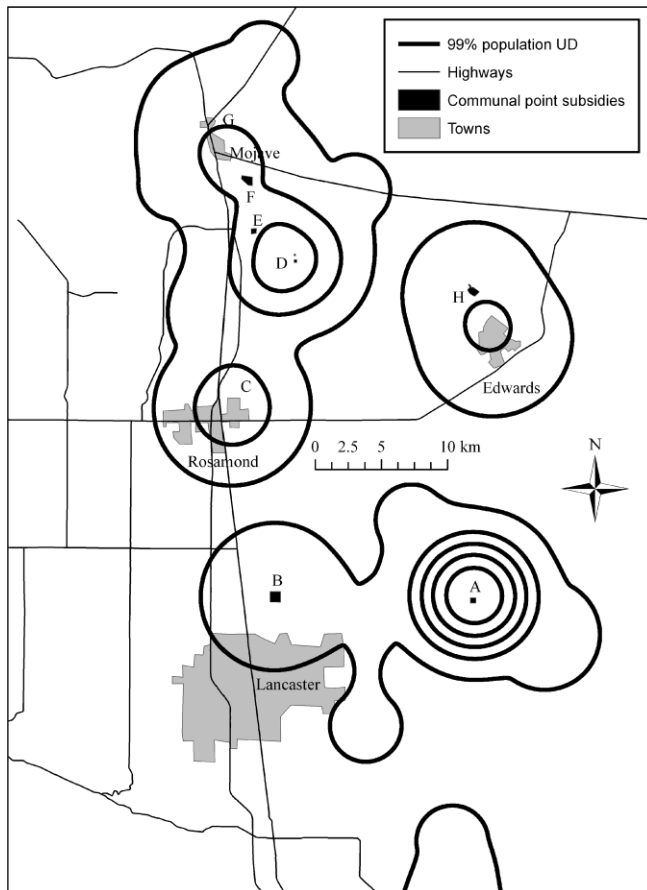


Figure 2. Ninety-nine percent fixed-kernel contours (thick dark lines) for the combined utilization distribution from dispersal locations for 42 juvenile common ravens with >10 dispersal locations in the western Mojave Desert, May 1999–March 2002. Contour intervals are 20%. Major roads are indicated with thin dark lines. Major towns are indicated by gray areas. Dark polygons represent the 8 communal point subsidies: (A) dairy, (B) Lancaster landfill, (C) Rosamond stables, (D) Rosamond hobby farm, (E) Mojave landfill, (F) Mojave sewage ponds, (G) Mojave shopping mall, and (H) Edwards Air Force Base landfill. UD = utilization distributions.

pogenic food and water sources and conspecific attraction were the strongest correlates of postfledging movements of juvenile ravens during our study, because most dispersal locations occurred at communal point subsidies, and UDs frequently overlapped entirely with other marked juveniles. Juveniles sighted outside their natal territory for the first time were nearly always located at communal point subsidies, often bypassing point subsidies located closer to their natal territories in favor of the more distant communally used ones.

Confined feeding operations represented an important resource for dispersing juvenile ravens. Although this land-use category represented a small fraction of the total study site (Table 1), we obtained a proportionally larger number (31%) of dispersal locations at this land-use type. The 3 primary communal point subsidies that fell into this category were the dairy, the Rosamond exurban hobby farms and stables, and the Rosamond urban hobby farm (Fig. 2). Confined feeding operations such as these present ravens with an abundant, concentrated, and continually

replenished source of food and water in the form of livestock feed, manure, refuse, water troughs, livestock carcasses, and others.

Movements of dispersing juveniles back and forth between the natal territory and communal point subsidies in combination with observations of broodmates in close proximity within the same flock suggested that broodmates undertook early dispersal movements together. Although we did not mark adult ravens, it is possible that dispersing juveniles located distant communal point subsidies with their assistance. Dispersing juveniles may have been led to communal point subsidies intentionally by adults attempting to wean their offspring from parental care or perhaps as a byproduct of hungry young juveniles following foraging adults. Previous demographic studies at this study site show decreased juvenile survival (Webb et al. 2004) and decreased nest productivity (Kristan and Boarman 2007) associated with increasing nest distance to point subsidies, which implies that breeding adults must forage outside their nesting territories in this resource-poor arid environment (Type B territory; Wilson 1976), and it is likely that juveniles follow adults to communal point subsidies.

