COMMON RAVEN JUVENILE SURVIVAL IN A HUMAN-AUGMENTED LANDSCAPE

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Abstract. Anthropogenic resource subsidies have contributed to the dramatic increase in the abundance of Common Ravens (*Corvus corax*) in the western Mojave Desert, California, during the past 30 years. To better understand the effects of these subsidies on raven demography, we examined whether survival to juvenile departure from the natal territory could be predicted by a set of environmental and morphological variables, such as nest proximity to anthropogenic resources and juvenile condition. We captured 240 juvenile ravens over 2 years and marked them prior to fledging. Nest proximity to anthropogenic resources and earlier fledging dates significantly predicted raven juvenile survival to departure from the natal territory. The best-fitting mark-recapture models predicted postdeparture survival as a function of time since fledging, nest proximity to anthropogenic resources, and year hatched. The positive effect of nest proximity to anthropogenic resources influenced postdeparture survival for at least 9 months after fledging, as revealed by the mark-recapture analysis. Annual survival was 47% for first-year, 81% for second-year, and 83% for third-year birds. Our results support the hypothesis that anthropogenic resources contribute to increasing raven numbers via increased juvenile survival to departure as well as increased postdeparture survival. We expect raven numbers to grow in concert with the growing human presence in the Mojave Desert unless raven access to anthropogenic resources is diminished.

Key words: Common Raven, Corvus corax, *dispersal, juvenile dispersal, juvenile survival, juvenile survivorship, mark-recapture.*

La Sobrevivencia Juvenil de *Corvus corax* en un Paisaje Mejorado por Humanos

Resumen. Los subsidios de recursos antropogénicos han contribuido al aumento dramático de la abundancia del cuervo *Corvus corax* en el occidente del desierto de Mojave durante los últimos 30 años. Para entender los efectos de estos subsidios en la demografía del cuervo, examinamos si la sobrevivencia hasta la salida de los juveniles del territorio natal podría ser predicha por un conjunto de variables morfológicas y ambientales, tales como su cercanía a los recursos antropogénicos y la condición de los juveniles. En dos años capturamos 240 cuervos juveniles y los marcamos antes que desarollaran plumas de vuelo. La cercanía del nido al punto de subsidio más cercano y las fechas tempranas de emplumamiento predijeron significativamente la sobrevivencia de los juveniles hasta su salida del teritorio natal. Los modelos de marcaje y recaptura más adecuados predijeron la sobrevivencia posterior a la salida del territorio como una función del tiempo desde el momento de emplumamiento, la cercanía al punto más cercano de subsidio y el año de nacimiento. Según el análisis de marcaje y recaptura, el efecto positivo de la cercanía a subsidios antropogénicos influye en la sobrevivencia después de la salida del territorio hasta por lo menos 9 meses después del emplumamiento. La sobrevivencia anual fue de 47% en el primer año, de 81% en el segundo año y de 83% para aves en su tercer año. Nuestros resultados apoyan la hipótesis de que los recursos antropogénicos contribuyen al crecimiento de los números de cuervos aumentando la sobrevivencia juvenil antes y después de su salida de los territorios natales. Esperamos que los números de cuervos aumenten en relación con la presencia humana en el desierto de Mojave a menos que su acceso a los recursos antropogénicos sea disminuido.

INTRODUCTION

Avian populations grow in response to increased availability of resources such as food supply and nesting substrates (Lack 1966, Braun and Balda 1989, Newton 1998). Human-modified landscapes may provide increased opportunities for generalist species, especially wide-ranging ones capable of exploiting both anthropogenic resources and those provided by surrounding, less disturbed landscapes (Hansson 1997). An example of such a species is the Common Raven (*Corvus corax*) in arid areas of southern California. Coinciding with an increasing human presence in the western Mojave Desert (U.S. Census Bureau 2000), annual Breeding Bird Surveys conducted by the U.S. Fish and Wildlife Service show a tenfold increase in Common Raven sightings in the region (Boarman and Berry 1995). The human population increase is significant because ravens forage at anthropogenic sites (Conner and Adkinson 1976, Boarman 1993, Knight et al. 1993, Restani et al. 2001).

Potential demographic mechanisms for the higher raven abundance as a function of anthropogenic resource subsidies include increased reproductive success (e.g., higher clutch sizes, hatching rates, fledging rates), increased immigration, decreased emigration, increased survival, or various combinations of these alternatives. Of these, juvenile survival and the associated limiting factors are notoriously difficult to study (Pulliam et al. 1992), due in part to the logistical constraints of mark-recapture studies. Raven abundance in the western Mojave provides a unique opportunity to study juvenile survival and the associated limiting factors because ravens occur in high density and can carry long-lasting radio-transmitters.

The distribution of anthropogenic resources in the western Mojave is also favorable for studying their influence on the survival of juvenile ravens. Most forms of anthropogenic resources (hereafter, point subsidies) in the region (e.g., sewage ponds, landfills) form distinct oases of rich, artificially maintained resources set within an otherwise resource-limited landscape. Breeding ravens construct nests throughout the landscape, and many feed their young at least partially with forage obtained at point subsidies (Kristan 2001).

We hypothesized that raven juvenile survival (to leaving the natal territory; hereafter, juvenile departure), could be predicted by a set of individual parameters (e.g., sex, mass) and environmental characteristics including nest proximity to point subsidies. We describe the relatively brief process of permanent emigration of fledglings from the natal territory as juvenile departure in order to distinguish it from natal dispersal *per se,* which encompasses the period between fledging and the first breeding attempt (Greenwood 1980), and which in ravens may not occur until 4 years after fledging (Boarman and Heinrich 1999). Since nutrition and other conditions prior to juvenile departure may affect postdeparture survival (Lack 1966, Dewey and Kennedy 2001), we extended our survival analysis into the postdeparture period. Since proximity to humans influences the risks of mortality in some species (Koenig et al. 2002, Rubolini et al. 2001), we also asked if nest proximity to anthropogenic activities such as roadways increased the risk of mortality, and whether any sources of anthropogenic mortality were either additive or compensatory (Nichols et al. 1984).

