

## DIFFERENCES IN SPACE USE BY COMMON RAVENS IN RELATION TO SEX, BREEDING STATUS, AND KINSHIP

WILLIAM C. WEBB<sup>1,3</sup>, JOHN M. MARZLUFF<sup>1</sup>, AND JEFF HEPINSTALL-CYMERMAN<sup>2</sup>

<sup>1</sup>University of Washington, College of the Environment, Box 352100, Seattle, WA 98195-2100

<sup>2</sup>University of Georgia, Warnell School of Forestry and Natural Resources, 108 East Green Street, Athens, GA 30602-2152

**Abstract.** Group differences in avian space use relate to group differences in resource use and demographic parameters. However, studies that consider year-round, intraspecific variation in the space use of noncooperatively breeding species are relatively rare. A greater understanding of factors relating to intraspecific variation in space use is especially important for managing human-subsidized predators, such as the Common Raven (*Corvus corax*). We hypothesized that sex, sociality, and the distribution of bonanzas of food should influence year-round space use by breeding and nonbreeding Common Ravens on the Olympic Peninsula of Washington State. We detected differences in space use between breeders and nonbreeders but not between the sexes. Breeders shared little space with their neighbors and displayed strong site fidelity, except in the fall and winter or after the death of a mate, when some breeding ravens moved extensively. Nonbreeders moved widely, were more gregarious, and their home ranges intersected a greater proportion of communal food resources than did those of breeders. Breeders shared little space with their adult neighbors, but they shared more space with nonbreeders when communal food resources fell within their territories. Pair bonds were broken only by the death of a partner, which in some cases was followed by extensive movements by the surviving adult prior to pairing with a new mate or settling in a new breeding territory. This study is the first to consider the space use of both nonbreeding and breeding Common Ravens in the same population simultaneously.

**Key words:** Common Raven, *Corvus corax*, dispersal, kinship, movements, space use, territoriality.

### Diferencias en el Uso del Espacio por *Corvus corax* con Relación al Sexo, Estatus de Cría y Parentesco

**Resumen.** Las diferencias de grupo en el uso del espacio por las aves se relacionan con las diferencias de grupo en el uso de los recursos y los parámetros demográficos. Sin embargo, los estudios que consideran la variación intra-específica a lo largo del año en el uso del espacio por parte de especies con reproducción no cooperativa son relativamente raros. Es importante lograr un entendimiento más profundo de los factores relacionados a la variación intra-específica en el uso del espacio para manejar a los depredadores subsidiados por los seres humanos, como *Corvus corax*. Hipotetizamos que el sexo, la socialidad y la distribución de las bonanzas de alimento deben influenciar el uso del espacio a lo largo del año por parte de individuos reproductivos y no reproductivos de *Corvus corax* en la Península Olímpic del Estado de Washington. Detectamos diferencias en el uso del espacio entre individuos reproductivos y no reproductivos pero no entre sexos. Los individuos reproductivos compartieron poco espacio con sus vecinos y mostraron una fuerte fidelidad al sitio, excepto en el otoño y el invierno o luego de la muerte del compañero, cuando algunos individuos reproductivos se desplazaron ampliamente. Los individuos no reproductivos se desplazaron ampliamente, fueron más gregarios y sus rangos de hogar interceptaron una proporción más grande de recursos alimenticios comunales que los de los reproductivos. Los individuos reproductivos compartieron poco espacio con sus vecinos adultos, pero compartieron más espacio con los individuos no reproductivos cuando los recursos alimenticios comunales cayeron dentro de sus territorios. Los lazos de pareja se rompieron sólo por la muerte de la pareja, lo que produjo en muchos casos que el superviviente se desplazara enormemente antes de encontrar una nueva pareja o un nuevo territorio reproductivo. Este estudio es el primero en considerar simultáneamente el uso del espacio de individuos no reproductivos y reproductivos de *C. corax* en la misma población.

## INTRODUCTION

Understanding the factors influencing intraspecific space use is important because variation in space use relates to differences in resource use, survival, and reproduction (Marzluff et al.

2004). Factors related to intraspecific variation in avian space use include age (Gustafsson 1988, Sol et al. 2000, del Mar Delgado et al. 2009) and sex (Matthysen 1999, Marra 2000, Safi et al. 2007). In species that establish dominance hierarchies, older birds usually dominate younger individuals (Partridge

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<sup>3</sup>E-mail: [webb@u.washington.edu](mailto:webb@u.washington.edu)

and Green 1985, Catterall et al. 1989, Sol et al. 2000), and in sexually dimorphic species, individuals of the larger sex usually dominate (Selander 1966, Aulén and Lundberg 1991). Social interactions between individuals, including behaviors such as territoriality (Stamps 1994), also influence space use within avian populations (Gauthreaux 1978, Wunderle 1991, Griesser et al. 2007). Kinship may also influence space use, for example, during cooperative breeding (Hatchwell 2009), during the fledgling-dependence period (Matthysen et al. 2010), and during natal dispersal (Matthysen et al. 2005). Resource specialization due to morphological differences (Phillips et al. 2004, Catry et al. 2005) or different nutritional requirements (Safi et al. 2007) also sometimes relate to differences in intraspecific space use.

