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Common Raven (*Corvus corax*) Juvenile Survival and Movements in a Human Augmented Landscape

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DEDICATION

This Thesis is dedicated to my family, friends, colleagues, and mentors; all of whom provided assistance, inspiration and support.

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ABSTRACT OF THE THESIS

Common Raven (*Corvus corax*) Juvenile Survival and Movements in a Human Augmented Landscape

by

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Annual surveys in the western Mojave Desert have shown a dramatic increase in Common Raven (*Corvus corax*) sightings during the past 30 years, coinciding with an increasing human presence in the region. Anthropogenic resource subsidies are suspected to contribute to the raven population increase, but the demographic relationship with such subsidies is uncertain. We asked whether raven juvenile survival could be predicted by a set of environmental variables such as nest proximity to the nearest anthropogenic resource (NAR) and a set of individual morphological variables such as mass. We also asked whether raven juvenile post-dispersal survival rates could be predicted by time, nest proximity to NAR, year, and sex. Common models for vertebrate dispersal involve resource competition, inbreeding avoidance, and social behavior. We evaluated the movements of juvenile Common Ravens using these categories of dispersal models.

We marked and followed two years of juvenile ravens in the western Mojave Desert. A total of 240 raven nestlings from 98 nests were captured and marked prior to fledging. Significant predictors of apparent survival to natal dispersal included nest proximity to the nearest anthropogenic resource and fledging date. The best-fitting mark-recapture models predicted post-dispersal survival as a function of time, nest proximity to the nearest anthropogenic resource, and differing between years. Juveniles fledging from nests closer to anthropogenic resources maintain higher rates of post-dispersal survival well into their first year. These results support the hypothesis that anthropogenic resources contribute to juvenile survival and the regional increase in raven numbers

We investigated post-dispersal habitat selection, looked for heritability in movement behavior, tested for sexual dimorphism in movements, and characterized interactions between siblings. Raven juvenile movements were relatively philopatric, and displayed no significant sexual dimorphism. Habitat selection of raven juveniles mirrored the distribution of anthropogenic resources. Lack of a sex-bias in movement behavior and low heritability for movement behavior contradicted predictions made by inbreeding avoidance models of natal dispersal. A lack of female-biased movements contradicted predictions based upon Greenwood's mating system model. Post-dispersal association between surviving sibling pairs suggested sibling recognition, which may function to prevent inbreeding. Overall, raven juvenile movements resembled an optimization process, rather than a strictly patterned behavior. They appeared to maximize their fitness by tracking resources in the environment and displayed the potential for avoiding future inbreeding by suggesting an ability to recognize close relatives.

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INTRODUCTION

Mobile vertebrates can rapidly access resource subsidies provided by humans. Due to their longevity, relatively large food requirements, and mobility, large vertebrates affect chemical, physical, and biological processes at the landscape level and can influence the spatial patterns of other organisms on the landscape (Harris, Hoctor, and Gergel 1996). The Common Raven (*Corvus corax*), the largest of all passerine birds, represents an ideal vertebrate for studying the impacts of anthropogenic subsidies on population biology.

The Common Raven ranges throughout the Northern Hemisphere. Eight subspeceis of the raven have been recognized worldwide. In the U.S., the western raven, *C. corax sinuatus*, is well recognized, and differs genetically and morphologically from *C.c. principalis*, the northern and eastern U.S. raven (Boarman and Heinrich 2000, Omland et al. 2000). Ravens mainly scavenge for food but they also hunt and steal from other birds. The Common Raven sometimes is similar ecologically to raptor species, although it is a passerine.

Predation and competition by ravens is postulated to have played a role in the declines of several threatened and endangered species in the western U.S., including the federally threatened Desert Tortoise (*Gopherus agassizii*) (Berry 1985). Ravens depredate juvenile Desert Tortoises by penetrating the incompletely ossified juvenile carapace or by removing exposed limbs (Boarman, 1993). In other regions, ravens negatively impact sensitive species including the California Condor (*Gymnogyps californianus*), Least Tern (*Sterna abtillarum*), and the Marbled Murrelet

(*Brachyramphus marmoratus*) (Boarman and Heinrich 2000).

Avian population dynamics respond readily to available resources such as food supply and nesting substrates. Annual surveys in the western Mojave Desert have shown a dramatic increased in raven sightings during the past 30 years (Boarman and Berry 1995), coinciding with an increasing human presence in the region (Knight et al. 1993). Ravens in the western Mojave are known to utilize anthropogenic resources (Boarman 1993, Knight et al. 1993) including landfills, dairies, refuse dumpsters, and irrigation runoff.

Anthropogenic resource subsidies probably contribute to the raven population increase, but the specific demographic mechanism is uncertain. Possible anthropogenic effects include increased juvenile survival, increased reproductive success, increased immigration, decreased emigration, decreased mortality, or various combinations of these alternatives. Juvenile survival is an important influence on population demographics and is relatively easy to measure.

The younger age classes in birds are subject to the highest mortality rates in general (Gill 1990). Shortages of resources such as food and water are major causes of death in juvenile birds (Miller et al. 1997), and changes in the abundance of resources can affect movement in and out of an area (Ferrer 1992). Anthropogenic resources may affect raven juvenile movement behavior by decreasing mortality and emigration and thereby influencing raven population dynamics.

The distribution of anthropogenic resources in the western Mojave is favorable for studying the anthropogenic influence on juvenile survival. Many forms of anthropogenic resources in the western Mojave (i.e. sewage ponds, landfills) form distinct point sources set within a natural landscape. Breeding ravens construct nests throughout the landscape, and juvenile ravens fledge from nests located at various distances from point sources. Since ravens are known to utilize these anthropogenic resources, nest proximity to the nearest point source can be used as a metric of juvenile access to anthropogenic resources.

Dispersal can be defined as the complete and permanent emigration from an individual's home range (Holekamp and Sherman 1998). Four definitions of dispersal can be distinguished. Breeding dispersal consists of the movement of adults between reproductive cycles. Natal dispersal is the emigration of young from their birthplace, and occurs in nearly all birds and mammals (Clobert and Lebreton 1991, Greenwood 1980). Greenwood (1980) defines natal dispersal as "the permanent movement from birth site to first breeding or potential breeding site ". Natal dispersal, which refers to individuals that may not have yet reproduced, is typically more extensive and over longer distances than breeding dispersal (Greenwood 1980). The two other defintions of dispersal are also discussed by Greenwood (1980). Greenwood distinguishes between effective and gross dispersal. Effective dispersal can be assigned only after reproduction has occurred, while gross dispersal refers to movement irrespective of reproduction. (Greenwood 1980).

Compared to other processes in population biology, relatively little is known about patterns of dispersal (Miller et al. 1997, Ferrer 1992, Newton 1991, Clobert and Lebreton 1991). The lack of information is partially due to practical problems encountered during empirical studies (Verhulst 1997, Holekamp and Sherman 1998). The need for additional studies of dispersal grows as the environment becomes increasingly modified and fragmented by anthropogenic activities. A better understanding of dispersal should play an important role in metapopulation analyses, population viability analyses, and wildlife conservation (Miller et al. 1997, Newton 1991). Dispersal is also central to the concept of source and sink areas, which become increasingly common in human-modified landscapes. Modeling shows that the viability of species of concern like the Northern Spotted Owl (*Strix occidentalis caurina*), are potentially sensitive to dispersal dynamics (Miller et al. 1997).

The present study uses natal dispersal theory to interpret the movements of juvenile Common Ravens. In terms of definitions, juvenile movements defined here can be understood in terms of natal ranging (Dingle 1996) or gross dispersal (Greenwood 1980), rather than true natal dispersal or effective dispersal (Greenwood 1980). Natal dispersal occurs between the first and second years in many passerine species. Ravens can also breed after their first year, but most will not attempt breeding until at least their 3rd year. Within the project's time frame, few of the marked individuals in the present study are likely to attempt breeding, and therefore could not satisfy the strictest definition of natal dispersal. The proximate and ultimate causes of behavior during the long juvenile period of Ravens and other long-lived species may differ from the behavior during natal dispersal *per se*. The existing literature does not distinguish between juvenile movement behavior and natal dispersal behavior. Nevertheless, the theory regarding natal dispersal remains the most relevant body of knowledge for evaluating juvenile movements.

Dispersal behavior can be examined by considering the costs and benefits in terms of individual fitness. Broadly speaking, animals that remain near their birthplace are considered philopatric while those that leave at some point are considered dispersive. The benefits of philopatry include familiarity with local terrain and food sources, benefits that may increase survival and decrease predation. Philopatric individuals benefit from a familiar social environment, the maintenance of kin associations, and reducing potential outbreeding depression. On the other hand, philopatric individuals incur costs such as resource shortages due to increased local competition (Gowaty 1993), and the potential risk of inbreeding depression (Greenwood 1980, 1983).

When the costs of philopatry outweigh the benefits, animals should disperse to improve their fitness (Horn 1983). For avian species, an individual that relocates further than 10 home ranges away is usually considered dispersive (Shields 1982). The fitness benefits of dispersal include less overcrowding, less competition with kin, and the improved fecundity in an environment with better resources. Dispersing individuals incur additional risks such as increased exposure to predators and increased energy requirements.

Various models exist to explain the motivations behind vertebrate dispersal. The most common dispersal models invoke resource competition (Murray 1967, Waser 1985, Walls and Kenward 1994), inbreeding avoidance (Howard 1960, Horn 1983,), and social behavior (Greenwood 1980, 1983). Under resource competition, dispersal is a response to population pressure. In the inbreeding avoidance model, dispersal is an adaptation to avoid the negative consequences of inbreeding (Horn 1983). Behavioral models, such as

Greenwood's (1980) mating system model, commonly assume that dispersal evolved as an inbreeding avoidance mechanism. Greenwood's behavioral model goes farther than inbreeding models in the sense that it attempts to explain the common patterns of sex-biased dispersal in birds and mammals. This model predicts the direction of sex-biased dispersal based upon mating system structure.

In the resource competition model, dispersal mainly functions to reduce intraspecific competition. Competition for resources such as food or nesting substrate cause some individuals to seek them elsewhere (Miller and Smallwood 1997). Populations swell after breeding and young animals in particular compete for resources. Since breeding expands numbers over local carrying capacities, it is unlikely that all the offspring could survive to reproductive age in the same location, and so at least some must move in order to survive.

Inbreeding avoidance models provide a genetic explanation for the evolution of dispersal. Dispersal plays a major role in gene flow and some animals are considered to be genetically predisposed to disperse, balancing the costs and benefits related to inbreeding or outbreeding (Horn 1983). In this view, the fitness benefits due to inbreeding avoidance and the subsequent increase in heterozygosity may outweigh the costs incurred during the process of dispersal. On the other hand, philopatry enhances fitness by maintaining locally adapted genes and avoiding the production of ill-adapted young.

Greenwood's (1980) mating system model represents the primary explanation of dispersal in terms of social behavior. This model explains the prevalence of sexual dimorphism in dispersal behavior (ones sex being dispersive, the other philopatric), and predicts the dispersive sex based upon the classification between mate-defense or resource-defense mating systems. In a resource-defense system, the resource defender’s fitness is enhanced by philopatry because he or she is more likely to establish a breeding territory in his or her natal area. On the other hand, dispersive sex can search for mate’s with the richest territory. In mate-defense systems, dispersal of the mate-defending sex occurs in part from low reproductive investment and the potential to maximize fitness through the acquisition of many mates over a lifetime.

Since Greenwood's 1980 analysis, many studies of avian dispersal have been published, some specifically designed to measure sex differences. In a recent reappraisal, Clarke et al. (1997) reviewed the avian literature for quantitative studies of sex biases in dispersal and found support for the general pattern of female-biased dispersal. In their analysis, they included studies that reported sex differences in dispersal patterns in natal or breeding dispersal as measured either by the proportion leaving or distance moved. The results indicated that 70% of species showed some sort of female bias in dispersal behavior. Surprisingly, at least 30% of species cited showed no sex differences. In addition, they found studies with evidence for male biased dispersal in 22 species representing 12 families. Contrary to Greenwood's predictions, species with male biased dispersal do not fall neatly into one mating system. They include communal breeders, polygynous species, lekking species, cooperative breeders, and other types of mating systems. A notable example is the cooperative breeding American Crow (*Corvus brachyrhynchos hesperis*) which displays male-biased dispersal.

Results from other empirical studies of avian dispersal also provide mixed support for the mating system model. Wheelwright and Mauck (1998) identified benefits of male philopatry in monogamous Savannah Sparrows (*Passerculis sandwichensis*). Male Savannah Sparrows raised within their study area recruited significantly more offspring than those raised outside the area. However, sex was a poor predictor of dispersal distance. In another monogamous species, Verhulst et al. (1997) observed female Great Tits (*Parus major*) dispersing greater distances than males. Cooperatively-breeding female Florida Scrub Jays (*Aphelocoma c. coerulescens*) moved farther from their nests than males (Wolfenden and Fitzpatrick 1991).