METHODS

STUDY AREA

The study site consisted of Edwards Air Force Base (34°38′N, 118°6′W) and surrounding communities in the western Mojave Desert, occupying approximately 4000 km^2, and lies within the Mojave Desert floristic province (Fig. 1; Hickman 1993). Mean annual precipitation is 112 mm, and falls mainly in the form of rain between November and March (MacMahon 2000). Mean annual temperature is 18.1°C, with hot summers (mean monthly daytime temperature 25–30°C, June–August), and cool winters (10–15°C, December–February; MacMahon 2000). The most common natural community types are Mojave creosote bush (*Larrea tridentata*) scrub and desert saltbush (*Atriplex* spp.) scrub. The most common anthropogenic community types include residential areas, agriculture, and ranching operations.

Ravens in the western Mojave Desert build nests in or on a variety of natural and anthropogenic substrates. The most common natural substrates are Joshua trees (*Yucca brevifolia*) and cliffs (Kristan 2001). Anthropogenic substrates include billboards, power poles, storefronts, and landscaped trees. Clutches consist of 1 to 5 eggs, laid in March or early April (Boar-
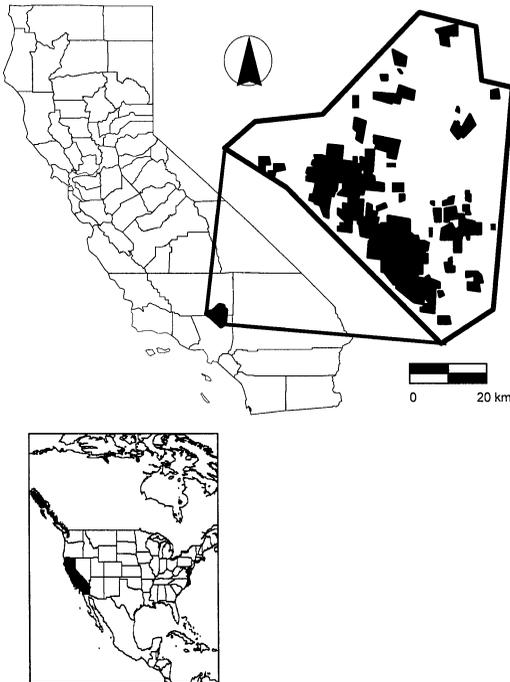
FIGURE 1. Location of the Mojave Desert study area in California. The dark polygons within the study area represent anthropogenic habitat, and the light portions represent natural habitat.

man and Heinrich 1999). Raven nestlings are altricial and fledge at approximately 5 weeks of age. Throughout the nesting period, adult ravens vigorously defend their territories against intruders. This aggressive behavior serves as an important clue to identifying active territories and their boundaries.

During the spring of 1999 and 2000, we conducted random searches for raven nests located in various substrates and distances from anthropogenic influence. Locations of nests were measured in universal transverse mercator (UTM) coordinates and plotted on a study site map constructed from ground observations, USGS 7.5-minute digital topographic maps, and USGS 7.5-minute digital orthophoto quarter quadrangles. For each nest we determined the distance to the nearest point subsidy and nearest human activity using mapping software (ESRI 1999). The nearest point subsidy to each nest was identified using *a priori* observations of the types of anthropogenic resources utilized by ravens foraging in the study site, including residences, artificial wetlands, landfills, sewage ponds, livestock

feedlots, shopping areas, agricultural fields, and golf courses. The nearest human activities to each nest included residences, paved roads, industry, etc. Thus, the distance to the nearest human activity was usually less than, but occasionally equal to, the distance to the nearest point subsidy.

MARK-RECAPTURE

We captured and marked a total of 240 (1999, *n* = 108; 2000, *n* = 132) raven nestlings from 98 nests at approximately 4.5 weeks of age, which was just prior to fledging. All nestlings were marked with individually coded patagial tags. Wings tags were applied to nestlings in the patagial area of both wings using either plastic clips or pop rivets. Wing tags were handmade from white, lightweight vinyl-coated nylon (''Herculite,'' Herculite Industrial Fabrics, Emigsville, Pennsylvania) cut into thin strips (170 × 26 mm) widening into teardrop-shaped ends (55 mm at the widest point). The general shape and application of the wing tags were similar to the methods of Stiehl (1983), but the wing tags were considerably narrower.

A subset (102) of the marked juveniles received radio-transmitters (ATS, Holohil Systems Ltd., Carp, Ontario, Canada), attached with a backpack-style harness (Buehler et al. 1995). Each harness was composed of two teflon ribbons (40 × 1 cm) threaded through each end of the unit casing. The rear ribbon passed behind the wings and the front ribbon draped over the shoulders. After fitting the ribbons beneath the contour feathers, we secured the four ends together near the furcula with an aluminum *J*-clip and high-strength adhesive. The transmitters used in this study weighed 22 g (approximately 3% of a fledgling's body mass) with a typical battery life of 18–24 months. We also took the following measurements from all captured juvenile ravens: mass, wing chord length, tarsus length, tarsus height, culmen length, culmen width, and culmen depth. All capture and experimental techniques strictly followed guidelines described by Gaunt and Oring (1997).

Since male and female ravens are morphologically indistinguishable, we used molecular techniques to identify sex. During visits to the nests, two small, growing feathers were sampled from each nestling, and sex was determined using a PCR reaction that amplifies the CHD genes on

the W and Z chromosomes (Griffiths et al. 1998).