The Common Raven (*Corvus corax*) is a wide-ranging generalist occurring in many biomes of the Northern Hemisphere. Different aspects of space use, behavior, and demography of breeding or nonbreeding ravens have been studied separately (Boarman and Heinrich 1999). Breeding ravens (hereafter, “breeders”) use the same year-round territory for feeding, mating, and nesting (type A territory; Nice 1941, 1943). Breeders dominate intruding conspecifics, and defend any food found on their territory (Marzluff and Heinrich 1991). Breeders rarely travel far from their territories, at least during the reproductive season (Marzluff and Neatherlin 2006). In contrast, nonbreeders, mainly juveniles and subadults (hereafter, “nonbreeders”), travel widely in search of concentrated food resources known as “food bonanzas” (Heinrich 1988a, Restani et al. 2001). Nonbreeders recruit conspecifics and share food bonanzas in order to prevent any resident breeders from monopolizing these resources (Marzluff et al. 1996, Wright et al. 2003). Large groups of mostly nonbreeders, sometimes numbering in the hundreds (Stahler et al. 2002, Marzluff et al. 1996), congregate at food bonanzas such as roadkill, carcasses left by hunters, landfills, and farms (Roth et al. 2004, Boarman et al. 2006, Webb et al. 2011a).

Studies that consider year-round, intraspecific variation in space use are rare, since following individually marked birds of known sex, age, and breeding status within a population is often difficult. Most studies of avian space use, including previous studies of the Common Raven (e.g., Roth et al. 2004, Webb et al. 2004), consider just one segment of the population (e.g., juveniles) or a restricted period (e.g., fledgling dependence). Simultaneous study of multiple groups within populations may improve our understanding of intraspecific variation in space use. Variation in the Common Raven’s use of space has not been previously studied by intensive following of breeding and nonbreeding, free-ranging, individually marked birds from the same population.

Understanding raven behavior and demography has become increasingly important as concerns for the potential negative effects of raven predation on sensitive species has increased in concert with the increase in abundance of this synanthropic species in many regions of North America (Boarman 2003). As the human footprint intensifies, the increase of features such

as landfills, sewage plants, fish hatcheries, and ranches provide ravens with anthropogenic resource subsidies, termed “point subsidies” (Webb et al. 2004). Natural food bonanzas such as animal carcasses are ephemeral and require ravens to locate them, but point subsidies provide super-abundant, permanently renewed, spatially fixed resources. We investigated intraspecific variation in space use within a population of Common Ravens on the Olympic Peninsula of Washington State, where both natural and anthropogenic food subsidies for ravens occur. We hypothesized that sex, sociality, and the distribution of point subsidies should influence breeding and nonbreeding ravens’ space use year round. In order to evaluate our hypothesis, we investigated patterns of space use by ravens as they related to sex, breeding status, and kinship. In particular, we characterized juvenile dispersal, year-round ranging behavior of nonbreeders and breeders, as well as year-round range overlap between nonbreeders and breeders.

## METHODS

### STUDY AREA

Our study encompassed the north and western portions of the Olympic Peninsula (Fig. 1). Over the past 100 years, large tracts of old-growth temperate rainforest have been transformed, mostly by logging, into a heterogeneous patchwork of relatively young seral stands (Franklin and Dyrness 1988, Scott 1999). These managed forests are dotted by a small number of human settlements and intersected by large rivers, streams, logging roads, and few paved roads. A more detailed description can be found in Marzluff and Neatherlin (2006) and Webb (2010).

### GEOSPATIAL ANALYSES

To characterize movements and space use by ravens, we constructed geospatial layers combining land cover (vegetation types) and land use (anthropogenic elements). Using 1991 Landsat Thematic Mapper imagery (Green et al. 1993), we created year-specific land-cover layers with supervised classification and 30-m pixel resolution resampled to 25 m, screen-digitizing land-use categories from orthophotos (1994, 1998, 2000, 2004, 2005, 2006) and Landsat Thematic Mapper satellite imagery (2000, 2003, 2004). We considered all land-use and land-cover classes as mutually exclusive in their spatial extent.

We defined resources as the suite of physical and biological components in the environment that led to ravens’ occupancy of a particular place. This definition included the local physical characteristics that produced forest of varying seral development, as well as a variety of human land uses (“habitat,” Block and Brennan 1993, Jones 2001). Resources within the study site included indigenous, ephemeral food bonanzas that attracted large numbers of ravens (deer, elk, and salmon carcasses) and more reliable anthropogenic food sources such as roadside refuse, roadkill, and hunter-killed carcasses. In addition, certain human land uses in the region (e.g., livestock ranches, landfills) provided superabundant and dependable food for ravens. Unlike ephemeral food bonanzas, these spatially fixed anthropogenic subsidies provided