Raptor dispersal studies also provide mixed support for Greenwood's model. Spanish Imperial Eagles (*Aquila adalberti*) (Ferrer 1992) and southeastern American Kestrels (*Falco sparverius*) (Miller and Smallwood 1997) do not display sexual dimorphism in dispersal. At the same time, other researchers found sex-biased dispersal in Burrowing Owls (*Athene cunicularia hypugaea*) (Millsap and Bear 1993), Merlins (*Falco columbarius*) (James et al 1987), and Buzzards (*Buteo buteo*) (Walls and Kenward 1994). Clarke et al. (1997:430) sums up current thoughts on sex-biased dispersal as follows: "the evolutionary origins of sex-biased dispersal remain a matter of debate, and most authors agree that we are unlikely to find a single hypothesis that elucidates the most important factors in all species."

The evolutionary role of sexual dimorphism in dispersal remains contentious (Pusey and Wolf 1996). Sexual dimorphism is especially common in outbreeding species. It is adaptive for outbreeding species by separating close relatives, thus preventing the deleterious effects of close inbreeding. However, if dimorphism is an adaptation to reduce inbreeding, it does not explain why some outbreeding species display a lack of dimorphism.

Kin recognition represents another mechanism of inbreeding avoidance in the absence of sexual dimorphism in dispersal (Keller 1997). Kin recognition is operationaly defined as the differential treatment of close relatives compared to unrelated individuals, and occurs in a number of species. The two traditionally hypothesized benefits of kin recognition are to enhance the fitness of more related individuals (nepotism), or to ensure an optimal balance between inbreeding and outbreeding. Evidence suggests that recognition and avoidance of close relatives as mates occurs in a variety of animals (Pusey and Wolf 1996, Radesater 1976, Burger 1998, Palestis and Burger 1999). Sibling recognition has been established in a number of birds (Burger 1998), and may represent a mechanism of sibling avoidance for the purpose of inbreeding avoidance (Keller 1998).

Dispersal behavior may also be flexible with respect to environmental variables. Several studies have compared dispersal behavior across different habitats, and dispersing juveniles appear to select certain habitats and also display lower mortality rates in higher quality habitats. Miller et al. (1997) found that juvenile mortality of Spotted Owls is generally caused by starvation. Spotted Owls preferentially utilize closed-canopy forests harboring greater prey densities. In Spain, habitat usage and rabbit densities were significantly correlated for dispersing juvenile Imperial Eagles (Ferrer 1992). Likewise, food supply during natal dispersal is critical to the survival of Tengmalm's Owl (*Aegolius funereus*) (Korpimaki and Lagerstrom 1988).

Little is known regarding the movements of non-breeding birds (Heinrich et al. 1994), including ravens (Knight et al. 1993). Whether raven juvenile dispersal behavior is relatively philopatric or dispersive is unclear. After the fledgling dependence period, raven juveniles join flocks composed mainly of other juveniles and non-territorial adults, otherwise known as vagrant flocks (Marzluff and Heinrich 1991). Members of vagrant flocks share resources, roost communally, and develop social hierarchies important for pair formation (Engel and Young, 1992a, Heinrich 1994). Flock size ranges from a few dozen to thousands of birds (Boarman and Heinrich 2000), often forming communal roosts near permanent or ephemeral resource concentrations like animal carcasses (Heinrich 1994). Marzluff and Heinrich (1991) found that floater flocks in New England take residence until the resource is depleted, and then migrate to the next clumped resource. In the western Mojave Desert, floater flocks also congregate at more persistent resources such as landfills and dairies. Juvenile raven siblings sometimes join the same floater flocks (Heinrich et al. 1994), interact with one another, and may recognize each other as close relatives.

The purpose of the present study was to investigate the patterns of raven juvenile survival and movements based upon the predictions of resource competition, inbreeding avoidance, and the mating system model. We asked four primary questions. (1) How do environmental and morphological variables affect raven juvenile survival to dispersal from natal territories? (2) Are predictions from common dispersal models supported by the patterns of raven juvenile movements? (3) Do raven juveniles exercise habitat selection after dispersal from natal territories? (4) Do raven juveniles movements provide evidence of sibling recognition?

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CHAPTER 1: Common Raven Juvenile Survival

ABSTRACT

Annual surveys in the western Mojave Desert show a dramatic increase in Common Raven (*Corvus corax*) sightings during the past 30 years, coinciding with an increasing human presence in the region. Anthropogenic resource subsidies probably contribute to the raven population increase, but the demographic effect of such subsidies is uncertain. We asked whether raven recruitment could be predicted by a set of environmental and morphological variables such as nest proximity to the nearest anthropogenic resource (NAR), and juvenile condition. We also asked whether raven juvenile post-dispersal survival rates could be predicted by time, year, and sex. Two annual cohorts were captured and marked prior to fledging. Significant predictors of apparent survival to natal dispersal included nest proximity to the nearest anthropogenic resource and fledging date. The best-fitting mark-recapture models predicted post-dispersal survival as a function of time, NAR, and year of hatching. Juveniles fledging from nests closer to anthropogenic resources maintained higher rates of post-dispersal survival well into their first year. They probably dispersed in better health, and were better suited to learn foraging techniques. Thus, anthropogenic resources appear to contribute to raven recruitment and the regional increase in raven numbers. Through increased juvenile survival, we should expect raven numbers to continue to grow in concert with the human presence in the desert unless raven access to anthropogenic resources is diminished.

INTRODUCTION

Avian populations may respond readily to changes in available resources such as food supply and nesting substrates. The effects of resource availability may be accentuated in human-modified landscapes (Blondel 1991). Annual surveys in the western Mojave Desert show a dramatic increased in raven sightings during the past 30 years (Boarman and Berry 1995), coinciding with an increasing human presence in the region. Ravens in the western Mojave are known to utilize anthropogenic resources (Boarman 1992, Knight et al 1993) including landfills, dairies, refuse dumpsters, and irrigation runoff.

Anthropogenic resource subsidies probably contribute to the raven population increase, but the demographic relationship with anthropogenic resources is unknown. Possible explanations for the raven population growth include increased reproductive success, increased immigration, decreased emigration, decreased mortality, or various combinations of these alternatives. Juvenile survival is one measure of reproductive success and can be quantified in relation to anthropogenic resource subsidies.

The distribution of anthropogenic resources in the western Mojave is favorable for studying its influence on recruitment. Many forms of anthropogenic resources in the western Mojave (e.g., sewage ponds, landfills) form distinct point sources set within a natural landscape. Breeding ravens construct nests throughout the landscape, and juvenile ravens fledge from nests located at various distances from point sources. Since ravens are known to utilize these anthropogenic resources, nest proximity to the nearest point source can be used as a metric of juvenile access to anthropogenic resources.

We asked whether raven juvenile survival could be predicted by a set of nesting environment and individual morphological variables. For example, could juvenile survival be predicted by morphological parameters such as sex or mass? Could juvenile survival also be predicted by nest site parameters such as proximity to the nearest anthropogenic resource, or the type of nest substrate? We also asked if proximity of a nest to human activities increased the risk of anthropogenic mortality?

METHODS

The study site was comprised of Edwards Air Force Base and surrounding communities in the western Mojave Desert, approximately 4000 km^2 (Fig. 1.1), which lie within the Mojave Desert Floristic Province (Hickman 1993). The habitat consists of a mixture of natural and anthropogenic types (CNDD 1999). 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 and various kinds of agriculture and ranching operations.

Ravens in the western Mojave build nests in a variety of natural and anthropogenic substrates. The most common natural substrates include Joshua Trees (*Yucca brevifolia*) and cliffs. Anthropogenic substrates include billboards, power poles, storefronts, and landscaped trees. The nesting chronology begins with a single clutch of 1 to 5 eggs, laid sometime in March or early April. Raven nestlings are altricial at hatching and fledge at approximately 5 weeks of age. Throughout the nesting period, nesting adult ravens vigorously defend their territories against intruders. This aggressive behavior serves as an important clue to identifying active territories and their boundaries.

We investigated the apparent survival rate of juvenile ravens to dispersal from the natal territory in relation to environmental and morphological parameters. The environmental parameters included the distance between each nest and the nearest anthropogenic resource (NAR), the distance between each nest and the nearest human activity (NHA), individual fledging date, nest substrate, and attachment of a radio transmitter. The anthropogenic resources considered for the analysis consisted of permanent point sources of food or water. The human activities included in the analysis were those posing potential harm to wildlife. The morphological parameters included the following measurements: sex, mass, wing cord length, tarsus length, tarsus height, culmen length, culmen width, and culmen height. Apparent survival to natal dispersal is defined as dispersal from the natal territory followed by subsequent observer detection.

We used program MARK (White 1998, Appendix 1) to extend our investigation of raven juvenile survival into the post-fledging time period. MARK is a mark-recapture software package that builds and compares demographic models. MARK computes the estimates of model parameters through numerical maximum likelihood techniques (White and Burnham 1999). The Akaike information criterion (AICc) is used to select the best model from the list of *a priori* models, and the model with lowest AICc can be used for statistical inference and parameter estimation.

MARK is flexible in the choice of starting models from which to choose, based upon the type of study and the type of data collected. Individual birds with and without radio transmitters met different data type assumptions. Individuals with radios can be resighted alive or recovered dead. Individuals without radios are resighted alive but unlikely to be recovered dead. As a result of the different data types, radio-tagged individuals were included in a Burnham analysis, and wing tag only individuals were included in a CJS (Cormack-Jolly-Seber) analysis. Burnham analyses incorporate live resighting and recovery data, while CJS analyses use live resightings only. Burnham analyses estimate 4 parameter types: survival rate (S), recapture rate (P), recovery rate (R), and site fidelity (F). CJS models estimate two parameter types: survival rates (Phi), and recovery rates (P). For both analyses, survival is our primary parameter of interest.

We constructed and tested mark and recapture models to compare parameters between sexes, among years, and in relation to the individual covariate NAR. Models were constructed by constraining each parameter separately and in combination with other model parameters. We constrained parameters as functions of time (*t*), sex (*g*), the individual covariate of NAR (*NAR*), and constancy (.) (table 1.1). We chose time as a constraint because post-fledging survival typically declines over time. We chose sex as a constraint because fledgling males and females may have different recapture and survival rates as a consequence of potentially dimorphic dispersal patterns (Wheelwright et al. 1995). We chose NAR as a constraint because pre-fledging resource availability has been shown to affect avian post-dispersal survival (Perrins 1980, Van Der Jeugd and Larsson 1998). These constraints test for time-dependence, group-dependence, covariate-dependence, and the null, respectively. We included modified constraints which allow for tests of interactions (*), additivity (+), and age or year differences (a2). We also included a combination of modified constraints that tests for time dependence with the covariate NAR. This involved simple time dependence combined with a temporary time-NAR interaction (t(t*NAR(# months)). Since survival and recapture rates were our primary parameters of interest, we did not constrain recovery rate or site fidelity in the Burnham analysis.

The nearest anthropogenic resource to each nest was identified using observations of raven foraging behavior (table 1.2). Nearest human activities included residences, paved roads, industry, or any human activity posing potential harm to wildlife. For each nest, the distance to the NAR and NHA was determined using a geographical information system (ESRI 1999). Locations of raven nests were measured in Universal Transverse Mercator 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 (Fig. 1.2). Human activities posing potential harm to wildlife (i.e. highways) are more widespread than clumped anthropogenic resources utilized by ravens (i.e. landfills). Thus, the distance to NHA was usually less than, but occasionally equal to, the distance to NAR.

During the springs of 1999 and 2000, raven nests were located in various substrates and distances from anthropogenic influence. A total of 240 raven nestlings from 98 nests were captured 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. A subset (102) of the marked juveniles received radio transmitters (ATS, Holohil Systems Ltd.) attached with a backpack-style harness. The transmitters used in this study weighed 22g and are approximately 3 % of the average fledgling's body mass. All capture and experimental techniques strictly followed guidelines described in Gaunt and Oring (1997).

Male and female raven nestlings are morphologically indistinguishable. During the marking process, two small growing feathers were sampled from each nestling. Nestling sex was determined using a PCR reaction that amplifies the CHD genes on the W and Z chromosomes (Griffiths 1998).

We monitored marked juveniles by returning to their natal territories at intervals of 1-3 times per week until the juveniles were known to have died or to have left their respective natal territories. The identity of all marked juveniles was confirmed by reading their patagial 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.

Juveniles were considered to have survived only if they were relocated alive outside their natal territories. This designation is termed "apparent survival", since it requires both departure from the natal territory and observer detection. Individuals never relocated alive outside the natal territory were not considered as survivors.

Juveniles that survived to depart from their natal territories were relocated by radio telemetry and by searching randomly throughout the study area. Relocation of radio-tagged juveniles was conducted mainly by motorized vehicle telemetry. Radio telemetry was accomplished using dual roof-mounted, 3-element Yagi antennas in tandem with an ATS R2000 portable radio receiver (Advanced Telemetry Systems, 1993). Hand-held portable 3-element and 2-element Yagi antennas were also used to search for radio-tagged juveniles. A Cessna 185 equipped with dual wing-mounted, 3-element Yagi antennas was used on 3 occasions to conduct a large-area aerial search for missing radio-tagged birds.

The apparent survival analysis was conducted using logistic regression (SAS PROC LOGISTIC) with forward selection predicting the two dichotomous categories of outcome (surviving or not surviving) from the set of predictor variables. A correlation matrix produced between all morphological characteristics showed high correlations between most characters (e.g., r = 0.64 mass vs. tarsus length). As a result, an individual health index was constructed and substituted for the morphological characters in the analysis. The index was comprised of the residual resulting from a regression between mass and tarsus length for each individual.