We monitored marked juveniles by returning to their natal territories 1–3 times per week until the juveniles were either known to have died, or had left their natal territories. The identity of all marked juveniles was confirmed by reading their wing tags with the aid of a spotting scope and binoculars. Since adult ravens vigorously defend active nesting territories against intruders, natal territories were defined as the area centered at the nest and defended by the nesting adult ravens. During repeated visits to each nesting territory, we observed that researchers, conspecifics, and heterospecifics such as Red-Tailed Hawks (*Buteo jamaicensis*) were typically intercepted by the resident pair between 0.5 and 1.0 km from the nest. Our estimates of natal territory sizes based upon such observations of adult defensive behavior were similar to the mean radius (1.0 km) between adjacent raven nests independently observed by Kristan (2001).

The natal territories of marked juveniles were monitored on a regular basis until each juvenile was located at least several kilometers outside the natal territory ($n = 90$), found dead ($n = 141$), or declared missing ($n = 9$). Juveniles were considered to have survived only if they were resighted alive outside their natal territories. To minimize the number of missing birds, each territory was thoroughly checked for signs of dead juveniles once all obvious signs of juvenile occupation had stopped. When juveniles turned up missing, radio-transmitters greatly aided the search for them. Survival checks were also greatly aided by strong juvenile preference for anthropogenic habitat (Webb 2001). The vast majority of surviving juveniles were first resighted outside their natal territories at point subsidies. Juveniles that were never resighted at point subsidies were usually found dead within their natal territory. Only nine marked juveniles were never relocated. Based on their continued absence from point subsidies throughout the region, these few missing juveniles were considered to have perished.

Juveniles that survived natal departure were relocated by radio-telemetry and by searching the study area (Kenward 1987, White and Garrot 1990, Winterstein et al. 2001). The entire study area was visited and searched monthly between June 1999 and February 2002, with the goal of maintaining an approximately uniform search effort throughout the study. Relocation of radio-tagged juveniles was conducted mainly by motorized vehicle telemetry. Signals were detected using dual 3-element Yagi antennas attached to a vehicle's roof by 1-m swiveling masts, in tandem with an ATS R2000 portable scanning radio receiver (Advanced Telemetry Systems 1993). Handheld portable 3-element and 2-element Yagi antennas were also used to search for radio-tagged juveniles by foot. On three occasions, we flew a Cessna 185 equipped with dual wing-mounted, 3-element Yagi antennas to conduct a large-scale aerial search for missing transmitter signals. Detectability of transmitter signals ranged from 1–50 km, depending upon the search mode (vehicle, foot, or aircraft), topography, and behavior of the individual birds.

The source of mortality was assessed as best as possible for all dead juveniles. In general, most cases of known mortality were classified as either natural or anthropogenic. The classification was further refined depending upon the amount of additional evidence, such as the location and timing of death, condition of the remains, and any markings left by predators.

We investigated the survival rate to departure of juvenile ravens in relation to environment and morphology. The environmental parameters included the distance from each nest to the nearest point subsidy, the distance from each nest to the nearest human activity, individual fledging date, nest substrate, air temperature during the nestling period, and attachment of a radio-transmitter. The point subsidies considered for the analysis consisted of permanent sources of food or water. The human activities included in the analysis were those posing potential harm to wildlife such as vehicle traffic and railroads. The morphological parameters included the measurements taken at capture. Juvenile departure was defined as movement from the natal territory, followed by subsequent observer detection.

STATISTICAL ANALYSES

Analysis of juvenile survival to departure was conducted using logistic regression (SAS PROC LOGISTIC; SAS Institute 1999) with forward selection predicting the outcome (surviving or not surviving) from the set of predictor variables. We substituted a condition index for each individual, composed of the residual from a regression of mass on tarsus length rather than using the entire suite of morphological parameters

because most were highly correlated (e.g., $r = 0.64$ for mass vs. tarsus length). In addition, we extended our survival analysis into the postdeparture period using open-population mark-recapture analyses (Cormack 1964, Jolly 1965, Seber 1965). We chose nest proximity to the nearest point subsidy as a factor because prefledging resource availability has been shown to affect avian juvenile survival (Perrins 1965, Van Der Jeugd and Larsson 1998). Although survival rates may decrease with age, we expected the postdeparture survival rate to increase with time as juveniles matured. We chose sex as a factor because we suspected that fledgling males and females might have different dispersal patterns (Wheelwright et al. 1995).

A mortality analysis was conducted to compare the relative contributions of anthropogenic and natural sources to predeparture mortality. We used logistic regression (SAS PROC LOGISTIC) with forward selection to predict the outcome (mortality by natural vs. anthropogenic means) in relation to nest distance from the nearest human activity.

We used program MARK (White and Burnham 1999) to build and test mark-recapture models to compare parameters between sexes, among years, and in relation to the individual covariate of nest distance to the nearest point subsidy (Williams et al. 2002). Our models were constructed using 3-months recapture intervals corresponding to the four seasons of the year. Program MARK estimates model parameters such as survival through numerical maximum-likelihood techniques. We used Akaike's information criterion (Akaike 1973) corrected for small sample size (AIC_c) and overdispersion ($QAIC_c$) to select the best model from the list of *a priori* models, and the model with lowest AIC_c or $QAIC_c$ was used for statistical inference and parameter estimation (Burnham and Anderson 1998).