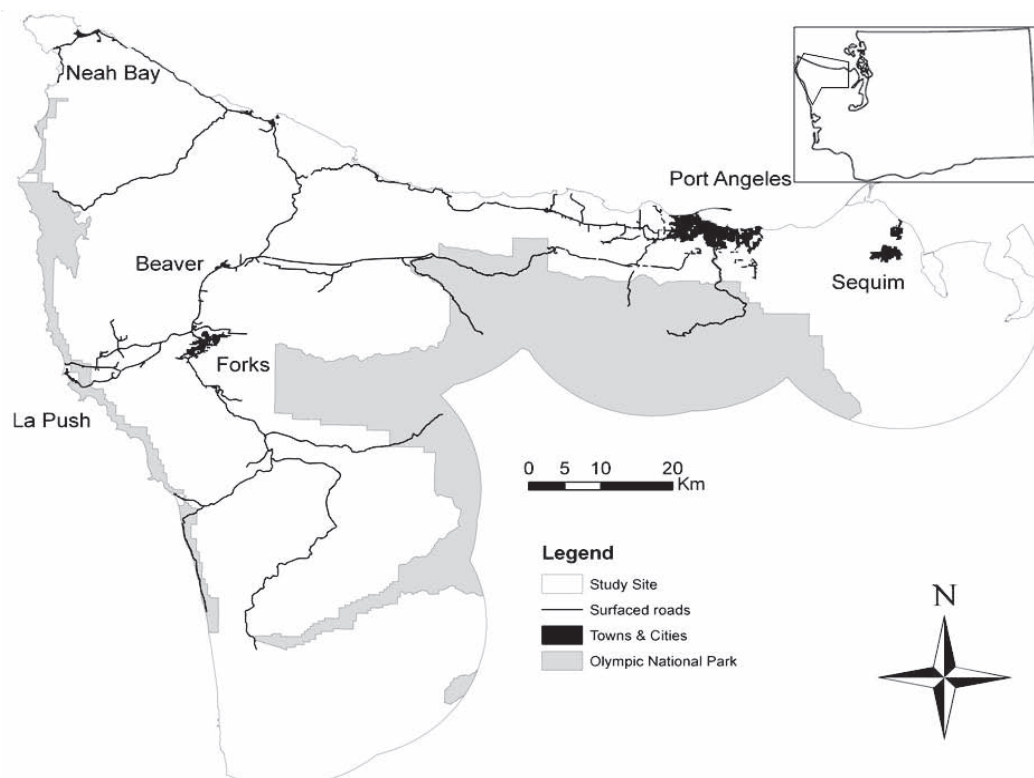


FIGURE 1. Map of the study site on the Olympic Peninsula of Washington State. Population centers include the cities of Port Angeles (population 18 982) and Sequim (5809) and the town of Forks (3120). Smaller population centers include the communities of Neah Bay (population 794), Beaver (633), and La Push (350).

consistently renewed food sources and are known as point subsidies (Webb et al. 2009).

#### CAPTURE AND MARKING

Between December 2002 and August 2005, we captured 60 ravens (22 juveniles 35 adults, and 3 subadults) with a remote-controlled portable net launcher (Coda Enterprises, Ltd.). We measured and color-banded each raven with a unique combination of plastic color bands and an aluminum U.S. Fish and Wildlife Service band. Each raven was outfitted with a backpack-mounted radio transmitter (Buehler et al. 1995) weighing 27 g (Advanced Telemetry Systems, Isanti, MN) with a projected lifespan of 40 months. We used a combination of plumage, mouth lining, and breeding behavior (Pyle et al. 1997, Heinrich and Marzluff 1992) to classify the age and breeding status of trapped ravens. Juveniles were birds of known age that had fledged from and were trapped within known territories during the breeding seasons of 2003 (6 juveniles), 2004 (7 juveniles), or 2005 (9 juveniles). Subadults were unpaired individuals of breeding age, as indicated by black mouth color (Heinrich and Marzluff 1992). Breeders were trapped in their territories, and subadults were trapped opportunistically during efforts focused on trapping breeders and their offspring. Since juveniles and subadults range similarly (Heinrich et al. 1994), we pooled these two nonbreeding

groups for statistical analyses. We used molecular techniques to sex the birds, sampling two small growing feathers from each individual and using a PCR reaction that amplifies the CHD gene fragments on the W and Z chromosomes (Griffiths et al. 1998).

#### RADIO TELEMETRY

We tracked ravens continuously from May 2003 to March 2007 (47 consecutive months) with an ATS R2000 portable scanning radio receiver (ATS, Isanti, MN, USA) attached to 4-element Yagi antennas on a truck and 2- and 3-element Yagi antennas held by hand. On one occasion during the middle of the study in May 2005, to search for missing birds within 200 km of the perimeter of the study, we used dual wing-mounted 3-element Yagi antennas attached to an airplane. During the spring and summer (March–September), we tracked ravens several times per month, during the rest of the year, for one week per month, until each bird died or its transmitter stopped functioning (mean 2.44, range 0.77–5.11 locations month<sup>-1</sup>). We followed two surviving juveniles and one subadult from the 2003 cohort with functioning transmitters into their fifth year, and three juveniles from the 2004 cohort into their fourth year, and three juveniles from the 2005 cohorts into their third year.

We used homing techniques (White and Garrot 1990) and triangulation to estimate ravens' locations (no more than once per

bird per 24 hr; Otis and White 1999). Typically we saw the tagged bird and recorded its location with a hand-held GPS unit. When this was not possible because of dense vegetation or the remoteness of parts of the study area, we triangulated (199 locations, or 6% of the total). We based estimates by triangulation on at least three compass bearings forming angles of 45–110°, obtained within 5 min of each other. Telemetry locations and error polygons were generated with LOCATE II (Nams 1990), and locations with error polygons >2.0 ha (a circular area with radius 80 m) were omitted. The detectability of transmitter signals ranged from 1 to 50 km, depending upon the search mode (vehicle, foot, or aircraft), topography, and behavior of the individual birds. Twice annually (once in the spring and fall) we used vehicle-based radio-receiving equipment to search extensively outside the study site by driving up to 150 km beyond its perimeter.