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, found dead, or declared missing. Natal territories were defined as the area surrounding each nest that was actively defended by the nesting pair. To reduce 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 non-surviving juveniles.

The source of mortality was assessed as best as possible for all relocated dead juveniles. The source of mortality was more apparent for dead juveniles found closer to the time of death. In general, most cases of known mortality were classified into either natural or anthropogenic causes. The classification was further refined depending upon the amount of additional evidence. Such evidence included the location of death, timing of death, condition of the remains, and any markings left by predators.

A mortality analysis was conducted to compare the relative contributions of anthropogenic and natural sources to pre-dispersal juvenile mortality. The mortality analysis was conducted using logistic regression (SAS PROC LOGISTIC) with forward selection predicting the two dichotomous categories of outcome (mortality by natural or anthropogenic means) in relation to distance from NHA.

RESULTS

Including both years, the overall survival rate for dispersal from natal territories was 38% (81 individuals) (table 1.3). Significant predictors of survival to natal dispersal included distance to NAR and fledging date (table 1.4, Figs. 1.3-5). Non-significant predictors included the health index, sex, nest substrate, year, distance to the NHA, and radio attachment (all $P > 0.05$). Thus, Ravens fledging from nests earlier in the season and closer to NAR were more likely to survive.

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

The best-fitting models based on AICc for the both the live recaptures (CJS) and Burnham analyses project survival as a function of time, NAR, and differing between years (tables 1.5, 1.6). The best Burnham model predicts survival as a function of NAR for a period of 6 months after fledging, followed by time-dependence alone. The best CJS model predicts survival as a function of NAR for 9 months after fledging, followed by time-dependence. The second best models incorporated NAR for 9 and 6 months for the Burnham and CJS models, respectively. For both analyses, no support was found for models incorporating differences between sexes. Monthly survival estimates were generally high except for decreases in the late summer and the mid-winter months (Figs. 1.6 – 9).

Juvenile mortality was recorded through February 2001. A total of 82 incidents of mortality were recorded, with 12 cases of unknown causes (15%) and 70 cases distinguishable between natural or anthropogenic causes (table 1.7). Most of the observed mortality (87%) occurred prior to dispersal from natal territories. Nest proximity to NHA was not a significant overall predictor of juvenile survival. However, for the known causes of mortality, nest proximity to NHA significantly predicted whether the mortality source was anthropogenic or natural. Juveniles fledging from nests closer to human activities had a significantly higher chance of dying from anthropogenic causes ($P < 0.0018$, SAS PROC LOGISTIC).

DISCUSSION

Initial raven fledging attempts are usually awkward. Raven juveniles spend several days on the ground or on nearby perches before learning to fly successfully. Most pre-dispersal juvenile mortality occurs between the initial fledging attempts and actual successful flight. The fledgling dependence period for surviving juveniles lasts anywhere from two to six weeks prior to dispersal from their natal territories. During this time, fledglings depend on parents for sustenance. Surviving juveniles usually disperse to locations of clumped resources. After dispersal, they are sometimes re-sighted within their natal territories, or more rarely within other active breeding territories.

The positive correlation between juvenile survival and proximity to NAR supports the hypothesis that anthropogenic resources increase juvenile survival rates. Ravens nesting within 1.0 km of NAR enjoyed the highest juvenile survival rates of nearly 60% (Fig. 1.3). Ravens fledging from nests further than 1.5 km survived at a rate of only 10 – 30 %. The regional increase in raven numbers may result in part from nesting raven access to anthropogenic resources. Nesting adult Ravens probably forage at nearby anthropogenic resources and return to deliver food to offspring. Nesting closer to anthropogenic resources probably reduces the physiological costs of foraging, may allow for increased food delivery rates and increased opportunity for adult vigilance against predators. Raven juveniles are particularly vulnerable to depredation during this time, as the most mortality occurs prior to departure from the natal territory (table 1.6).

The best Burnham and CJS post-dispersal survival models also support the hypothesis that anthropogenic resources increase juvenile survival rates. Juveniles fledging from nests closer to anthropogenic resources maintain higher rates of post-dispersal survival. A better health index (one not confounded with development) would probably reveal that juveniles fledging from nests closer to anthropogenic resources are likely to disperse in better health, and therefore have a good head start on survival. The monthly post-dispersal survival rates are generally high (Figs 1.6. A-D.), mostly with the exception of declines during the late summer and mid-winter. The late summer decline might be due to the effect of the initial fledging condition, or cessation of parental care. The mid-winter effect might be due to the annual poaching efforts (which are conducted during that time by landowners), or changing conditions due to the season.

Avian juvenile mortality is typically very high. The apparent survival rate for juvenile ravens (38%) falls within expected values for a stable or growing population. Woolfenden and Fitzpatrick (1989, 1991) found mortality rates as high as 75% in the Florida Scrub Jay, a confamilial species. The current apparent survival estimate is conservative, because it relies upon successful relocation for categorization of survival. It is unlikely that many surviving juveniles escaped detection, but any errors would only increase the estimated survival rate.

Juvenile survival was negatively correlated with fledging date. Juveniles fledging later in the season had a significantly lower survival rate (Figs. 1.4, 1.5). Juveniles fledging prior to May 28th survived at a rate of 75% in 1999. The 1999 survival rate until mid- June ranged between 36 – 45%, dropping off dramatically afterwards. This pattern of decreasing juvenile survival over time correlates negatively with the seasonal trend of increasing air temperature.

The increasing desert air temperatures during the nesting season must present significant physiological stress on both adults and juveniles. Extreme air temperature probably restricts adult foraging activities, causes additional adult energy expenditure during brooding, and slows juvenile development (Peterson 1986). Although ravens employ heat avoidance behavior such as panting or seeking shade during hot conditions, those nesting in natural substrates appear more vulnerable. Heat stress is probably increased by the lack of cover found in most natural nesting substrates compared to anthropogenic substrates. Natural substrates such as Joshua Trees and cliffs provide less insulation than anthropogenic substrates like billboards and landscaped trees.

Some of the non-significant predictors of juvenile survival illuminate the relative efficacy of the methodological approaches. For example, it is possible that aspects of juvenile morphology such as mass and wing cord length are negatively correlated with distance to NAR. It is reasonable to predict that juveniles whose nests are closer to NAR should display different morphologies compared to juveniles of the same age but located farther from NAR. However, morphological measurements may represent unreliable or non-interpretable predictors of juvenile survival if taken at different ages. Without a reliable age estimate of individual nestlings, differences in morphology related to distance from NAR will be confounded by age differences. Unfortunately, without marking individual chicks at hatching, it was not possible to age a nestling accurately enough to compare morphology between individuals. Nestlings grow quickly and the use of fledging date alone is not accurate enough for individual comparison. Because eggs might be laid on consecutive days, sibling age at marking may differ anywhere from 1 to 4 days, depending upon the initial clutch size and onset of incubation.

The non-significant effect of transmitter attachment on survival reinforces the appropriateness of this marking technique. Females from the 1999 year appear at first glance to be strongly affected by transmitter attachment, surviving at only a 6% rate (table 1.3). However, statistical analysis indicates that this result is most likely an effect of fledging date rather than radio attachment. Logistical difficulties resulted in acquiring a late shipment of transmitters in the spring of 1999. As a result, juveniles fledging later in the season were more likely to receive a transmitter. Radio-tagged females in the 1999 year had the latest fledging date (June 20th) of all groups from table 1.3. Overall, only 7 of 51 (14%) birds that fledged after June 9th survived to natal dispersal. Out of 240 juveniles marked, only one instance of possible complications resulting from marking was observed. This individual suffered minor callusing from slightly loose patagial tags. It was not clear if the injury had a significant effect on the individual's health. No individuals required euthanasia at any time during the study.

This study supports the hypothesis that anthropogenic resources aid the western Mojave raven population. In areas like the western Mojave where resource levels are naturally low, the impacts of artificial resources can be dramatic, and help explain increasing raven numbers. Since human influence in the region will likely increase, land managers should expect raven numbers to grow in concert with the growing human presence, unless raven access to anthropogenic resources is diminished.

Adjustments could easily be made to reduce raven access to anthropogenic resources. Among those adjustments, a general education initiative should take a high priority. The public is generally unaware of the conservation issues regarding ravens. Many people unwittingly contribute to the conservation problem by actively or inadvertently feeding ravens, which often attracts and supports large numbers of ravens. Animal enthusiasts often directly supply food to ravens. Ravens also utilize food and water left outside by livestock and pet owners for their animals. Eliminating the practice of actively or inadvertently feeding ravens would significantly reduce the available anthropogenic resources.

At the present, research regarding raven commensalism with humans represents an effective approach to finding viable long-term conservation solutions. However, private landowners within the study site currently poach ravens illegally by poisoning or shooting. Current illegal poaching efforts have significant short-term effects in raven survival, but are extremely misguided. Poaching interferes with conservation research, breaks state and federal laws, and brings collateral damage to non-target wildlife species. Our data indicates that current poaching efforts have only temporary effects, and mostly kill juveniles and other non-breeders. One possible suggestion for effective long-term population management would include an educational effort toward the reduction of raven access to anthropogenic resources in combination with a concerted poaching effort by many private landowners

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Table 1.1. Program MARK model-building examples. Parameter types include survival rate (S), recapture rate (P), recovery rate (R), and site fidelity (F).

Example	Parameter	Constraint
1	S	constant
	p	constant
	r	constant
	F	constant
2	S	changes over time
	p	constant
	r	constant
	F	constant
3	S	changes over time
	p	changes over time
	r	constant
	F	constant
4	S	differs between groups (males and females)
	p	constant
	r	constant
	F	constant
5	S	differs between groups (males and females)
	p	differs between groups (males and females)
	r	constant
	F	constant

Table 1.2. Types of nearest anthropogenic resources (NAR)

Type	# nests
residences	37
artificial wetlands	15
landfills	15
sewage ponds	12
livestock feeding operations	8
strip malls	8
agricultural fields	5
golf courses	1

Table 1.3. Apparent survival to natal dispersal in juvenile Common Ravens

Cohort	Sex	Radio	No Radio	Survived	% survived	Mean Fledge Date
1999	Males	34		9	26%	6/17/1999
1999	Males		30	14	47%	6/3/1999
1999	Females	16		1	6%	6/20/1999
1999	Females		28	18	64%	5/31/1999
2000	Males	23		13	57%	5/29/2000
2000	Males		33	7	21%	6/6/2000
2000	Females	28		11	39%	6/4/2000
2000	Females		48	17	35%	6/4/2000
	Totals:	67	139	81	38%	6/7

Table 1.4. Results of logistic regression of apparent survival to natal dispersal

Parameter	DF	Estimate	S.E.	$\chi2$	P
intercept	1	1.473500	0.375000	15.4395	<0.0001
NAR	1	-0.000400	0.000097	16.7878	<0.0001
fledging date	1	-0.068900	0.016200	18.0583	<0.0001
health index	1	-0.002180	0.002660	0.6686	0.4135
sex	1	0.186500	0.171900	1.1772	0.2779
nest substrate	1	-0.072800	0.177200	0.1686	0.6814
year	1	-0.262100	0.172400	2.3127	0.1283
NHA	1	0.000031	0.000156	0.0392	0.8430
radio	1	-0.060800	0.128200	0.1282	0.7203

Table 1.5. Burnham model results for the post-dispersal survival of juvenile Common Ravens

Model	AICc	D AICc	wAICc	K	Deviance
S(a2-t(t*nar(6))/t(t*nar(6) p(t) r(.) F(.)	659.04	0.00	0.84	30	594.92
S(a2-t(t*nar(9))/t(t*nar(9) p(t) r(.) F(.)	663.33	4.29	0.10	33	592.32
S(a2-t(t*nar(3))/t(t*nar(3) p(t) r(.) F(.)	664.23	5.19	0.06	30	600.10
S(t+nar) p(t) r(.) F(.)	673.72	14.68	0.00	23	625.31
S(t*nar) p(t) r(.) F(.)	675.45	16.41	0.00	28	615.87
S(t) p(t) r(.) F(.)	720.17	61.13	0.00	43	625.53
S(t) p(.) r(.) F(.)	743.95	84.91	0.00	24	693.32
S(.) p(.) r(.) F(.)	765.00	105.96	0.00	4	756.92
S(g) p(g) r(.) F(.)	769.90	109.97	0.00	6	756.83

Key:

Parameters (K)	Constraint	Modifiers
survival rate (S)	time (t)	interaction (*)
recapture rate (p)	cohorts (a2)	additivity (+)
recovery rate (r)	constancy (.)	# of months for interaction (#)
fidelity rate (F)	anthropogenic resources (NAR)	
	group/sex differences (g)	

Table 1.6. CJS model results for the post-dispersal survival of juvenile Common Ravens.