Because of differences in detection probabilities, we analyzed juveniles marked with transmitters separately from juveniles that were marked with wing tags only. Although transmitters increased the recapture probability for raven juveniles, data obtained from radio-transmitters in our study did not meet the assumptions of known fate data because ravens are highly mobile and the radio-transmitters were relatively weak in comparison to the size of the study area. Thus, the data from radio-tagged juveniles were incorporated in a Burnham joint live recaptures and dead recoveries analysis (Burnham 1993), while the recaptures-only data from juveniles with wing tags only were used in a Cormack-Jolly-Seber live-recoveries analysis (Cormack 1964, Jolly 1965, Seber 1965).

Survival and recapture rates were our parameters of interest for both the CJS and Burnham analyses. CJS models estimate two parameter types: survival rate (Φ), and recovery rate (p), and provide only minimum estimates of true survival because mortality is confounded with permanent emigration. The parameter space for Burnham models includes four parameter types: survival rate (S), recapture rate (p), recovery rate (r), and site fidelity (F). Since survival and recapture rates were our primary parameters of interest, we did not constrain recovery rate or site fidelity in the Burnham analysis.

Mark-recapture analyses were conducted by testing the global models and then constraining parameters according to our *a priori* hypotheses. Model notation follows that of Lebreton et al. (1992) and Franklin et al. (2000). We constrained parameters as functions of time (t), sex, age, the individual covariate of nest distance to the nearest anthropogenic resource (*proximity*), and constancy (.). We evaluated the impact of nest distance to the nearest anthropogenic resource with an ANODEV test (Skalski et al. 1993, White and Burnham 1999), which compared the amount of deviance explained by a covariate against the amount of deviance not explained by the covariate.

Goodness-of-fit tests are typically used to confirm that data analyzed in information-theoretic models met the assumptions of those models (Anderson et al. 2001). Program MARK provides a parametric bootstrapping approach (White and Burnham 1999) for goodness-of-fit testing for most types of models with the notable exception of models containing individual covariates. We created our own goodness-of-fit program for the CJS analysis that emulates the parametric bootstrapping approach in MARK. However, a similar program for Burnham analyses is not currently available.

RESULTS

PREDEPARTURE JUVENILE SURVIVAL

The overall survival rate to departure was 38% (90 of 240 marked individuals). Significant pre-
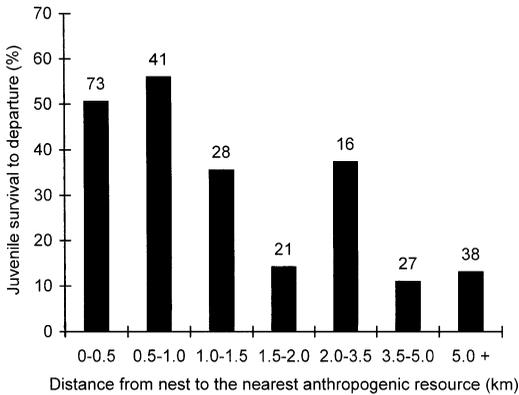
FIGURE 2.   Survival to departure from the nest territory and nest distance to the nearest anthropogenic resource (e.g., sewage pond, landfill) for juvenile Common Ravens hatched in 1999 and 2000. Increments increase above 2.0 km for descriptive purposes because sample sizes were smaller at these distances. Numbers above bars are sample sizes (individuals).

dictors of survival to departure included nest distance to the nearest anthropogenic resource ($\chi^2 = 16.8$, $P < 0.001$) and fledging date ($\chi^2 = 18$, $P < 0.001$; Fig. 2). Sixty percent of juvenile ravens nesting within 1.0 km of anthropogenic resources survived to depart from their natal territory, while only 10–30% of those nesting farther than 1.5 km survived. Juvenile ravens fledging prior to 28 May in 1999 experienced greater than 70% survival while those fledging after 18 June experienced only 15% survival (Fig. 3). A similar pattern of survival occurred in 2000, with higher survival for juvenile ravens fledging prior to 26 May, and lower survival for juvenile ravens fledging later than 3 June. Nonsignificant predictors of survival to departure included the condition index, sex, nest substrate, year, distance to the nearest human activity, and transmitter attachment (all $P > 0.05$). Thus, ravens fledging earlier in the season and closer to the nearest point subsidy were more likely to survive to depart from their natal territories.

It was unlikely that juveniles that survived to depart from their natal territories escaped detection. The vast majority of survivors were relocated within 2 months after fledging. Only two individuals located for the first time outside their natal territories were found dead at that time.

POSTDEPARTURE JUVENILE SURVIVAL

We tracked 90 ravens for 33 consecutive months between June 1999 and March 2002, obtaining 2451 postdeparture locations. Overall, juvenile ravens survived better during the postdeparture period if their nests had been closer to anthropogenic resources. Those fledging in 2000 survived better than those fledging in 1999. The best-fitting CJS and Burnham models were both functions of time, nest distance to the nearest anthropogenic resource, and year (Table 1, 2). The effect of distance to the nearest anthropogenic resource was detectable for up to 9 months after departure. The best CJS model predicted survival as a function of nest distance to the nearest anthropogenic resource for three recapture intervals (9 months) after fledging, followed by time-dependence alone. This model was over four times as well supported as the next best model, and the individual covariate of nest distance from the nearest anthropogenic resource explained a highly significant proportion of the deviance (ANODEV $F_{2,87} = 4.5$, $P < 0.001$). The best Burnham model predicted survival as an additive function of nest distance to the nearest point subsidy, and was over 42 times as well supported as the next best model. The individual covariate of nest distance to the nearest point subsidy accounted for a highly significant proportion of the deviance (ANODEV $F_{4,53} = 5.2$, $P < 0.001$).

No support was found for any models incorporating differences in survival or recapture between the sexes. Burnham survival estimates (based upon radio-equipped birds) were generally higher than CJS estimates, suggesting that CJS methods underestimated true survival rates. Seasonal survival estimates were typically higher than 75%, with the lowest values usually occurring during the winter. Cumulative survival was estimated from the product of seasonal survival estimates calculated separately for CJS and Burnham estimates and then averaged. Mean annual survival was 50% for hatch-year, 81% for second-year, and 83% for third-year birds. After 33 months, an estimated 28% of the juvenile Common Ravens that survived departure were still alive (Fig. 4).