Adult aggression towards unrelated conspecifics could be another explanation for the high frequency of first dispersal sightings at communal point subsidies. Because adult ravens defend territories from conspecifics (Marzluff and Heinrich 1991), territorial defense of point subsidies by adults in territories adjacent to dispersing juveniles may prevent juveniles from accessing those resources and funnel dispersal towards communal point subsidies where abundance of resources prevents their defense by resident pairs of adult ravens. Juvenile and other vagrant ravens actively recruit conspecifics to large resources, most likely preventing the monopoly of resources by resident pairs (Marzluff et al. 1996). Thus, initial dispersal to communal subsidies may also result from active recruitment of naïve dispersers by knowledgeable conspecifics.

Birds of many species are attracted to locations where they can observe conspecifics feeding (Krebs 1973, Avery 1994), resulting in flocks that range in size and composition from just a few family members to thousands of unrelated individuals (Nicholls et al. 2000). The preeminent explanations for the benefits of social foraging emphasize the benefits of reduced predation risk and foraging enhancement (Beauchamp 2004). In our study, juvenile raven mortality primarily occurred during the few days between fledging and independent flight (Webb et al. 2004), and survival was considerably higher once juveniles dispersed from their natal territories. Once juvenile ravens become capable of flight, they have few diurnal predators in this region (Webb et al. 2004), and thus reduced predation is not a likely proximate explanation for social foraging. Enhanced foraging is a more likely explanation of social foraging by juvenile ravens.

Individuals can use the presence of other foragers to locate clumped food patches more efficiently (Giraldeau and Beauchamp 1999). Foragers not only provide cues to others

about where to eat, but also when and what to eat (Galef and Giraldeau 2001). This kind of public information (Valone 1989) could be especially important for generalist species such as ravens that forage on a wide range of food types and risk ingesting harmful foods, especially novel anthropogenic foods that sometimes occur in places such as landfills. Ravens exhibit extra caution in the presence of novel food types but hesitate less when they observe conspecifics foraging on the same food type (Heinrich 1989). Other potential benefits of sociality for ravens include mate finding. In Washington State, widowed adult ravens visit communal flocks where they are more likely to find a mate (W. C. Webb, unpublished data).

For a long-lived species such as the common raven, the subadult period is an important life-history component and the efficiency with which birds conduct movements during this phase could impact lifetime reproductive success (Baker 1993). Anthropogenic resources provide superabundant and dependable year-round food and water supplies and may substantially increase juvenile survival by providing food and water in an otherwise resource-poor arid environment. After their first year, annual juvenile survival in the western Mojave population is 88% (Webb et al. 2004). Anthropogenic resources have likely contributed to increased raven abundance in part by elevating the survival rate of the juvenile age class. Anthropogenic resources such as those provided at confined feeding operations not only provide food and water for survival but also increased social opportunities for juveniles to establish dominance relationships with other nonbreeders, search for potential mates, and wait for breeding vacancies (Zack and Rabenold 1989, Stutchbury 1991). Unless dispersal behavior changes when juveniles begin to breed, and the birds begin to range more widely, then it is unlikely there is substantial emigration from the study site.

MANAGEMENT IMPLICATIONS

Drawn by abundant resource subsidies, juvenile ravens spend most of their time in areas of anthropogenic land use and spend very little time in areas with undisturbed native land cover. This pattern of resource use suggests that juvenile ravens rarely encounter potential prey species such as the desert tortoise (*Gopherus agassizii*) that require undisturbed native plant communities (USFWS 1994, 2006). However, if juvenile ravens depredate desert tortoises, then it is likely to be incidental, occurring mainly from chance encounters during transit between anthropogenic point subsidies. Reduced availability of anthropogenic resources to juvenile ravens would decrease the likelihood of depredation of desert tortoises by this segment of the raven population.

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