We used vocal and visual cues to estimate the abundance of conspecifics within a 100-m radius of each radio-tagged bird. We verified distance radii for abundance estimates in the field with a hand-held GPS unit. On the basis of consistently high raven abundance at locations providing the birds dependable sources of food, we identified eight communal point subsidies within the study area: three livestock ranches, two waste facilities, one hobby farm, a fish hatchery, and a prison. To compare the relative importance of point subsidies for breeders and nonbreeders, we quantified the volume of intersection of the home ranges of breeders and nonbreeders with a 500-m buffer around each communal point subsidy.

#### SPACE-USE ANALYSES

An important measure of avian space use is the home range. We estimated ravens' home ranges as the two-dimensional extent of their three-dimensional utilization distributions (UDs) on the basis of point locations in ArcGIS 9.2 with the Home Range Tools (HRT) for ArcGIS 9.x (Rodgers et al. 2005) by implementing a 99% fixed-kernel estimator (Seaman et al. 1999). We estimated home ranges for ravens with 10 or more locations and for juvenile ravens with 10 or more locations of dispersal outside the natal territory. Consistent with previous findings with this species (Webb et al. 2009), we established that this definition of adequate sample size was sufficient to quantify relative differences in space use (Garton et al. 2001) by determining that there was no positive correlation between sample size and home range ( $R^2 = 0.01$ ,  $P = 0.49$ ) (Webb et al. 2011a). Using an objective criterion that minimizes the risk for oversmoothing or undersmoothing (Worton 1989, Sain et al. 1994), we selected the smoothing parameter by first buffering each location by 625 m. This scale relates to data collection (the square of the minimum resolution of spatial data, 25 m), forest management, and reflects a priori distances thought relevant to ravens' behavior and their sensory abilities. We then generated provisional home ranges with different proportions of HREF until the provisional home range with a continuous outer isopleth closely approximated the 625-m buffer around the largest grouping of locations for each individual. We chose the smoothing parameter based on the proportion of HREF associated with

the closest-matching provisional UD. We generated individual home ranges for each raven and separate sets of group home ranges for breeders and nonbreeders. We calculated a group home range for each individual (the focal individual) by using locations for all members of the group (breeding or nonbreeding) except the focal individual. We used a two-factor ANOVA to compare average home range area across all years between birds of different sex, different breeding status, and their interaction.

In a tagged population, the distances birds move between locations where they are radio-tracked represent another important aspect of their space use. Therefore, in addition to quantifying home ranges, we measured three indices of breeders' and nonbreeders' movement, including the median, initial, and maximum distance ravens were located from the location where they were initially trapped. We defined a breeder's extraterritorial movements as any movement farther from the location of initial trapping than the diameter of the largest contiguous isopleth of its home range.

#### STATISTICAL ANALYSES

Using two-factor ANOVAs for breeders and nonbreeders (subadults with >10 locations and juveniles with >10 post-dispersal locations), we compared movement indices by sex and breeding status, as well as their interaction. We defined natal dispersal as the movements of juvenile ravens between their natal territory and first breeding territory (Greenwood 1980). Although there are few records of their natal dispersal, most ravens probably do not breed until their fourth year or later (Webb 2010). Therefore, we defined juvenile dispersal as the subset of movements juvenile ravens made outside their natal territory prior to natal dispersal. We defined a juvenile's initial movement distance as its first dispersal location outside its natal territory. Based upon observations of territorial behavior of breeders, this area usually extended 0.5 to 1.0 km from the nest. We restricted our analyses of space use between relatives to known relationships between juveniles, broodmates, and their parents established by observing reproductive behavior.

Since our study was much shorter than the lifespan of many ravens, and we were unable to radio-tag every individual within each family group, our knowledge of family relationships between birds was incomplete. We assumed that all known parent-offspring relationships were genetic since extra-pair copulation is rare among ravens (Boarman and Heinrich 1999), and we did not observe evidence of this behavior. To characterize the duration of the bonds between adults and their offspring, we also investigated the degree of post-dispersal association between juveniles, broodmates, and their parents by quantifying the frequency and timing of locations recorded inside the natal territory after initial dispersal from the natal territory.

The amount of space conspecifics share is an important characteristic of space use and provides insight into social behavior. We quantified space-sharing by ravens by the index statistic volume of intersection (VI) (Seidel 1992, Kernohan et al. 2001). The VI index determines the proportion of an animal's UD which is shared, and



ranges from 0 for no overlap to 1 for complete overlap. In calculating VI, we analyzed data for each year separately. We estimated the VI between adult ravens occupying neighboring territories to quantify the extent of space sharing by neighboring territory holders. To characterize the degree of association between nonbreeders and adults, we compared the VI that individual nonbreeders and individual breeders shared with the population of nonbreeders. To determine whether broodmates preferentially associate, we compared the VI shared by broodmates to the VI shared between those same birds and the rest of the unrelated nonbreeding population.