CAUSES OF MORTALITY

Juvenile mortality was recorded through March 2002. A total of 82 mortalities were recorded, with 12 cases of unknown source (15%) and 70 cases distinguishable between natural or anthropogenic sources. Most of the observed mortality (71 of 82 cases, or 87%) occurred prior to de-
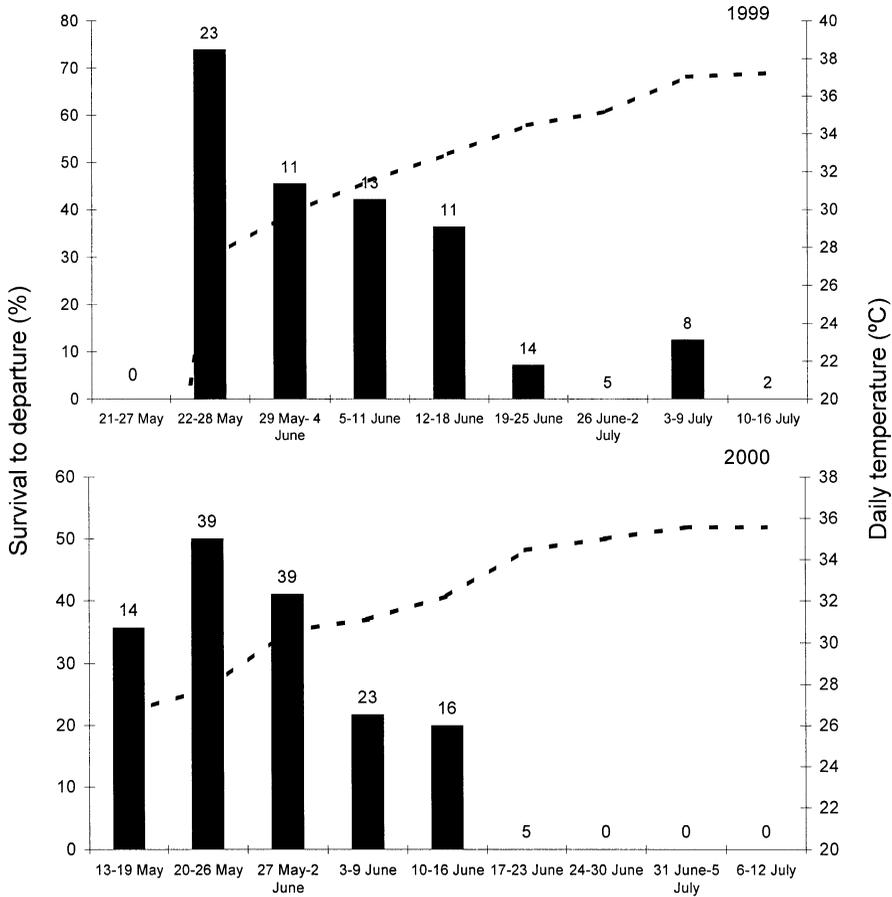
FIGURE 3. Survival of juvenile ravens to departure from the natal territory in relation to fledging date and the mean daily maximum temperature during the nestling period in 1999 and 2000. The fledging group dates are organized by weeks mainly for descriptive purposes, but also represent the relative number of juveniles fledging in the population. Numbers above bars are sample sizes (individuals).

parture from natal territories, and predation accounted for the majority of the known causes (52 of 70 cases, or 74%). Mammalian predation was the primary identifiable source of mortality (44 of 70 cases, or 63%), and of these, coyotes (*Canis latrans*) were the most common (16 of 21 cases, or 73%). Although nest proximity to the nearest human activity was not a significant overall predictor of mortality prior to juvenile departure, nest proximity to the nearest human activity did significantly predict whether the source of mortality was either anthropogenic or natural. Juveniles fledging from nests closer to human activities were more likely to die from an anthropogenic source ($\chi^2 = 9.79$, $P < 0.02$). Thus, anthropogenic sources of mortality compensated for natural sources of mortality rather

than adding to the overall mortality rate (Nichols et al. 1984).

DISCUSSION

The positive correlation between survival to juvenile departure and nest proximity to the nearest point subsidy supports our hypothesis that anthropogenic resources increase raven recruitment. A physiological or behavioral threshold may exist for Mojave ravens in regards to nest distance from resources. Working in the eastern Mojave, Sherman (1993) observed that nesting ravens usually foraged within 1.5 km of their nest. In the western Mojave, nesting ravens forage at anthropogenic resources near their nests (Kristan 2001), and a nest distance of 1.5 km from the nearest point subsidy appears to rep-

TABLE 1.   Ranking of Cormack-Jolly-Seber models for postdeparture survival of 56 juvenile ravens, comparing survival (Φ) and recapture probability (p) among sex, age (two age classes), and in relation to the individual covariate of nest distance to the nearest anthropogenic resource (proximity). We used Akaike's information criterion (Akaike 1973) corrected for small sample size (AIC_c) and overdispersion ($QAIC_c$) to select the best model from the list of *a priori* models. The best model predicted survival as a function of nest distance to the nearest anthropogenic resource for three recapture intervals after fledging (equivalent to nine months), followed by time dependence alone. The best model also supported unique survival and recapture rates between age groups. Proximity*$t(x)$ terms describe the effect of nest proximity over x recapture intervals. t = time; ($\cdot$) = constancy.