model	AICc	DAICc	wAICc	K	Deviance
Phi(a2-t(t*nar(9))/t(t*nar(9) P(a2-t/t) r(.) F(.)	1621.63	0.00	1.00	46	1522.84
Phi(a2-t(t*nar(6))/t(t*nar(6) P(a2-t/t) r(.) F(.)	1648.83	27.20	0.00	45	1552.34
Phi(a2-t(t*nar(3))/t(t*nar(3) P(a2-t/t) r(.) F(.)	1668.68	47.06	0.00	44	1574.49
Phi (a2-t/t) P (a2-t/t)	1694.36	72.73	0.00	54	1576.92
Phi (a2-t/t) P (t)	1707.34	85.71	0.00	47	1606.25
Phi (t +nar) P (t)	1707.94	86.31	0.00	30	1645.57
Phi (t) P (t)	1728.42	106.79	0.00	39	1680.55
Phi (a2-t/t*nar) P (t)	1767.91	146.28	0.00	41	1680.55
Phi (.) P (.)	1844.49	222.86	0.00	2	1840.47
Phi (g) P (g)	1847.69	226.06	0.00	4	1839.63

Key:

Parameters	Constraint	Modifiers
survival rate (Phi)	time (t)	interaction (*)
recapture rate (P)	cohorts (a2)	additivity (+)
	constancy (.)	temporary (# months)
	anthropogenic resources (NAR)	
	group/sex differences (g)	
	parameters	

Table 1.7. Causes of mortality in juvenile Common Ravens

Type	Source	Pre-dispersal	Post-dispersal
natural	bobcat	2	0
	coyote	16	0
	disease	1	0
	Great Horned Owl	6	0
	unknown mammal	22	1
anthropogenic	dog	3	1
	electrocution	0	3
	vehicle	4	1
	train	6	0
	poaching	0	4
known cause		60	10
unknown cause		11	1
total		71	11

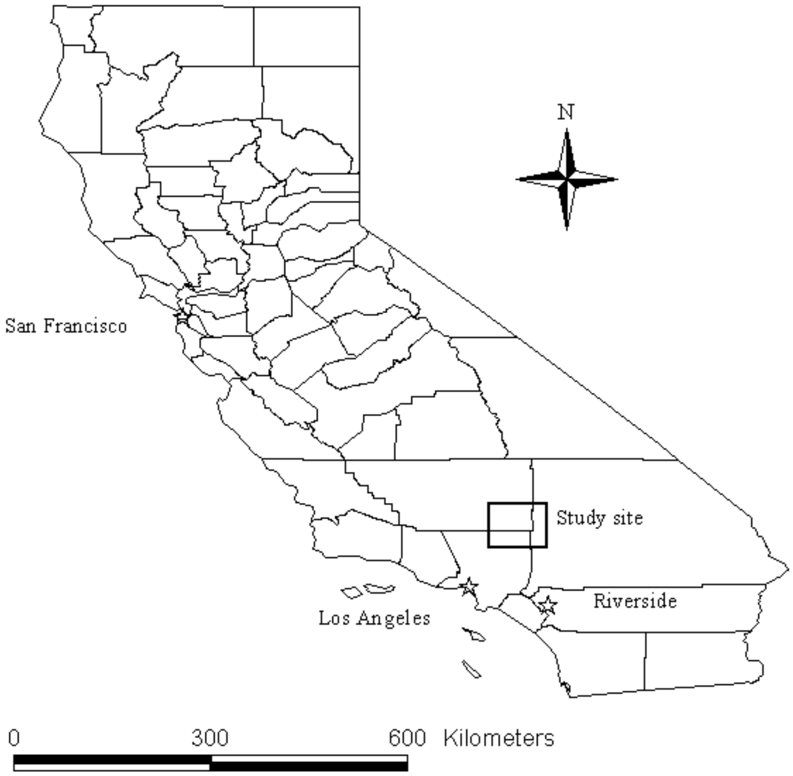

FIGURE 1.1. Study site

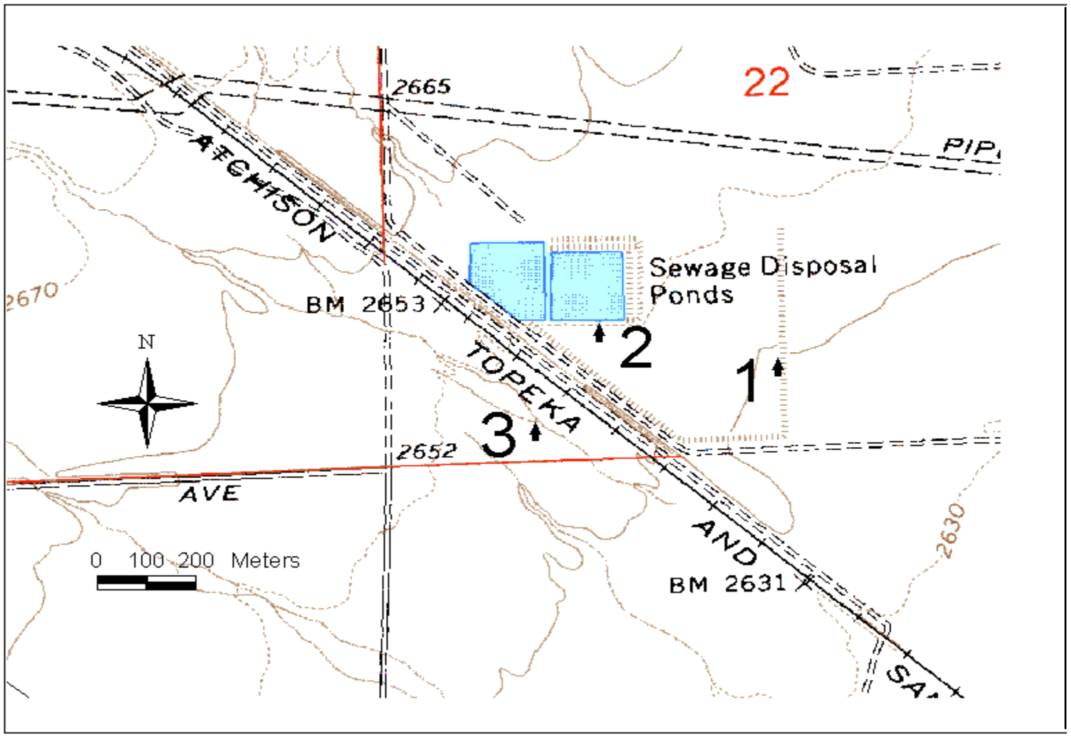

FIGURE 1.2. Example of measuring the nearest anthropogenic resource (NAR; 3) to a Common Raven nest (1), and the nearest human activity (NHA; 2). In this case, the NHA is a railroad. Several juveniles were killed by trains on this and other tracks. Juveniles fledging from nests near railroads may not perceive trains as threats because of habituation. Observations indicated that unimproved roads in the area were not used often enough to be considered significant sources of human activity.

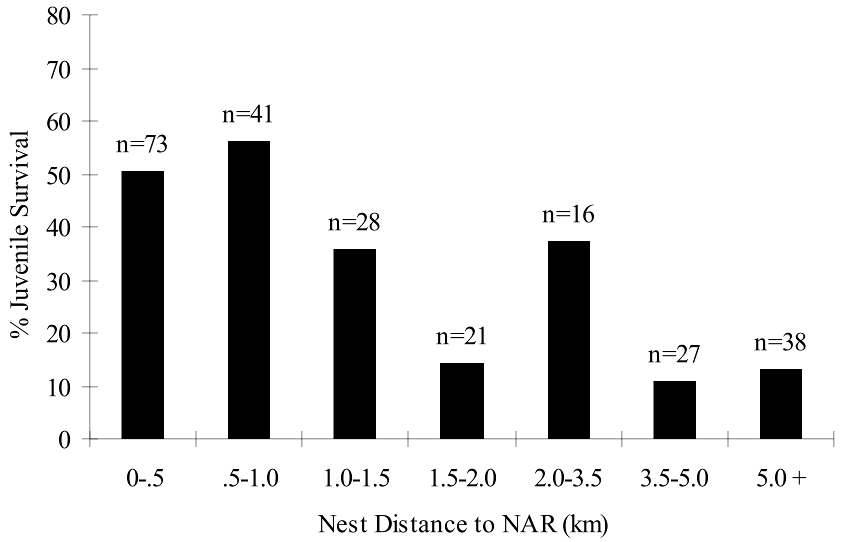

FIGURE 1.3. Apparent juvenile survival to leave the natal territory and nest distance to NAR.

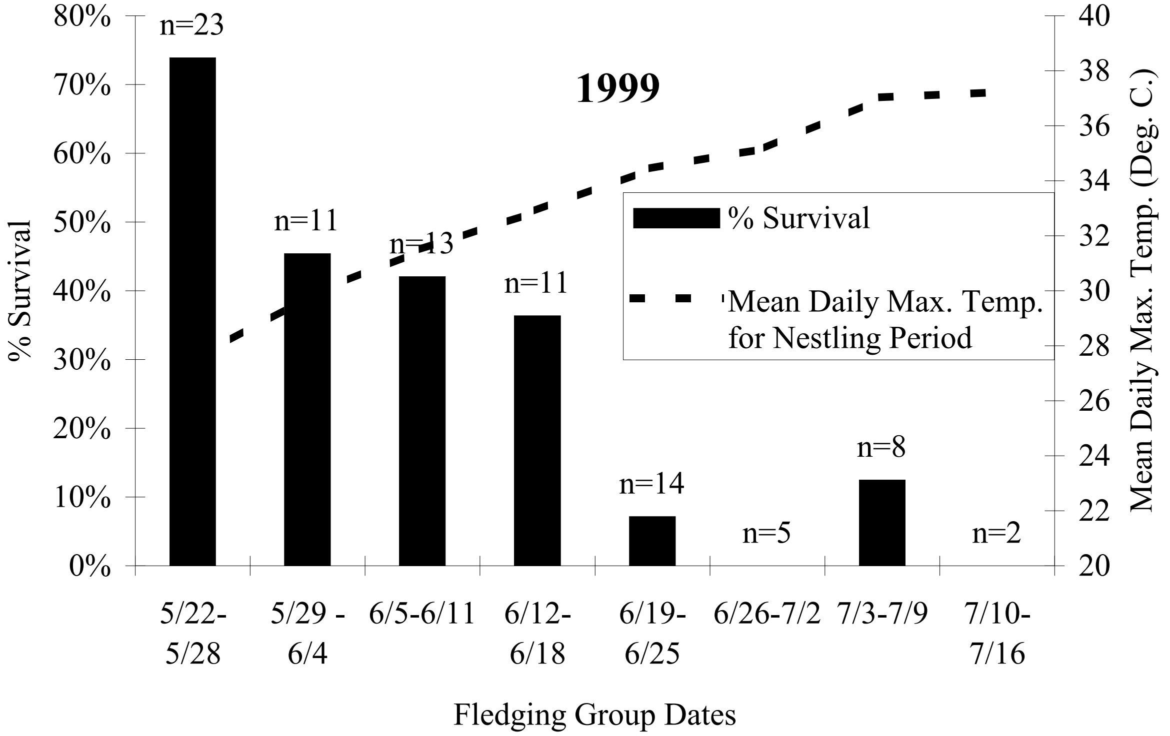

FIGURE 1.4. Apparent juvenile survival to leave the natal territory by fledging date, 1999 cohort.

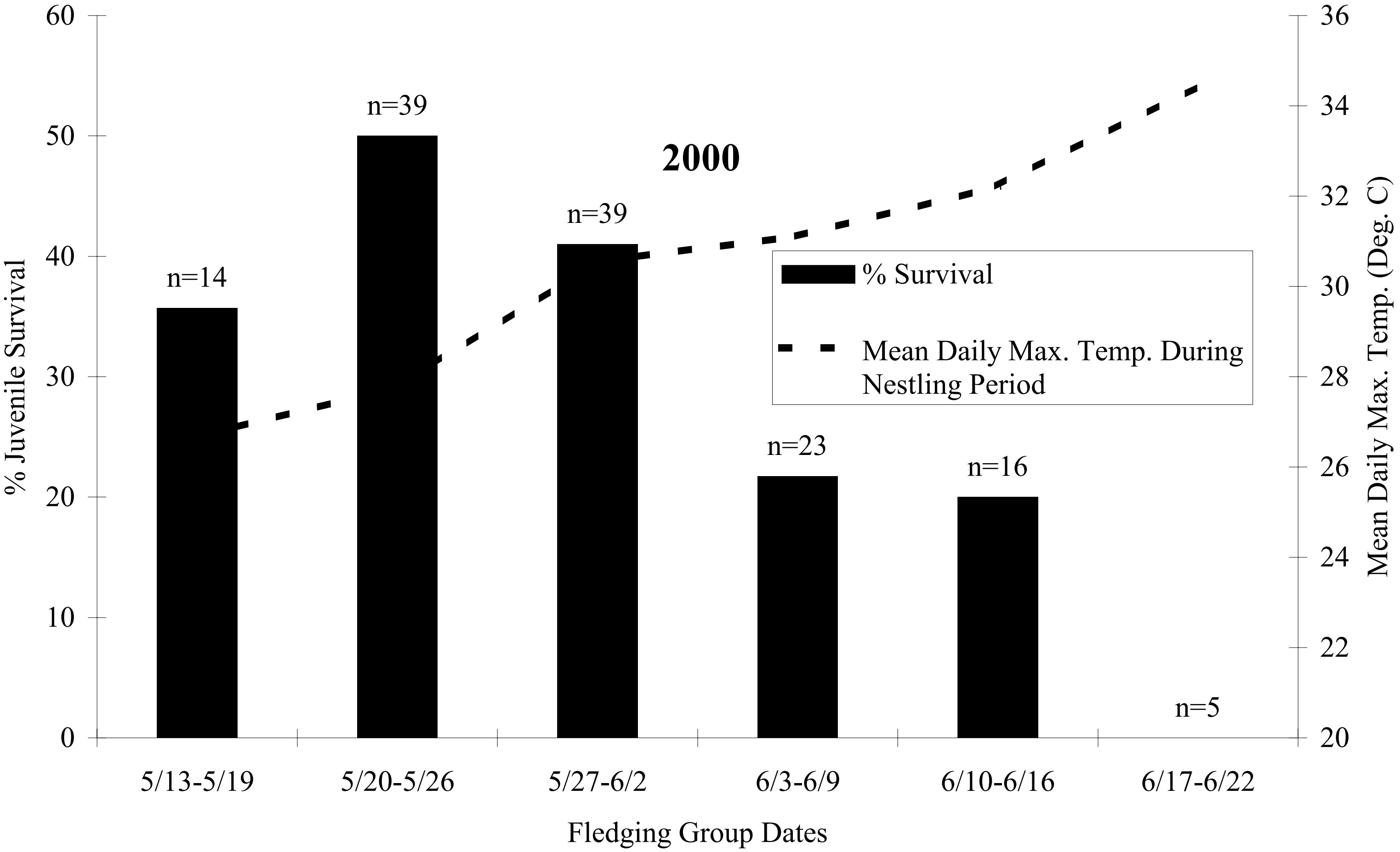

FIGURE 1.5. Apparent juvenile survival to leave the natal territory by fledging date, 2000 cohort.