We defined neighbors as any pair of unrelated breeders with their largest contiguous isopleths  $\leq 625$  m apart, a quantity related to the spatial scale of analysis, and also too narrow for an intervening third pair's home range. Although most breeding ravens' home ranges ( $n = 34$ ) lay near at least one neighbor (range 0–7), the density of tagged neighbors numbered less than the geometrical hypothetical maximum of 12 neighbors from 6 adjacent territories (assuming roughly hexagonal territories, Wilson 1975:272). We estimated the VI shared by neighboring breeding ravens by regressing the mean number of neighboring breeding ravens for each breeding raven across years with the mean VI with the home range from the population of unrelated breeding ravens across years.

Unless otherwise indicated, we used SPSS (SPSS 2004) for our analyses. We applied  $P < 0.05$  as the significance level along with two-tailed tests. We checked for normality with the Kolmogorov–Smirnov goodness-of-fit test, and tested for homogeneity of variance with Levene's test. To meet the assumptions of general linear models, we used arcsin or natural log transformations in all parametric analyses. For all analyses, we pooled subadults with juveniles into the class of nonbreeders. We analyzed data for an individual separately if it moved to a new territory or transitioned to a new breeding status. The values reported under Results are means  $\pm$  SD.

## RESULTS

### RESULTS OF RADIO TRACKING

We obtained 3215 locations by radio-tracking ravens from February 2003 until June 2007 (Table 1). Four juveniles perished before we obtained 10 locations outside their natal territories, and another disappeared before the sample reached 10, so we excluded these 5 individuals from relevant analyses. Of these 60 birds (including 4 analyzed separately after they moved to a new territory or transitioned to a new breeding status) we recorded 1–9 locations for 5, 10–29 locations for 12, 30–49 locations for 17, 50–69 locations for 20, and  $\geq 70$  locations for 10. The length of time that individual birds were followed after they were radio-tagged ranged from 67 to 1455 days ( $678 \pm 365$  days).

### FATE OF TAGGED RAVENS

Through the end of the study, 25 ravens died, 4 disappeared, 2 dropped their transmitters while still alive, 10 transmitter

batteries died while the birds were still alive, and 19 remained alive with functioning transmitters. No individuals were known to have left the study area. Aside from 9 deaths of unknown cause, the causes of mortality and their frequency included predation by owl or raptor (7), shooting (6), broken wing (1), crushed by falling tree (1), and entangling of the transmitter harness in a tree canopy (1). Given breeders' strong site fidelity, at least three cases of disappearance were likely shootings that also destroyed the transmitters and precluded recovery of the carcass.

We radio-tagged both members of 15 mated pairs, and among 8 of these, one member (3 males, 5 females) perished prior to its mate. All 5 males remated by the following breeding season and remained in the same territory, although one male temporarily moved extensively, as expected for a nonbreeder (located 7.2–20.2 km outside his territory), between October and February near the time of his mate's death in December 2005. He could not be found in March but reappeared back in his territory in April 2006 with a new mate. Two of the females remated by the breeding season following the deaths of their mates; one remained on the same territory, while the other settled in an adjacent territory after a brief period of extensive movements that lasted 5 weeks, during which she was located up to 16 km from the location of her initial trapping (Fig. 2). After her mate perished in August 2005, the third female left her territory in which she had fledged four offspring earlier that

TABLE 1. Locations of radio-tracking of breeding and nonbreeding Common Ravens on the Olympic Peninsula by year and season.

Year and season <sup>a</sup>	Locations ( <i>n</i> )	Unique ravens located ( <i>n</i> )	Mean and SD
2003			
Spring	32	9	3.56 $\pm$ 3.00
Summer	273	20	13.65 $\pm$ 5.87
Fall	115	19	6.05 $\pm$ 1.90
2004			
Winter	55	11	3.73 $\pm$ 0.65
Spring	193	20	9.65 $\pm$ 6.59
Summer	343	34	10.06 $\pm$ 6.95
Fall	116	29	4.00 $\pm$ 1.39
2005			
Winter	101	30	3.37 $\pm$ 1.38
Spring	449	45	9.98 $\pm$ 8.07
Summer	455	50	9.10 $\pm$ 4.69
Fall	162	41	3.95 $\pm$ 1.70
2006			
Winter	107	35	3.06 $\pm$ 1.41
Spring	350	37	9.49 $\pm$ 5.06
Summer	280	29	10.00 $\pm$ 6.42
Fall	99	28	3.54 $\pm$ 1.45
2007			
Winter	83	25	3.32 $\pm$ 1.18
Spring	12	10	1.50 $\pm$ 0.71

<sup>a</sup>Winter, January–March; spring, April–June; summer, July–September; fall, October–December.