Model	No. of parameters	$\Delta QAIC_c$[a]	$QAIC_c$ weight
Φ(age t (proximity*$t(3)$))/(t proximity*$t(3)$) p(age t/t)	31	0.00	0.76
Φ(age t (proximity*$t(4)$))/(t proximity*$t(4)$) p(age t/t)	33	2.84	0.18
Φ(age t (proximity*$t(5)$))/(t proximity*$t(5)$) p(age t/t)	35	6.24	0.03
Φ(age t (proximity*$t(6)$))/(t proximity*$t(6)$) p(age t/t)	36	7.64	0.02
Φ(age t (proximity*$t(2)$))/(t proximity*$t(2)$) p(age t/t)	29	9.27	0.01
Φ(age t (proximity*$t(1)$))/(t proximity*$t(1)$) p(age t/t)	27	13.46	0.00
Φ(age proximity + t)/(proximity + t) p(age t/t)	26	13.64	0.00
Φ(t) p(t)	19	37.15	0.00
Φ($\cdot$) p($\cdot$)	2	47.83	0.00
Φ(sex) p(sex)	4	51.53	0.00
Φ(age proximity*t)/(proximity*t) p(age proximity*t)/ (proximity*t)	89	112.20	0.00

[a] The lowest $QAIC_c$ value was 609.62; $\hat{c}$ = 1.29.

resent a cutoff between high and low survival rates. Nesting closer to anthropogenic resources probably reduces the physiological costs of foraging, and may allow for increased food delivery rates and permit increased adult vigilance against predators. Although nesting near anthropogenic resources is a successful strategy, the distribution of nest distances from point subsi-

TABLE 2.   Ranking of Burnham models for postdeparture survival (S) and recapture (p) probability for 34 juvenile Common Ravens. Models analyzed the effect of sex, age (two age classes), and in relation to the individual covariate of nest distance to the nearest anthropogenic resource (proximity). We used Akaike's information criterion (Akaike 1973) corrected for small sample size (AIC_c) and overdispersion ($QAIC_c$) to select the best model from the list of *a priori* models. The best model also supports unique survival and recapture parameters between age groups. t = time; ($\cdot$) = constancy term; g = gender term. Proximity*$t(x)$ terms describe the effect of nest proximity over x recapture intervals. Recovery rate (r) and site fidelity (F) were held constant for all analyses.

Model	No. of parameters	$\Delta QAIC_c$[a]	$QAIC_c$ weight
S(age proximity + t)/(proximity + t) p(age t/t)	16	0.00	0.93
S(age proximity + t/proximity + t) p(t)	16	7.49	0.02
S(age proximity + t/proximity + t) p($\cdot$)	10	8.27	0.01
S(age proximity*$t(1)$)/t(proximity*$t(1)$) p(age t/t)	17	8.36	0.01
S(age t (proximity*$t(2)$)/t(proximity*$t(2)$ p(age t/t)	18	10.66	0.00
S(t + proximity) p($\cdot$)	10	10.83	0.00
S(t + proximity) p(t)	16	10.92	0.00
S(age t (proximity*$t(3)$) p(age t/t)	20	13.24	0.00
S(t) p($\cdot$)	14	10.07	0.00
S(t) p(t)	23	27.79	0.00
S($\cdot$) p($\cdot$)	4	37.42	0.00
S(g) p($\cdot$)	5	37.94	0.00
S(age proximity*t)/(proximity*t) p(age proximity*t)/ (proximity*t)	56	86.53	0.00

[a] The lowest $QAIC_c$ value was 434.12; $\hat{c}$ = 1.26.
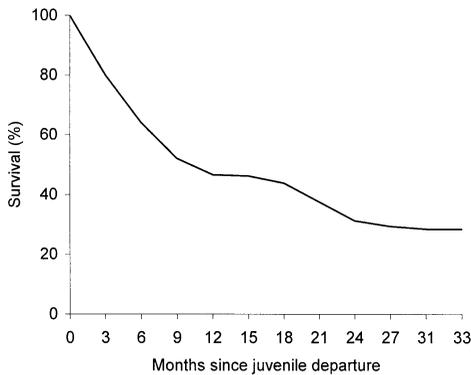
FIGURE 4. Cumulative survival curve for 90 juvenile Common Ravens. The values are the product of seasonal survival estimates from both Cormack-Jolly-Seber and Burnham analyses for birds hatched in 1999 and 2000. Data for birds hatched in 2000 were available for the first 21 months only.

dies does not appear strongly leptokurtic. This suggests ravens are reluctant to contract their territories simply in order to nest near point subsidies, even though the natural resources within their territories may be scarce. Point subsidies are larger than a single nesting pair can defend and therefore must be shared with unrelated ravens. Marzluff and Neatherlin (unpubl. data) observed a similar conflict between raven territorial behavior and increased reproduction and survival associated with proximity to anthropogenic resources on the Olympic Peninsula, Washington, a substantially different ecological setting.

Closer proximity to anthropogenic resources may increase juvenile survival through increased opportunity for adult vigilance against predators prior to juvenile departure (Arcese and Smith 1988, Dewey and Kennedy 2001), the period when juvenile ravens are most susceptible to predation. Raven juveniles are particularly vulnerable between fledging and first successful flight, spending considerable time on the ground, and appear generally naïve to threats from intruders. The lack of dense vegetation near most nesting substrates probably reduces the ability of juvenile ravens to hide from predators before they can fly. When present, adult nesting ravens display aggressively toward observers prior to juvenile departure. The relatively low survival rate of juvenile ravens to departure (38%) was in large part due to predation by coyotes, also a

human-subsidized predator (Tigas-Lourraine et al. 2002).