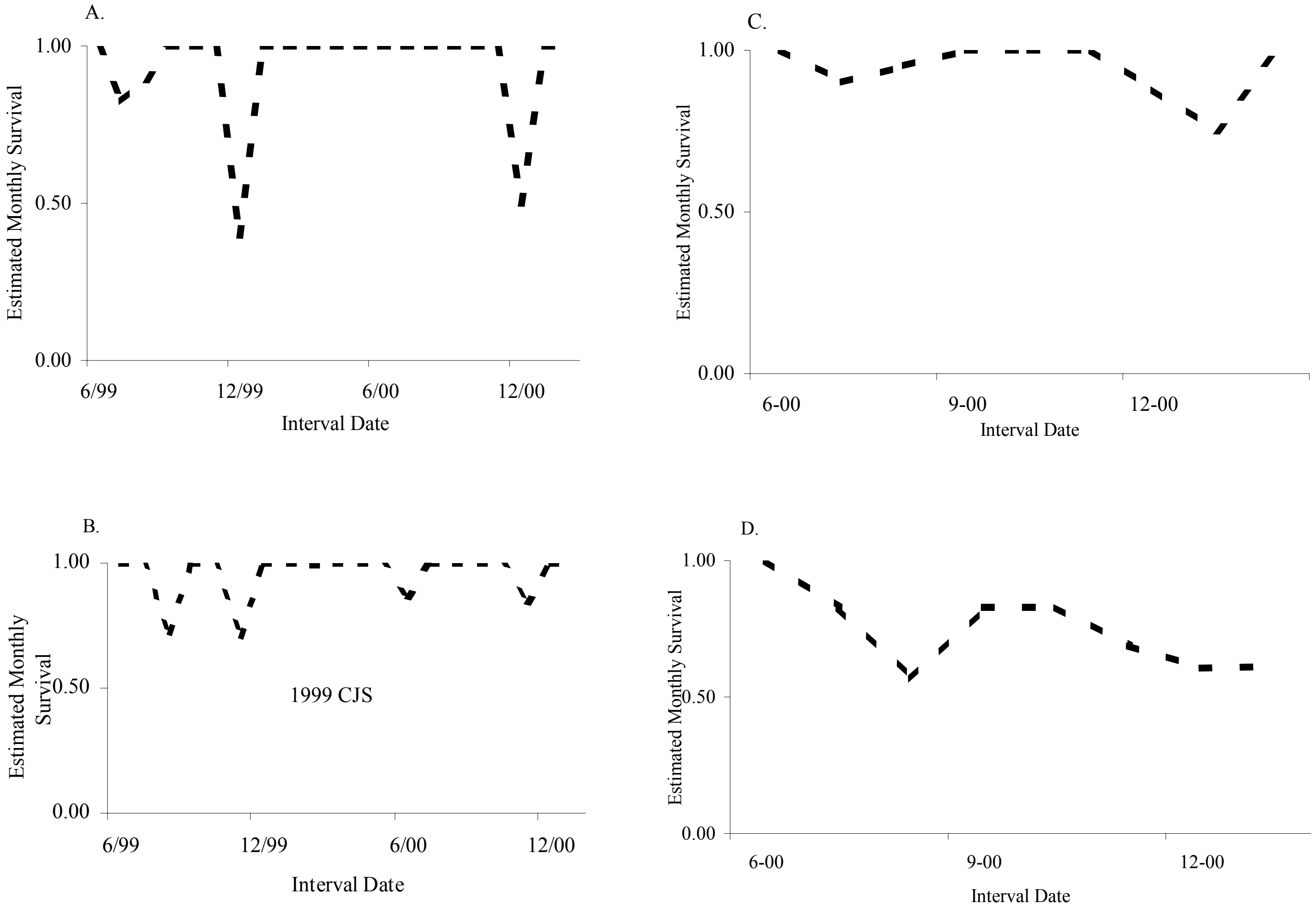

FIGURE 1.6. (A.) Burnham model monthly survival estimates, 1999 cohort. (B.) CJS model monthly survival estimates, 1999 cohort. (C.) Burnham model monthly survival estimates, 2000 cohort. (D.) CJS model monthly survival estimates, 2000 cohort.

Chapter 2: Common Raven Juvenile Movements

ABSTRACT

Common models for explaining avian natal dispersal involve resource competition, inbreeding avoidance, and social behavior. We evaluated the movements of juvenile Common Ravens in the context of each of these categories of dispersal models. We marked and followed two annual cohorts of juvenile ravens in the western Mojave Desert. We investigated habitat selection, looked for heritability in movement behavior, tested for sexual dimorphism in movements, and characterized interactions between siblings. Raven juvenile movements were relatively philopatric, and displayed little sexual dimorphism. Habitat selection of raven juveniles mirrored the distribution of anthropogenic resources. Low heritability in movement behavior and a lack of sexual dimorphism contradicted predictions based on inbreeding avoidance and Greenwood's (1980, 1983) mating system model. Juvenile philopatry and patterns of habitat selection related to resource abundance supported resource-based competition models. Locations of raven juveniles showed that siblings tend to associate more than unrelated individuals. The function of sibling association is unknown, but provides evidence for sibling recognition which may play an eventual role in inbreeding avoidance as juveniles reach sexual maturity. Overall, raven juvenile movements resembled an optimization process, rather than a strictly patterned behavior. They appeared to maximize their fitness by tracking resources in the environment and displayed the potential for avoiding future inbreeding by suggesting an ability to recognize close relatives.

INTRODUCTION

Dispersal is a life history trait with important ecological and genetic implications for populations. It is a demographic process relevant to the distribution and abundance of organisms (Johnson and Gaines 1990). The young constitute the majority of dispersers, and natal dispersal occurs in nearly all birds (Clobert and Lebreton 1991). Various models exist to explain the adaptive significance of avian natal dispersal. The most general dispersal models involve resource competition (Murray 1967, Waser 1985, Walls and Kenward 1994, Lambdin 1994), and inbreeding avoidance (Howard 1960, Horn 1983). In the resource competition model, dispersal functions to alleviate population pressure. In the inbreeding avoidance model, dispersal plays a major role in gene flow, balancing the costs and benefits related to inbreeding or outbreeding. Behavioral models such as Greenwood's (1980) mating system model assume that dispersal evolved as an inbreeding avoidance mechanisms, and also predict the direction of sexually dimorphic dispersal behavior.

These general models of avian natal dispersal are not considered to be mutually exclusive, but do present testable predictions. For example, resource competition models assume that the distribution of resources influences the pattern of natal dispersal. Some proponents of inbreeding avoidance models (Howard 1960, Reed and Oring 1992) propose that dispersal behavior is genetically inherited by juveniles as a mechanism to reduce matings between close relatives. Other researchers suggest that some species may possess the ability to recognize close relatives in order to avoid them during reproduction

(Pusey and Wolf 1996, Wheelwright and Mauck 1997). Finally, the behavioral model proposed by Greenwood (1980) predicts the prevalence of female biased dispersal for avian species with resource defense mating systems.

Our goal was to employ natal dispersal models in evaluating the movements of juvenile Common Ravens (*Corvus corax*). The term juvenile movements is substituted for natal dispersal, since natal dispersal is defined as "the permanent movement from birth site to first breeding or potential breeding site " (Greenwood 1980:1141). Juvenile movements defined here can be understood in terms of natal ranging (Dingle 1996) or gross dispersal (Greenwood 1980), rather than true natal dispersal or effective dispersal (Greenwood 1980). Although ravens can breed after their first year, most do not attempt breeding until at least their 3rd year. Thus, within our project's 2-year time frame, few of the marked individuals in the present study were likely to attempt breeding, and therefore would not satisfy the stricter definition of natal dispersal.

The proximate and ultimate causes of behavior during the long juvenile period of ravens and other long-lived species may differ from the behavior during natal dispersal *per se*. However, the existing literature does not distinguish between juvenile movement behavior and natal dispersal behavior. Thus, the current theory regarding natal dispersal remains the most relevant body of knowledge for evaluating juvenile movements.

We therefore asumed that movements during the birds' first year or two adequately characterized the nature of their pre-breeding movements. Based upon related studies in the same system (Boarman 2001, unpublished data), we have no reason to suspect that raven juvenile movements defined here would strictly differ from the movements of older pre-breeding individuals. Both sub-adult and juvenile Common Ravens in the western Mojave appear to heavily utilize anthropogenic resources (such as landfills and sewage ponds) and concentrate in anthropogenic habitat.

Our specific objectives were to examine raven juvenile movements in order to determine i) whether there is sex bias in juvenile movements; ii) investigate habitat selection to determine the relationship between resource distribution and juvenile movements; iii) test for the heritability of juvenile movement behavior; iv) look for evidence of sibling association during juvenile movements.

METHODS

The study site included Edwards Air Force Base and surrounding communities in the western Mojave Desert, (approximately 4000 km^2 ; Fig. 1.1), which lies within the Mojave Desert Floristic Province (Hickman 1993). The habitat consists of a mixture of natural and anthropogenic types (CNDD 1999). 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 and various kinds of agricultural and ranching operations. See table 2.1 for a complete list of habitat types occurring in the study area.

During the spring of 1999 and 2000, raven nests were located and nestlings were captured and marked at approximately 4.5 weeks of age. Juveniles typically fledged in their 5th week (pers. obs.). All nestlings were marked with individually coded wing tags. A subset of the marked juveniles received radio transmitters attached with a backpackstyled harness. All capture and experimental techniques strictly followed guidelines described in Gaunt and Oring (1997).

Since male and female ravens are morphologically indistinguishable, only molecular techniques differentiate individuals of either sex. During visits to the nests, two small growing feathers were sampled from each nestling. Nestling sex was determined using a PCR reaction that amplifies the CHD genes on the W and Z chromosomes (Griffiths 1998).

Juveniles were tracked at regular intervals to monitor their survival rate, post-dispersal movements, and behavior. We monitored marked juveniles by returning to their respective natal territories at frequencies of 1-3 times per week until the juveniles were known to have left their natal territories or to have died.

Juveniles which left their natal territories were relocated by radio telemetry and searching randomly throughout the study area. We surveyed the entire study site during each tracking bout in order to locate the maximum number of individuals. Each tracking bout lasted one to three days, and the number of bouts varied from two to ten per month. To maximize the range of obtainable information, including behavioral data, the majority of tracking efforts occurred during daylight hours. During post-dispersal re-sightings, individual identity was confirmed by reading patagial tags with a spotting scope and binoculars

Relocation of dispersed juveniles was conducted mainly by vehicle. Radio telemetry was accomplished using dual roof-mounted, 3-element Yagi antennas in tandem with an ATS R2000 portable radio receiver (Advanced Telemetry Systems, 1993). Hand-held portable 3-element and 2-element antennas were also used to search for radio-tagged juveniles. On 3 occasions, a Cessna 185 equipped with dual wing-mounted 3-element Yagi antenna elements was used to search for missing radio-tagged birds.

Locations of juveniles were recorded in Universal Transverse Mercator (UTM) coordinates utilizing hand-held Global Positioning System (GPS) units (Magellan GPS 300, Department of Defense PLGR). The DOD-issued PLGR maintains an accuracy of less than 10m error. The PLGR was used until selective availability was discontinued, after which the Magellan (less than 15m error) was utilized. Locations of juveniles were plotted on a study site map constructed using GIS (ESRI 1999).