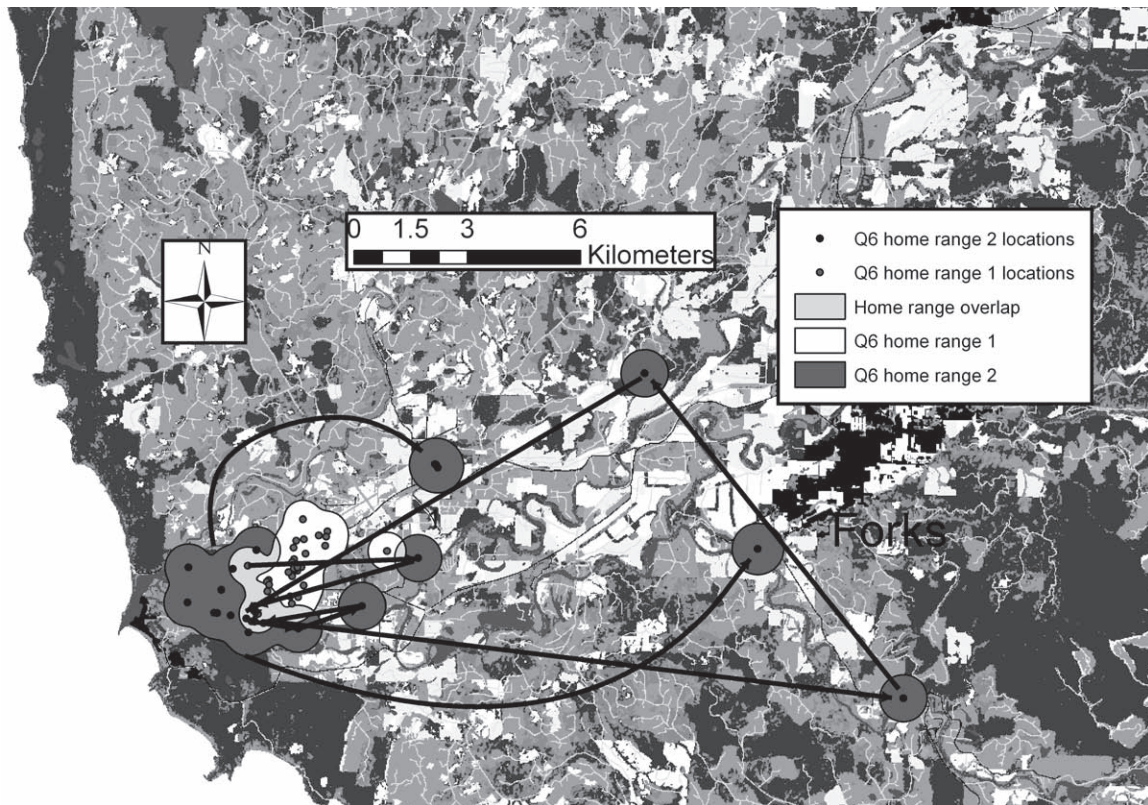


FIGURE 2. Locations of radio tracking and extent of home range (99% outer isopleth) of a breeding female Common Raven (Q6) trapped in April 2005 and followed until the end of the study in March 2007. This bird used home range 1 until her mate was shot in June 2006. After her mate's death, Q6 appeared to wander outside home range 1 (represented by dark straight lines) until settling in home range 2 with a new mate in August 2006. During the subsequent fall, Q6 was located on several occasions attending two separate food bonanzas several kilometers from the core of her territory (curved arrows). In both cases the food bonanzas were slaughtered cow carcasses that attracted several dozen ravens, including some that were radio-tagged.

season and did not breed through the end of the study, while two untagged breeders took residence in her former territory.

#### JUVENILE AND NATAL DISPERSAL

All 22 radio-tagged juveniles survived dispersal from their natal territory, although we did not obtain an accurate radio location for one of these until after it had died. We briefly detected a radio signal from this juvenile in August 2005 ~10 km south of the natal territory, which indicated the bird was flying rapidly, preventing recording of a reliable location. The signal for this juvenile was not detected again until May 2006 when we recovered its carcass 48.6 km from the nest. The mean date when juveniles were first observed outside their natal territories, 2003–2005, was 9 August ( $n = 21$ ), range 9 July–25 September. Of 17 juveniles with radio-tagged family members, in six cases a broodmate accompanied the dispersing juvenile, and in one case a breeding raven was with its offspring at the juvenile's first dispersal location. Once located outside the natal territory, most (16/22) juveniles did not return to their natal territories. The other six juveniles were sighted within their natal territory off and on for an additional period (range 5–26 days) after their initial dispersal.

Following independence, most (12/22) juveniles were located at least once inside their parents' home ranges (95% UD), but only as members of a large group attracted to communal resources—food bonanzas or point subsidies. One male juvenile that fledged in 2003 was located the majority of the time (83% of all locations) within his parents' home ranges, which also encompassed a point subsidy. The mean population frequency of juveniles' post-dispersal locations inside the natal territory was generally low ( $0.08 \pm 0.17$ , range 0–0.83). A male trapped as a juvenile in 2003 bred unsuccessfully in his fourth year but fledged two young in his fifth year in a territory 4.9 km from his natal territory where his father still resided. Another bird trapped in 2003, a female subadult of unknown age, fledged one young after 3 years in a territory 11.7 km from the location where she was trapped.

#### HOME RANGES AND SITE FIDELITY

The median distance of movement from the location of initial trapping was 0.9 km for breeders (range 0.3–2.5 km), and 9.9 km for nonbreeders (range 1.4–63.4 km, Table 2). Distances moved by nonbreeders were significantly greater than those

TABLE 2. Movement metrics for adult and nonbreeding ravens with >10 locations recorded on the Olympic Peninsula. Of the 60 ravens radio-tagged, five juveniles perished before we obtained 10 locations outside the natal territory. Data from four ravens were analyzed separately after these birds moved to new territories or transitioned between social classes. All values are means except for movement distance, which is the median.