A negative relationship between the probability of recruitment and breeding date has been observed in several species and attributed to various causes including food availability (Daan et al. 1989), parental quality (Spear and Nur 1994), and predation pressure (Naef-Daenzer et al. 2001). The pattern of decreasing juvenile survival and fledging date parallels the seasonal trend of increasing air temperature in the western Mojave. Survival rates plummeted when air temperatures regularly exceeded 30°C during the late stages of the nesting season in June and July. Extreme air temperature probably restricts adult foraging activities, causes additional adult energy expenditure during brooding, and slows juvenile development (Peterson et al. 1986).

Heat stress is probably increased by the lack of cover found in most natural nesting substrates such as Joshua trees and cliffs compared to anthropogenic substrates like billboards and landscaped trees. Steenhof et al. (1993) attributed higher raven nesting success in transmission-line towers in comparison to natural substrates to better protection from heat. Nesting substrate was not a significant predictor of raven juvenile survival to departure in our study, however, perhaps because the differential insulation between natural and anthropogenic substrates affected the nestling stage more strongly than the fledgling stage. Nestlings from late-season nests were unlikely to survive to fledging age, and thus could not be included in the study.

The population dynamics of many species are sensitive to juvenile survival (Levin et al. 1987, Kushlan 1988, Davis and Levin 2002). It is likely that anthropogenic resources have contributed to the increase in raven abundance, at least in part through increased juvenile survival. However, the relative impact of juvenile survival on raven population dynamics in the western Mojave is unclear because other demographic parameters such as the mean lifespan, age of first reproduction, and emigration and immigration rates are poorly documented (Boarman and Heinrich 1999).

MANAGEMENT IMPLICATIONS

This study supports our hypothesis that anthropogenic resources subsidize the western Mojave raven population. Moreover, it indicates that one demographic mechanism by which this is

achieved is increased juvenile survival (both survival to departure from the natal territory and postdeparture survival) as nest proximity to anthropogenic resources increases. In areas like the western Mojave where resource levels are naturally low, the impacts of artificial resources can be dramatic, and their influence helps explain the increased abundance of ravens. Unfortunately, ravens have been implicated as human-subsidized predators (Soulé 1988) of sensitive species, including the federally threatened desert tortoise (*Gopherus agassizii*) in the Mojave Desert (Camp et al. 1993), and thus their sustained high abundance is of considerable conservation concern. Land managers should expect raven numbers and conflicts with humans to grow in parallel to the human population, unless raven access to anthropogenic resources is diminished. Eliminating or altering management practices that inadvertently provide resource subsidies to ravens should reduce their population density and associated negative impacts on biodiversity in the western Mojave.

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LITERATURE CITED

ADVANCED TELEMETRY SYSTEMS. 1993. Receiver manual for models R2000/R2100/R4000. Advanced Telemetry Systems, Inc., Isanti, MN.

AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle, p. 267–281. *In* B. N. Petran and F. Csaki [EDS.], International symposium on information theory. 2nd ed. Akademiai Kiadi, Budapest.

ANDERSON, D. R., W. A. LINK, D. H. JOHNSON, AND K. P. BURNHAM. 2001. Suggestions for presenting the results of data analyses. Journal of Wildlife Biology 65:373–378.

ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. Journal of Animal Ecology 57:119–136.

BOARMAN, W. I. 1993. When a native predator becomes a pest: a case study, p. 191–206. *In* S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz [EDS.], Conservation and resource management. Pennsylvania Academy of Science, Easton, PA.

BOARMAN, W. I., AND K. H. BERRY. 1995. Common Ravens in the southwestern United States, 1968–92, p. 73–75. *In* E. T. Laroe [ED.], Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. USDI National Biological Service, Washington, DC.

BOARMAN, W. I., AND B. HEINRICH. 1999. Common Raven (*Corvus corax*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 476. The Birds of North America, Inc., Philadelphia, PA.

BRAUN, J. D., AND R. P. BALDA. 1989. Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities? Condor 90:61–71.

BUEHLER, D. A., J. D. FRASER, M. R. FULLER, L. S. MCALLISTER, AND J. K. D. SEEGAR. 1995. Captive and field-tested radio transmitter attachments for Bald Eagles. Journal of Field Ornithology 66:173–180.

BURNHAM, K. P. 1993. A theory for combined analysis of ring recovery and recapture data, p. 199–213. *In* J. D. Lebreton and P. M. North [EDS.], Marked individuals in the study of bird population. Birkhäuser Verlag, Basel, Switzerland.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

CAMP, R. J., R. L. KNIGHT, H. A. L. KNIGHT, M. W. SHERMAN, AND J. Y. KAWASHIMA. 1993. Food habits of the nesting Common Ravens in the eastern Mojave Desert. Southwestern Naturalist 38:163–165.

CONNER, R. N., AND C. S. ADKINSON. 1976. Concentration of foraging Common Ravens along the trans-Canada highway. Canadian Field Naturalist 90:496–497.

CORMACK, R. M. 1964. Estimates of survival from sightings of marked animals. Biometrika 51:429–438.

DAAN, S., C. DIJKSTRA, R. DRENT, AND T. MEIJER. 1989. Food supply and the annual timing of avian reproduction. Proceedings of the International Ornithological Congress 19:392–407.

DAVIS, J. L. D., AND L. LEVIN. 2002. Importance of pre-recruitment life-history stages to population dynamics of the woolly sculpin *Clinocottus analis*. Marine Ecology Progress Series 234:229–246.

DEWEY, S., AND P. KENNEDY. 2001. Effects of supplemental food on parental-care strategies and juvenile survival of Northern Goshawks. Auk 188:352–365.

ESRI. 1999. Arcview GIS v 3.2. Environmental Systems Research Institute, Inc., Redlands, CA.

FRANKLIN, A. B., D. R. ANDERSON, R. J. GUTIÉRREZ, AND K. P. BURNHAM. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs 70:539–590.