We measured movement variables that included a suite of movement distances, three movement indices, and home range size. The suite of movement distances included the mean, initial, and maximum distance individuals were located from their nests. The movement indices included the mean distance moved between locations, the rate of movement between locations (velocity), and Sheilds' (1982) criteria for relative philopatry. Sheilds' criteria uses a distance equivalent to 10 home ranges to classify individuals as either dispersive or philopatric. We estimated the diameter of the mean breeding adult homerange based upon the mean distance between nests (Kristan and Boarman, in prep.) For simplification, we assumed a circular homerange. We then classified juvenile ravens as philopatric or dispersive by comparing their mean movement distance with the diameter of 10 mean adult homeranges.

The juvenile home ranges were calculated implementing a 95% fixed kernel estimator (Hooge et al. 1999). A fixed kernel estimator was chosen because kernel methods free the utilization distribution estimate from parametric assumptions and provide a means of smoothing locational data (Worton 1989). The smoothing parameter was chosen using least squares cross-validation (Worton 1989).

We estimated the heritability of movement behavior from the regression coefficient from paired observations of mean movement distance between same year siblings (Price and Burley 1993, Greenwood et al. 1979). Only those individuals with at least 5 locations outside the natal territory were included in the analysis. To account for the possibility of sex biased movements, we also separately analyzed same sex and opposite sex sibling pairings.

We investigated the degree of post-dispersal association between surviving siblings by comparing the spacing between siblings and non-siblings. We compared the physical distance between the locations of siblings located on the same day with the distance between a randomly selected pair of unrelated juveniles located on the same day. In the case of nests with more than two survivors, the sibling pair included in the analysis was randomly chosen. Each sibling pair was used once in the analysis The date used for each sibling pair was randomly selected from the set of days in which the sibling pair and at least 5 additional unrelated juveniles were located on the same day. From the random date, two non-sibling juveniles were randomly selected. The distances among the sibling and non-sibling pairs were compared using a Wilcoxon's matched-pairs signed ranks test.

If inbreeding avoidance influences movement behavior, one might expect the frequency of sibling association to differ between same sex and opposite sex pairs. To investigate the role of sex in sibling association, we compared the proportion of opposite sex pairs involved in same day sightings with the overall proportion of opposite sex pairs in the tagged juvenile population. Only those sibling pairs for whom both members had a reasonable chance of detection were included in the analysis (5 or more locations for both siblings).

Habitat selection was determined by comparing the proportions of habitat use and availability (White and Garrot 1990). A habitat map of the study site was constructed using GIS (ESRI 1999). Raven juvenile locations were plotted onto the digital map and each location was classified by habitat type.

Data on habitat type were obtained from the California Gap Analysis Project (Davis et al 1998). The California Gap Analysis Project classifies habitat types according to plant communities recognized by the California Natural Diversity Database (CNDD 1999). The GAP data were ground-truthed for accuracy and combined with USGS 7.5-Minute Digital Raster Graphics (DRG's) and USGS 7.5 -Minute Digital Orthophoto Quarter Quadrangles. Overall, 20 uniquely identifiable habitat types occurred within the study site (table 2.1).

RESULTS

Two hundred and forty ravens from 98 nests were marked as nestlings with patagial tags, 101 of which were also equipped with radio transmitters. We calculated the apparent survival rate for dispersal from natal territories. The apparent survival rate is an estimate of the true survival rate, and is defined as juvenile dispersal from the natal territory combined with observer detection. Including both years, the apparent survival rate for dispersal from natal territories was 38% (81 individuals) (table 1.3). A total of 1401 post-natal territory dispersal locations of juveniles from both years were obtained through February 2001.

Movement variables were calculated for the sub-sample of individuals with 10 or more post-dispersal locations for data collected through February 2001 (n = 15 females, 24 males; n = 19, 1999 cohort, n= 20, 2000 cohort). No sex-related differences were observed in the suite of movement distances: mean, initial, and maximum distance located from the nest (SAS PROC TTEST, table 2.2). The distribution of mean movement distances ranged from 1-27 km (fig. 2.1). No significant sex-related differences occurred within the movement indices: mean distance moved between locations, and the rate of movement between locations (velocity) were not significantly different between males and females (SAS PROC TTEST, table 2.2). The majority of juveniles were relatively philopatric in their movements (table 2.2). The mean movement distances for both males and females was less than half of Sheilds'criteria (19 km). Only 13% of the juveniles (3 females and 2 males from 39 total) had mean movement distances large enough to classify them as dispersive.To characterize habitat selection, proportions were calculated for the amount of habitat available and the amount of habitat used. Since the proportions of use and availability were very low for many categories, the habitats were lumped into 3 categories: natural, urban, and agricultural (table 2.1). The null hypothesis of habitat use being in proportion to availability was rejected. Raven juveniles utilized anthropogenic habitat (urban and agricultural habitats) more than expected, while under-utilizing natural habitats (SAS PROC FREQ, χ^2 = 142.3225, P

<0.0001). Only 3% of the total post-dispersal juvenile locations occurred in natural habitat in comparison to the number of locations in urban (64%) and agricultural habitat (33%) (table 2.1, Fig. 2.2).

If there was a strong genetic component to movement behavior, then one would expect similarities in the movements between siblings, especially those of the same sex. However, the regression for mean movement distance indicated low heritability for movement behavior. The regression coefficient for the mean movement distance for all sibling pairs was $r^2 = 0.07$ (df =23, P > 0.21, SAS PROC REG, table 2.3, fig 2.3). The results for same sex pairs was similar, $r^2 = 0.22$ (df =12, P > 0.22, SAS PROC REG) for same sex siblings

If there was no connection between siblings, then you would not expect to find them closer together than other marked juveniles. However, the distances separating sibling pairs were significantly less than non-sibling pairs observed within the same day, (n =22, S = -70.5, P > 0.0103**,** SAS PROC UNIVARIATE). This suggests some level of sibling association (table 2.4).

If inbreeding avoidance affects movement behavior, one might expect the overall movements to be greater for opposite sex sibling pairs than same sex pairs. To test for this, we compared the mean movement distance of same sex pairs with opposite sex pairs. However, there was no significant difference in the mean movement between opposite sex pairs (mean = 10.8 km) and same sex pairs (mean = 9.7 km) (df = 46; t = 0.60; P > 0.55; SAS PROC TTEST, table 2.3).

If opposite sex siblings avoid each other, then we also would expect a significant difference in distances between opposite sex and same sex pairs when located on the same day. Unfortunately, the sample size of same day sightings for opposite sex pairs (n=6) was quite small for comparison with same sex pairs (n= 16). One might similarly expect the overall frequency of same day sightings to differ between same sex and opposite sex pairs relative to their proportion in the tagged juvenile population overall. The frequency of opposite sex pairs sighted within the same day (table 2.3) was not significantly less than expected (n = 6 of 22 total, chi-square = 1.69, P > 0.19, SAS PROC FREQ) based upon the proportion of opposite sex sibling pairs with 5 or more post natal dispersal locations (n = 11 of 24, table 2.3). Thus, it can be interpreted that individuals were equally likely to associate with siblings of either sex.

DISCUSSION

After fledging, most juvenile ravens spend a considerable time (1-4 weeks) within their natal territories before departing. During this time, adults continue bringing food to the fledglings. Since nest proximity to anthropogenic resources is a significant predictor of juvenile survival to natal dispersal, most breeding ravens probably utilize anthropogenic resources located outside breeding territories to feed their young. Utilization of anthropogenic resources by nesting ravens suggests that natal territories are relatively resource-deficient, and eventual departure from the natal territory is probably a prerequisite for juvenile survival. To the best of our knowledge, juveniles either departed from their natal territories or died before they could leave; none appeared to stay.

The departure process from natal territories probably begins as adults begin to wean fledglings. Hungry fledglings probably begin to follow adults as they forage, which is most likely to the nearest anthropogenic resource. Adults eventually cease feeding juveniles, and surviving juveniles join vagrant flocks roosting near clumped communal resources.

Resource competition models would predict that juvenile movements after dispersal from the natal territory should track resource availability. The relative philopatry of raven juveniles and the pattern of habitat selection for resource-rich anthropogenic habitat uphold the predictions of the resource competition model. The majority of juveniles (87%) were classified as highly philopatric according to Shields' criteria. Shields' benchmark of 10 homerange diameters is arbitrary, and relative philopatry will vary depending upon the methods used for home range calculation. However, we believe that our population of juveniles is highly philopatric. No individuals were known to leave the study site based upon aerial telemetry and occasional long-range searches outside the study site.

Raven utilization of anthropogenic habitat is consistent with observations of expanding raven numbers in the western Mojave (Knight et al. 1993a). Over 95% of juvenile post-dispersal locations were found in anthropogenic habitat, either in urban or agricultural settings. Anthropogenic resources probably serve as the main raven attraction in these settings. Sewage ponds, landfills, refuse dumpsters, and irrigation water represent some of the urban resources utilized by raven juveniles. Agricultural practices provide resources for juvenile ravens in the form of livestock feed, manure, irrigation water, livestock carcasses, and others. Raven juveniles can be frequently observed trailing combines during the harvest, foraging upon crop remnants, disturbed insects, and small vertebrates.

Other researchers have found evidence for resource competition models by establishing strong connections between resources and individual movement (Ferrer 1992, Walls and Kenward 1994). Miller and Smallwood (1997) found that natal dispersal in southeastern American Kestrels (*Falco sparverius*) was determined in part by competition for breeding sites. In some species, a few dominant juveniles may occasionally establish themselves when the natal area is vacated through adult mortality. However, most juveniles can maximize their fitness only if they leave the natal territory, in spite of the risks involved.

It could be argued that the pattern of raven juvenile habitat selection we observed follows from observer bias towards locating juveniles in the convenience of anthropogenic habitat. However, the study site landscape is in reality more conducive to locating individuals in natural habitat. While vehicle access was exceptionally good in both natural and anthropogenic habitat types, there are less distractions and fewer obstructions to the observer in natural habitat. Human structures, landscaping, and other vehicle traffic in anthropogenic habitat present significant obstacles to the observer. On the other hand, the natural habitats mainly consist of sparsely-vegetated desert plains with many roads that present few vehicle hazards. Careful attention in avoiding observer habitat bias was made throughout the study; the proportion of time spent searching in natural habitat was much greater than the relative frequency of locations in natural habitat.

The negative effects of inbreeding depression have been well documented, especially in captive animals (Pusey and Wolf 1996). The severity of inbreeding effects are thought to be significant enough to select for inbreeding avoidance mechanisms. Dispersal is commonly assumed to be an evolutionary response to the negative effects of inbreeding depression. The inbreeding avoidance hypothesis suggests that dispersal is an innate mechanism for reducing the chance of mating with close relatives. However, it is difficult to distinguish absolutely between inbreeding avoidance and alternative hypotheses because they are not mutually exclusive.

The inbreeding avoidance hypothesis suggests there is an innate stimulus that might motivate certain individuals but not others to leave the vicinity of their birthplaces. Various researchers provide support for a genetic component to dispersal behavior (Dice and Howard 1951, Lidicker 1975, Comins et al. 1980). If there is a strong genetic component to inbreeding avoidance, then a correlation between the movement behavior of siblings might be expected. However, the lack of heritability in sibling movement behavior in our study provides no evidence for a strong genetic component. These results corroborate those of Wheelwright and Mauk (1998), who found a non-significant correlation of natal dispersal distances between parents and their offspring, suggesting low heritability of this trait. The lack of a strong genetic component weakens the hypothesis that dispersal evolved as an adaptation for inbreeding avoidance.

If dispersal is an adaptation for inbreeding avoidance, one might also expect birds to adjust their movements in relation to close relatives of the opposite sex. However, the movements of opposite sex sibling pairs are similar to those of same sex sibling pairs, and therefore provide little evidence for avoidance. Similar mean movement distances between same sex and opposite sex sibling pairs suggests that birds do not simply flee the presence of opposite sex siblings. In addition, pairs of siblings located on the same day were equally likely to be the same or opposite sex. This indicates that opposite sex siblings associate as much as same sex sibling pairs.

Greenwood’s widely accepted behavioral model is based on the assumptions of the inbreeding avoidance hypothesis. The model argues that the type of mating system dictates the pattern of sexually dimorphic natal dispersal in avian and mammalian species. Most avian and mammalian mating systems are classified as either resource-defense or mate defense. Resource defense systems are most common in birds. In this model, the resource defender maximizes fitness by gaining local familiarity through philopatry, while the other sex maximizes fitness by choosing between resource defenders during dispersal. Thus, resource defense mating systems favor philopatry of the resource defender and dispersal of the other sex.

Greenwood’s mating system model would predict female-biased dispersal in the raven because behavioral evidence suggests that ravens have a resource-defense mating system (Heinrich 1989, Stiehl 1978). Greenwood’s model would predict female-biased dispersal in the raven. However, raven juvenile movements do not display a female bias, and therefore do not support Greenwood’s model. It may be that for some species, communal foraging at clumped resources may allow females to select among available mates without having to disperse greater distances than males (Wheelwright and Mauck 1997). In fact, pair-bonding is believed to be one of the social behaviors occurring in vagrant flocks of ravens (Heinrich 1989).