Movement metric	♂ ( <i>n</i> = 30)		♀ ( <i>n</i> = 29)		<i>F</i>	<i>P</i>	Adults ( <i>n</i> = 38)		Nonbreeders ( <i>n</i> = 21)		<i>F</i>	<i>P</i>
	$\bar{x}$	SE	$\bar{x}$	SE			$\bar{x}$	SE	$\bar{x}$	SE		
Home range (ha)	1534	206	1275	212	0.11	0.74	859	176	1950	237	39.44	<0.01
Movement distance (m)	4487	1262	7572	2550	3.57	0.06	1309	238	14498	3226	131.04	<0.01
Maximum distance (m)	19512	4536	17701	3863	0.01	0.91	5497	763	42373	5083	133.02	<0.01
Initial distance (m)	3590	1285	6936	2041	1.04	0.31	1446	319	12861	2806	37.62	<0.01

traveled by breeders (all  $P < 0.01$ , Table 2). Neither sex nor the interaction between sex and breeding status explained significant variation in movement. Dispersed juveniles and subadults were located in significantly larger groups ( $9.04 \pm 4.54$ ) than were breeders ( $1.83 \pm 0.43$ ;  $t_{62} = -9.4$ ,  $P < 0.01$ ).

Overall, breeders maintained strong site fidelity (Fig. 3). However, on 55 occasions (2.52% of locations of breeding ravens), we encountered breeders farther from the site of their initial trapping than the maximum diameter ( $3887 \pm 941$  m) of the largest continuous isopleth within their respective UD. We describe these movements as extraterritorial because they were greater than the usual distance breeders moved and required traversing the home ranges of one or more unrelated breeders. We recorded 1 or 2 excursions by 7 breeders, 3–5 by 5, and 8–11 by 3. The majority (41/55) of extraterritorial movements occurred from October through January, and the majority (40/55) involved visits to food bonanzas. Six pairs of breeding ravens of which both birds carried radio tags accounted for a total of 22 extraterritorial movements, including three pairs in which both mates appeared together at least once for a total of six occasions.

Nonbreeders maintained larger home ranges than did breeders (two-way ANOVA,  $F_{3,55} = 39.4$ ,  $P < 0.01$ ), but home-range size did not differ by sex ( $F_{1,55} = 0.1$ ,  $P = 0.74$ ), nor was there a significant interaction for home-range area between breeding status and sex ( $F_{1,55} = 0.4$ ,  $P = 0.62$ , Table 2). The volume of the home range intersecting point subsidies buffered by 500 m was greater for nonbreeders ( $0.36 \pm 0.18$ ) than for breeders ( $0.06 \pm 0.14$ ; Wilcoxon rank sum test,  $W_5 = 816.5$ ,  $P < 0.01$ ).

#### SPACE SHARING

Breeding pairs of Common Ravens shared a high proportion of their space ( $0.75 \pm 0.09$ ). The area breeders shared increased with the number of neighbors [VI =  $0.009 + 0.006(\text{no. neighbors})$ ] (Fig. 3). Thus, given the hypothetical geometric maximum of 12 adult neighbors (Wilson 1975), the VI (95% CI) between adult neighbors is  $0.081 \pm 0.067$  (range 0.014–0.148). Nonbreeders shared greater VIs ( $0.40 \pm 0.22$ ; independent samples  $t$ -test,  $t_{57} = -3.9$ ,  $P < 0.01$ ) with the population UD of other nonbreeders than breeders shared

with the population of nonbreeders ( $0.07 \pm 0.09$ ). The VIs shared by broodmates did not differ from the VIs that broodmates shared with the population UD for unrelated juveniles (Wilcoxon signed-rank test:  $n = 11$ ,  $Z = -0.71$ ,  $P = 0.47$ ).

#### DISCUSSION

In our study, we evaluated the hypothesis that sex, sociality, and the distribution of point subsidies influence year-round space use by breeding and nonbreeding ravens. We detected no differences in space use between the sexes, but space use by breeders and nonbreeders differed substantially. Breeders departed their exclusive territories rarely. Nonbreeders moved widely, associated with a greater number of conspecifics, and used point subsidies more than did breeders. Family members sometimes associated outside the natal territory during juvenile dispersal, but this pattern was short-lived and did not extend beyond the juveniles' dependence period. Our results are valuable because space use relates to resource use, which influences survival and reproduction.

#### SEX, BREEDING STATUS AND SPACE USE

Sex-related differences in dispersal occur in most avian species (Greenwood 1980), but in the raven we observed no sex-related differences in home-range size or movement distances, including the mean, initial, and maximum distances at which ravens were located from locations of their initial trapping. This absence of sex-related differences in space use on the Olympic Peninsula agrees with results for breeding ravens in northern California (Roth et al. 2004) and juvenile ravens in the Mojave Desert (Webb et al. 2004). Moreover, on the Olympic Peninsula nonbreeders were considerably more mobile than breeders, such that home ranges and movement indices for nonbreeders were an order of magnitude larger than those registered by breeders.