GAUNT, A. S., AND L. W. ORING. 1997. Guidelines to the use of wild birds in research. Ornithological Council. Washington, DC.

GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behavior 28:1140–1162.

GRIFFITHS, R., M. C. DOUBLE, K. ORR, AND R. J. G. DAWSON. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

HANSSON, L. 1997. The relationship between patchiness and biodiversity in terrestrial systems, p. 146–155. In S. T. A. Picket, R. S. Osterfeld, M. Shachak, and G. E. Likens [EDS.], The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York.

HICKMAN, J. C. [ED.]. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. Biometrika 52:225–247.

KENWARD, R. 1987. Wildlife radio tagging. Academic Press, London.

KNIGHT, R. L., H. A. KNIGHT, AND R. J. CAMP. 1993. Raven populations and land-use patterns in the Mojave Desert, California. Wildlife Society Bulletin 21:469–471.

KOENIG, J., R. SHINE, AND G. SHEA. 2002. The dangers of life in the city: patterns of activity, injury and mortality in suburban lizards (Tiliqua scincoides). Journal of Herpetology 36:62–68.

KRISTAN, W. B. 2001. Effects of habitat selection on avian population ecology in urbanizing landscapes. Ph.D. dissertation, University of California, Riverside, CA.

KUSHLAN, J. A. 1988. Conservation and management of the American crocodile. Environmental Management 12:777–790.

LACK, D. L. 1966. Population studies of birds. Clarendon Press, Oxford, UK.

LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

LEVIN, L. A., H. CASWELL, K. D. DEPATRA, AND E. L. CREED. 1987. Demographic consequences of larval development mode: planktotrophy vs. lecithotrophy in Streblospio benedicti. Ecology 68:1877–1886.

MACMAHON, J. A. 2000. Warm deserts, p. 286–322. In M. G. Barbour and W. D. Billings [EDS.], North American terrestrial vegetation. Cambridge University Press, Cambridge, UK.

NAEF-DAENZER, B., F. WIDMER, AND M. NUBER. 2001. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. Journal of Animal Ecology 73:730–738.

NEWTON, I. 1998. Population limitation in birds. Academic Press, San Diego, CA.

NICHOLS, J. D., M. J. CONROY, D. R. ANDERSON, AND K. P. BURNHAM. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Transactions of the North American Wildlife and Natural Resources Conference 49:535–554.

PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit Parus major L. Journal of Animal Ecology 34:601–647.

PETERSEN, K. L., L. B. BEST, AND B. M. WINTER. 1986. Growth of nestling Sage Sparrows and Brewer's Sparrows. Wilson Bulletin 98:535–546.

PULLIAM, H. R, J. B. DUNNING JR., AND J. LIU. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications 2:165–177.

RESTANI, M., J. M. MARZLUFF, AND R. E. YATES. 2001. Effects of anthropogenic food sources on movements, survival, and sociality of Common Ravens in the Arctic. Condor 103:399–404.

RUBOLINI, D., E. BASSI, G. BOGLIANI, P. GALEOTTI, AND R. GARAVAGLIA. 2001. Eagle Owl (Bubo bubo) and power line interactions in the Italian Alps. Bird Conservation International 11:319–324.

SAS INSTITUTE. 1999. The SAS system for Windows, release 8.0. SAS Institute, Inc., Cary, NC.

SEBER, G. A. 1965. The multi-sample single recapture census. Biometrika 49:330–349.

SHERMAN, M. W. 1993. Activity patterns and foraging ecology of nesting Common Ravens in the Mojave Desert, California. M.Sc. thesis, Colorado State University, Fort Collins, CO.

SKALSKI, J. R., A. HOFMAN, AND S. G. SMITH. 1993. Testing the significance of individual and cohort level covariates in animal survival studies, p. 9–28. In J. D. Lebreton and P. M. North [EDS.], Marked individuals in the study of bird populations. Birkhäuser Verlag, Basel, Switzerland.

SOULÉ, M. E. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75–92.

SPEAR, L., AND N. NUR. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in Western Gulls. Journal of Animal Ecology 63:283–298.

STEENHOF, K., M. N. KOCHERT, AND J. A. ROPPE. 1993. Nesting by raptors and Common Ravens on electrical transmission line towers. Journal of Wildlife Management 57:271–281.

STIEHL, R. B. 1983. A new attachment method for patagial tags. Journal of Field Ornithology 54:326–328.

TIGAS-LOURRAINE, A., D. H. VAN-VUREN, AND R. M. SAUVAJOT. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation 108:299–306.

U.S. CENSUS BUREAU. 2000. Population estimates for cities with populations of 10,000 and greater by: July 1, 1999. USDC Census Bureau, Population

Estimates Program, Population Division, Washington, DC.

VAN DER JEUGD, H. P., AND K. LARSSON. 1998. Prebreeding survival of Barnacle Geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology 67:953–966.

WEBB, W. C. 2001. Common Raven juvenile survival and movements in a human augmented landscape. M.Sc. thesis, University of California, Riverside, CA.

WHEELWRIGHT, N. T., G. TRUSSELL, J. P. DEVINE, AND R. ANDERSON. 1995. Sexual dimorphism and population sex ratios in juvenile Savannah Sparrows. Journal of Field Ornithology 65:520–529.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

WHITE, G. C., AND R. A. GARROT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA.

WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. Analysis and management of animal populations. Academic Press, San Diego, CA.

WINTERSTEIN, S. R., K. H. POLLOCK, AND C. M. BUNCK. 2001. Analysis of survival data from radiotelemetry studies, p. 351–380. *In* J. J. Millspaugh and J. M. Marzluff [EDS.], Radio tracking and animal populations. Academic Press, San Diego, CA.