A male bias in juvenile movements, although contrary to Greenwood's predictions, would be consistent with the inbreeding avoidance hypothesis because it would still provide a mechanism for separating the sexes of close relatives. The total lack of any sex bias does not support the inbreeding avoidance hypothesis. Among closely related species, the results are mixed: female-biased dispersal occurs in Florida Scrub Jays (*Aphelocoma coerulescens*) (Woolfenden and Fitzpatrick 1978), and Pinyon Jays (*Gymnorhinus cyanocephalus*) (Marzluff and Balda 1989), but is male biased in American Crows (*Corvus brachyrhynchos*) (Caffrey 1992), and Australian Magpies (*Gymnorhina tibicen*) (Veltman and Carrick 1990).

It could be argued that the timing of breeding behavior provides another possible explanation for the lack of sex-biased movements. Although they reach sexual maturity after their first year, ravens typically don't begin breeding attempts until their 3rd year (Boarman and Heinrich 1999). Thus, the full expression of raven sexual dimorphism in dispersal may not occur until breeding activity commences, which is outside the scope of the current investigation. At the completion of this study, the 1999 and 2000 years began their 3rd and 2nd years, respectively. No individuals were known to have attempted breeding. However, based on related studies of adult ravens (including several breeding individuals), we have no reason to suspect that the pattern of juvenile and adult movements significantly differ in the western Mojave. Both juvenile and adult ravens heavily utilize anthropogenic resources and concentrate in anthropogenic habitat (Boarman and Kristan, unpublished data).

If dispersal does not function to prevent inbreeding, then selection should favor the evolution of other inbreeding avoidance mechanisms. Kin recognition is one mechanism that may play an important role in inbreeding avoidance (Keller 1997). Discrimination of kin from non-kin has been demonstrated in a number of animal species including mammals, birds, reptiles, amphibians, social insects, colonial invertebrates and others. Evidence suggests that recognition and avoidance of close relatives as mates occurs in a variety of animals (Pusey and Wolf 1996, Radesater 1976, Burger 1998, Palestis and Burger 1999). Individuals choosing mates avoid siblings, littermates, or nestmates for breeding. Sibling recognition has been established in a number of birds (Burger 1998), and may represent a mechanism of sibling avoidance for the purpose of breeding (Keller 1998).

Studies of kin recognition in birds have usually focused on parent-sibling interactions while studies of sibling recognition are relatively rare (Radesater 1976, Medvin et. al 1992). The physical proximity of dispersed raven siblings suggests some form of active sibling association, and the possibility of sibling recognition which may function in part for the purpose of inbreeding avoidance.

Like many avian species, raven populations support a large non-breeding component. After dispersing from their natal territories, juvenile ravens join large flocks of non-territorial birds including other juveniles and other non-breeders. These vagrant flocks seek out and congregate at clumped food resources, often roosting nearby until the resource is depleted. Numerous vagrant flocks occurred throughout our study site, and frequently contained a number of marked juveniles. Although dispersed juvenile were located throughout the study site, we observed that siblings often joined the same vagrant flock. Although floater flocks are large and contain several marked individuals, we frequently observed siblings within floater flocks to be in close physical proximity to each other.

Most observations of sibling association occur in the first few months after dispersal from the natal territory when juveniles first appear in vagrant flocks. It is possible that juveniles first arrive at vagrant flocks while following their parents and siblings to clumped resources. High mortality occurs during the immediate post-fledging period, and selection might favor siblings with the ability to recognize close relatives for the purpose of sharing resources during this time period. If the ability for sibling recognition during the juvenile period is not lost, then birds reaching sexual maturity could later also utilize it for inbreeding avoidance.

Parker et al. (1994) also observed close relatives within raven vagrant flocks, but dismissed the possibility of resource sharing between kin as a primary explanation. Using DNA fingerprinting, they found that vagrant flocks were not composed of cohesive genetic clans. In the western Mojave, ravens in vagrant flocks often number in the hundreds, and it is unrealistic to expected these large flocks to consist of cohesive genetic groups. Moreover, vagrant flocks congregate where resources are abundant, and would be impossible for a subset of birds to control. In contrast to the ecology of Parker's study site, communal resources in the western Mojave tend to be permanent rather than ephemeral. Since resources are abundant and accessible, it is doubtful that birds rely on nepotism for resource access.

Even if juveniles first reach vagrant flocks by following close relatives, it is unclear why they would continue to associate with each other after reaching the resource. They could just as easily follow other flock members to the clumped resource. It is possible that post-fledging association between siblings functions in some sort of extended imprinting process. Raven fledglings are known for their heightened curiosity, or “neophilia” (Heinrich 1994) during the first few weeks after fledging. Regardless of its true adaptive significance, the process of sibling association suggests that raven juveniles possess the ability to recognize close relatives. Sibling recognition in turn may function to help prevent inbreeding, especially in the absence of other inbreeding avoidance mechanisms.

The argument could be made that observations of sibling association are spurious. They could be interpreted as resulting instead from juvenile dispersal to the nearest clumped resource or mere association based upon wearing patagial tags. It is generally true that juveniles dispersing from natal territories tend to join the vagrant flock at the nearest communal resource. However, this is not always the case. Dispersing juveniles are often observed at more distant communal resources, and siblings regularly join separate flocks. Moreover, the probability of observing siblings in close spatial proximity by chance alone, even when joining the same flock, are slim. The members of vagrant flocks typically spread over several hectares while foraging on communal resources.

Vagrant flocks typically contain several tagged juveniles, so siblings have the opportunity to interact with a number of unrelated tagged juveniles. Because only related individuals tend to associate, it is unlikely that juveniles associate merely because they wear patagial tags.

Numerous variables affect bird movements (Heinrich et al. 1994) and interspecific variation complicates the likelihood for development of a unifying theory. Recent authors (Newton 1991,Verhulst 1997) suggest that problems related to dispersal models may stem from the treatment of dispersal as a fixed trait while ignoring the ability of animals to respond to environmental cues. Dispersal behavior may be more highly influenced by behavioral plasticity than previously acknowledged (Verhulst 1997). Researchers argue that individuals use multiple cues to maximize their fitness during dispersal and recent development in this field treat dispersal as an optimization process rather than as a fixed trait. Individuals may readily optimize their dispersal behavior in response to environmental cues such as the distribution of resources or conspecifics (Wheelwright and Mauck 1997). Similarly, Pusey and Wolf (1996) suggest that evidence supports the existence of kin recognition in many outbreeding species. If inbreeding avoidance is the ultimate cause for dispersal, then selection should favor the evolution of mechanisms for kin recognition. However, it is likely that no single mechanism can explain the motivations for dispersal either within a population at a given time or within a given species (Clarke et al. 1997). A comprehensive understanding of dispersal may only come from considering a combination of models.

In conclusion, raven juvenile movements resemble an optimization process , rather than a strictly patterned behavior. They appear to maximize their fitness by tracking resources in the environment and display the potential for avoiding future inbreeding by appearing to possess an ability to recognize close relatives. The relative philopatry of raven juveniles and their selection of resource-rich anthropogenic habitat uphold the predictions of resource competition models of natal dispersal, and support observations of increasing raven numbers due to anthropogenic resource subsidies. Dispersal models based on inbreeding avoidance assume a genetic component to dispersal behavior. Results from a sib-sib regression of mean movement distance suggest low heritability for this trait. Behavioral models for natal dispersal such as Greenwood’s mating system model assume that dispersal evolved for the purpose of inbreeding avoidance. Raven juvenile movements did not show a sex-bias, therefore not supporting the predictions of Greenwood nor the inbreeding avoidance models. Locations of raven juveniles show that siblings tend to associate more than unrelated individuals. The function of sibling association is unknown, but provides evidence for sibling recognition which may play an eventual role in inbreeding avoidance.

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Table 2.1. Habitat availability and use for juvenile Common Ravens

Habitat type	Proportion of area	Proportion of use	Locations observed	Locations expected
Natural				
Mojave Creosote Bush Scrub	0.5209	0.005	7	729.79
Desert Saltbush Scrub	0.1654	0.037	52	231.71
Mojave Mixed Woody Scrub	0.0546	0.001	2	76.56
California Annual Grassland	0.0493	0.000	0	69.11
Alkali Playa Community	0.0348	0.000	0	48.75
Semi-Desert Chapparal	0.0258	0.000	0	36.17
Mojave Juniper Woodland	0.0154	0.001	1	21.58
Sagebrush Scrub	0.0039	0.000	0	5.40
Other	0.0018	0.000	0	3.15
Subtotal	0.8720	0.044	62	1222.22
Urban				
Commercial and services	0.0550	0.004	6	77.10
Residential	0.0518	0.439	615	72.52
Other Urban	0.0039	0.004	5	5.47
Industrial	0.0013	0.192	269	1.89
Subtotals	0.1124	0.639	895	156.97
Agricultural				
Irrigated hayfield	0.0082	0.058	81	11.52
Irrigated row and field crops	0.0064	0.004	6	8.96
Orchards, Vineyards, Nurseries	0.0008	0.004	6	1.16
Confined Feeding Operations	0.0001	0.251	351	0.17
subtotals	0.0156	0.317	444	21.81
total anthropogenic	0.1280	0.9557	1339	178.78
Grand totals	1.000	1.000	1401	1401.0

Table 2.2. Movements of juvenile Common Ravens in the western Mojave Desert.

	males (n=24)		females(n=15)			
movement variable	mean	s.e	mean	s.e	(t)	P value
homerange (km^2)	142	71	188	10	0.38	0.70
homerange diameter (m)	8890	2106	10380	3073	0.41	0.68
Movement Distance (m)	8584	1242	8846	1998	-0	0.97
Maximum Movement Distance (m)	17828	2320	18362	3627	0.13	0.90
Initial Movement Distance (m)	5778	1387	5984	1908	0.09	0.93
Distance Between Relocations (m)	2897	518	4100	1256	0.89	0.39
Velocity Between Relocations (m/day)	624	136	576	181	-0.2	0.83
Sheilds' criteria (m)*	19000		19000			
philopatric individuals	22		12			
dispersive individuals	2		3			

*Calculated as 10 x diameter of the mean nesting territory (Kristan and Boarman, in prep.)

Table 2.3. Juvenile Common Raven Sibling Movements in the Western Mojave Desert

Nest	Cohort	Sib 1	Sex	Distance (m)	Sib 2	Sex	Distance (m)	Pairing
wcw48	2000	3e	m	9170	4e	f	10221	opposite sex*
jcs7	1999	l4	m	7032	l3	f	19990	opposite sex
jcs7	1999	l3	f	19990	l5	m	10059	opposite sex
wbk28	1999	n4	m	9767	n2	f	9696	opposite sex*
wbk28	1999	n3	f	27665	n4	m	9767	opposite sex
wbk87	1999	3s	f	9637	3r	m	3498	opposite sex*
tg12	1999	h1	f	1907	h4	m	1904	opposite sex*
wcw89	2000	7t	f	19964	7x	m	16161	opposite sex*
wcw9	2000	1y	f	3601	1x	m	4858	opposite sex
wcw9	2000	1x	m	4858	1w	f	16803	opposite sex
wbk5	2000	3z	m	10662	3m	f	10690	opposite sex*
							Opposite sex sibling mean: 10814	
wbk40	1999	c1	f	3572	c4	f	3249	same sex*
wbk28	1999	n2	f	9696	n3	f	27665	same sex
ka27	2000	2f	f	5961	2u	f	2018	same sex*
wcw85	2000	4m	f	6757	4p	f	7373	same sex*
wcw85	2000	4p	f	7373	4r	f	7953	same sex
wcw85	2000	4r	f	7953	4m	f	6757	same sex
gcg91	1999	x4	f	6293	x5	f	8214	same sex*
wcw9	2000	1w	f	16803	1y	f	3601	same sex*
jcs7	1999	l4	m	7032	l5	m	10059	same sex*
wcw1	2000	1g	m	10662	1h	m	10690	same sex*
pf3	1999	g4	m	15902	g1	m	21815	same sex*
gcg69	1999	4c	m	17401	3c	m	12750	same sex*
wcw1	2000	1h	m	7159	1g	m	7941	same sex*

* Indicates sibling pairs observed on the same day   Same sex sibling mean: 9717

Table 2.4. Association Between Juvenile Common Raven Siblings in the Western Mojave Desert

Sib pair	Sex	Nest	Yr	Date	Sibs (m)*	Non-sibs (m)*	Non-sib pair
V1, V2	f,f	WBK57	1999	7/1/1999	0	127	L4,C1
C1, C4	f,f	WBK40	1999	7/19/1999	0	23437	H4,G4
4C, 3C	m,m	GCG69	1999	9/6/1999	0	0	H4, J1
2F, 2U	f,f	KA27	2000	7/5/2000	0	15817	1R,S2
3D, 2D	f,m	WCW31	2000	7/9/2000	0	165	L3, 1i
3G, 2S	f,f	WBK87	2000	7/13/2000	0	12488	2F,2N
L4, L5	m,m	JCS7	1999	10/22/2000	0	29237	3M,1Y
7T, 7X	f,m	WCW89	2000	10/23/2000	0	41950	N2,1i
3E, 4E	m,m	WCW48	2000	9/7/2000	103	193	3X,6E
N4, N2	m,f	WBK28	1999	7/17/2000	175	14368	1V, 4M
3S, 3R	f,f	WCW13	2000	7/31/2000	231	827	1H,3Z
4M, 4P	f,f	WCW85	2000	7/27/2000	296	12802	3P,6F
4G, 4V	f,f	WCW90	2000	11/12/2000	348	29536	N3,2N
1H, 1G	m,m	WCW1	2000	7/11/2000	1110	728	N3, 3Z
H1,H4	f,m	TG12	1999	9/3/1999	1785	917	L3,G1
6G, 6D	m,m	TG15	2000	8/18/2000	2468	23725	P4, 3X
X4, X5	f,f	GCG91	1999	7/10/1999	4195	4146	H4,C1
E7, E1	m,f	WBK30	1999	8/16/1999	4455	40365	H1,G1
1W, 1Y	f,f	WCW9	2000	9/15/2000	12699	24451	N4,1i
4Q, 2M	m,m	WBK78	1999	9/7/2000	14167	0	4E,1C
3Z, 3M	m,f	WBK5	2000	11/12/2000	25591	29715	4T,3P
G4, G1	m,m	PF3	1999	8/16/1999	40365	0	H4,J1

* A value of zero signifies individuals were observed less than 1m apart

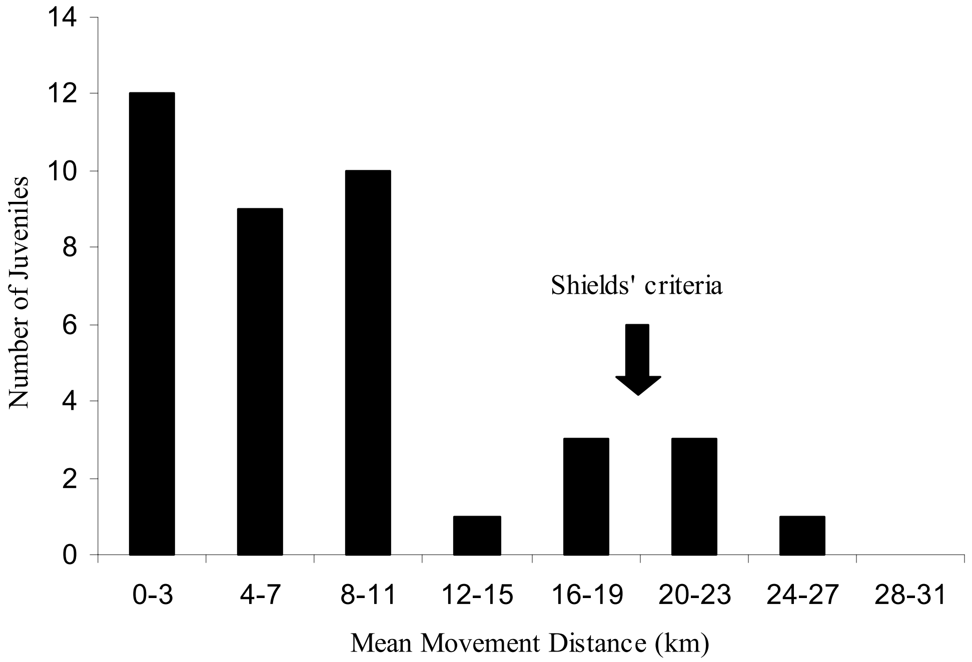

FIGURE 2.1. The distribution of mean movement distances for juvenile Common Ravens.

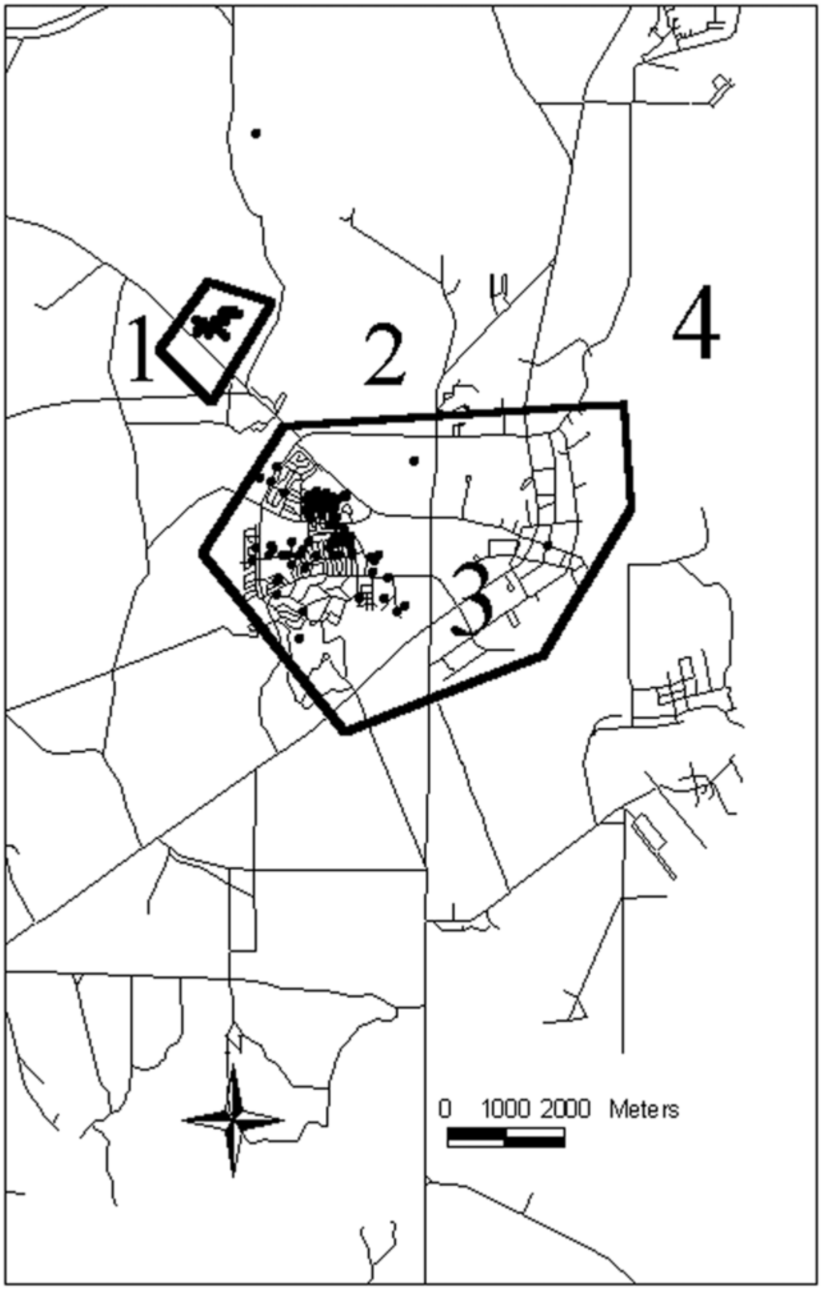

FIGURE 2.2. An example of habitat selection for juvenile Common Ravens. The black dots represent juvenile locations on a portion of the study site near Edwards, California between June 1999 and July 2001. The heavy black line outlines anthropogenic habitat (3), including the Edwards landfill (1), from natural habitat such as Mojave creosote bush scrub (2). The vast majority of locations occur within anthropogenic habitat. The thin black lines are roads. Edwards Dry Lake, where the space shuttle lands, is nearby (4).

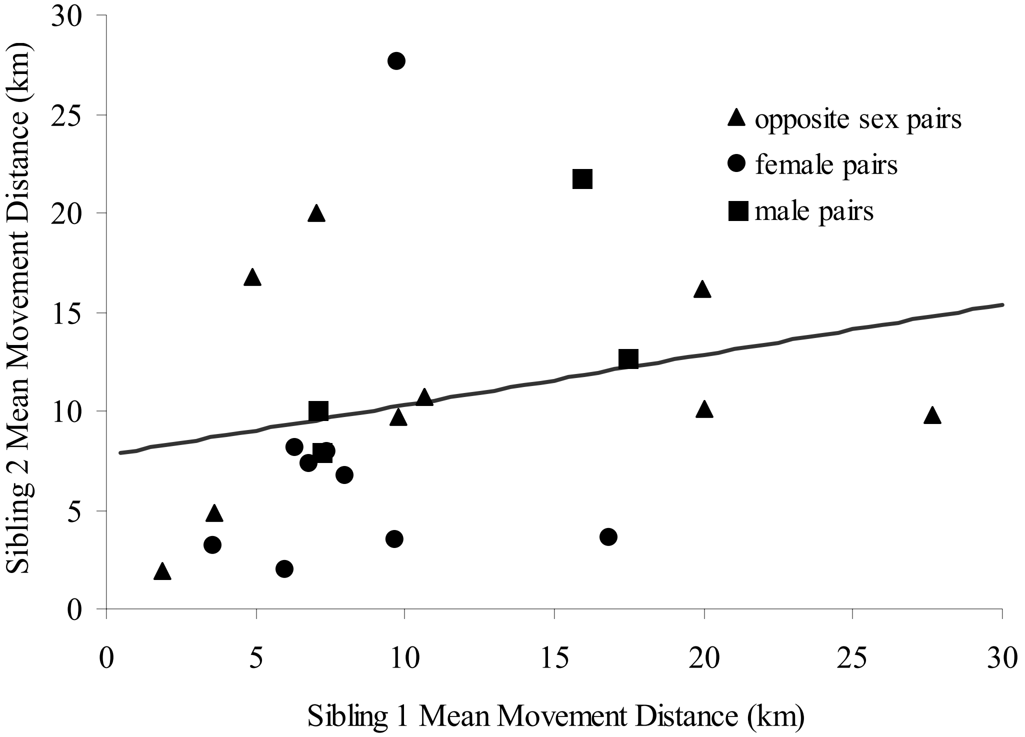

FIGURE 2.3. Regression of mean movement distances for pairs of sibling juvenile Common Ravens with 5 or more locations outside the natal territory.

CONCLUSION

Increased juvenile survival is an important demographic influence of anthropogenic resources on the west Mojave raven population. The positive correlation between juvenile apparent survival and proximity to NAR support the hypothesis that anthropogenic resources contributes to juvenile survival. By selecting nest sites near anthropogenic resources, nesting adult ravens probably reduce the physiological costs of breeding and provide more resources to their offspring. Mark-recapture analyses suggest that the influence of nest proximity on juvenile survival extends several months into a juvenile's first year.

There is a general lack of fit between the predictions of the mating system model and the observed patterns of raven juvenile movements. A female bias in movements is the major prediction of this model. Various explanations exist for this general lack of fit. The model itself may be inaccurate in its treatment of dispersal behavior as a fixed trait. The phenology of dispersal behavior provides another possible explanation. The full expression of raven sexual dimorphism in dispersal may not occur during juvenile movements prior to breeding, but only when individuals begin to establish breeding territories. However, concurrent studies of adult ravens in the same study site suggest that juvenile and adult movements are similar.

Inbreeding avoidance models of dispersal predict movements structured to prevent inbreeding. Evidence of sibling association support this prediction. The proximity of dispersed siblings suggests the possibility of sibling recognition. Based upon reports of raven intelligence (Koehler 1951, Heinrich 1995b), it is not unreasonable to accept the possibility that ravens recognize conspecifics on an individual basis. Sibling recognition in ravens is probably related to inbreeding avoidance rather than resource-sharing.

The general prediction of the resource competition model is that raven juvenile movements should track resource availability. The vast majority of raven relocations occurred in resource-rich anthropogenic habitats. This pattern of habitat selection combined with the relative philopatry of juvenile ravens upholds the resource competition model predictions. It appears that little motivation exists for juvenile ravens to become dispersive because sufficient resources already exist within the study site.

Numerous variables affect bird movements (Heinrich et al. 1994) and intraspecific variation complicates the likelihood for development of a unifying theory. More recent authors (Newton 1991,Verhulst 1997) suggest that problems related to dispersal models may stem from the treatment of dispersal as a fixed trait while ignoring the ability of animals to respond to environmental cues. Dispersal behavior may be more highly influenced by behavioral plasticity than previously acknowledged (Verhulst 1997). Individuals may readily optimize their dispersal behavior in response to environmental cues such as the distribution of resources or conspecifics (Wheelwright and Mauck 1998). However, it is likely that no single mechanism can explain the motivations for dispersal either within a population at a given time or within a given species (Clarke et al. 1997). A comprehensive understanding of dispersal may only come from considering a combination of models.

This study supports the hypothesis that anthropogenic resources contribute towards the growing western Mojave raven population. In areas like the western Mojave where resource levels are naturally low, the impacts of artificial resources can be dramatic. Since human influence in the region will likely increase, land managers should expect raven numbers to grow in concert with the growing human presence, unless raven access to anthropogenic resources is diminished. In turn, the negative impacts of Ravens on other wildlife should increase as well. Research regarding raven commensalism with humans represents the most effective approach to finding viable long-term conservation solutions.

APPENDIX 1: Model selection and parameter estimation in Program MARK

AICc = -2log Likelihood + 2K + 2K(K + 1)/(n-ess - K - 1) where K is the number of parameters and n-ess is the effective sample size. Delta AICc is the difference between consecutive models. The QAICc Weight of a model = exp(-1/2 * Delta QAICc of the model) / [sum for all models of exp(-1/2 Delta QAICc)] . The sum of the QAICc weights is 1, and these weights are used in model averaging. Deviance is defined as the difference in -2log(Likelihood) of the current model and -2log(Likelihood) of the saturated model. The saturated model is the model with the number of parameters equal to the sample size.