#### NONBREEDERS' PHILOPATRY

Distances nonbreeders moved on the Olympic Peninsula and in the Mojave Desert of California (Webb et al. 2009) were considerably smaller than in some previous reports, which found



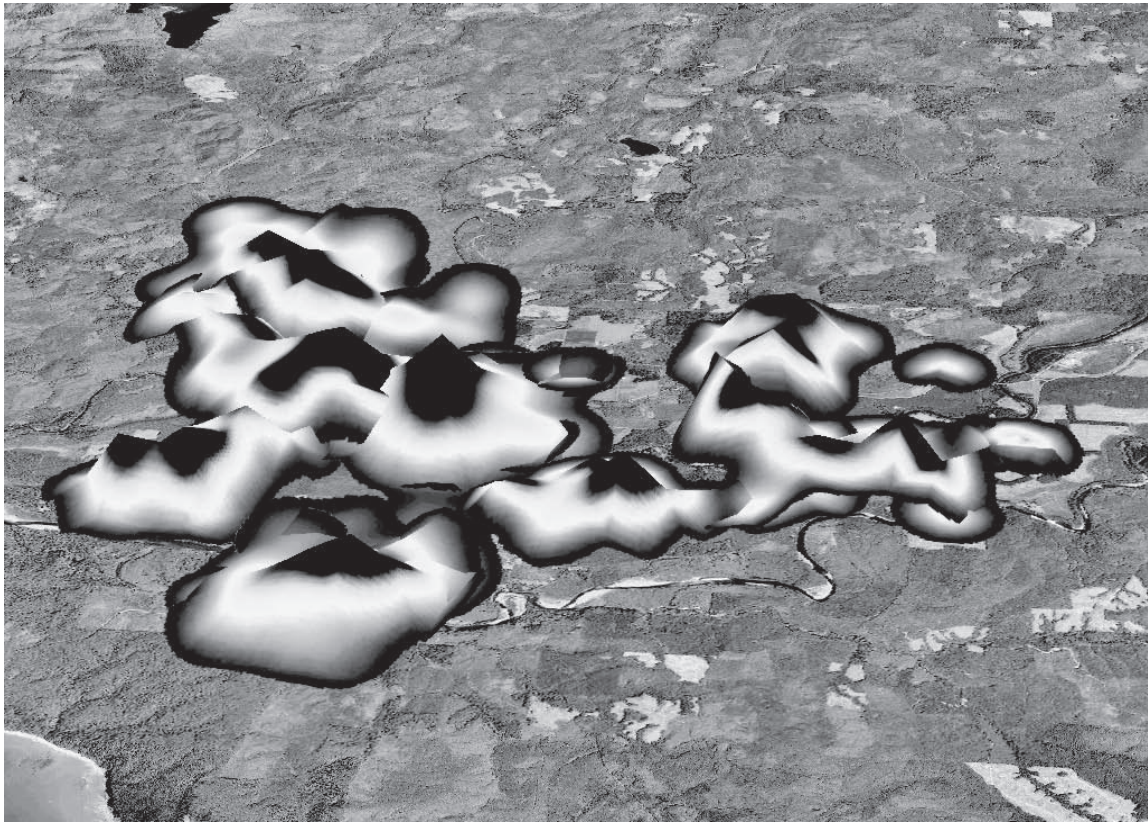


FIGURE 3. A portion of the study site depicting volume of intersections (VI) of utilization distributions (UD) of breeding Common Ravens with adjacent home ranges. Within a UD, taller-appearing portions represent regions of greater use.

nonbreeders wandering hundreds of kilometers (Bruggers 1988, Heinrich et al. 1994, Restani et al. 2001). Potential explanations for these differences in nonbreeders' philopatry might include geography, relative harshness of climate, seasonal migration patterns, and the relative abundance of point subsidies. For example, ravens in the Arctic and Greenland migrate seasonally (Restani et al. 2001), and ravens breeding in the Mojave Desert appear to relax their territoriality outside the breeding season (Webb et al. 2009). The philopatry of juvenile ravens on the Olympic Peninsula and in the western Mojave Desert is probably influenced in large part by geographic barriers. Our study area on the Olympic Peninsula is surrounded by the Pacific Ocean to the west, the Strait of Juan de Fuca to the north, and the Olympic Mountains to the east. The western Mojave Desert study area (Webb et al. 2009) is surrounded by three large mountain ranges to the north and west and relatively inhospitable open desert to the south and east. Differences in the density of point subsidies could also explain the apparent inconsistencies in nonbreeders' vagility reported in the scientific literature. Although those authors did not report on the density of point subsidies, it is likely that their study sites in Minnesota (Bruggers et al. 1988), New England (Heinrich et al. 1994), and Greenland (Restani et al. 2001) were characterized a lower density of point subsidies than existed on the Olympic Peninsula or in the western Mojave Desert (Webb et al. 2009). A high

density of point subsidies in the western Mojave Desert and the Olympic Peninsula might preclude the need for nonbreeders to search for less abundant natural but ephemeral food bonanzas scattered over much larger areas.

#### TERRITORIALITY AND SPACE USE

Avian territories cover a spectrum ranging from complete overlap with no apparent defense to exclusive domains with clearly defined, well-defended boundaries (Newton 1998). On the Olympic Peninsula, breeding ravens shared a high degree of space with their own mates, but they shared very little space with their breeding neighbors. Because food bonanzas attracted large numbers of nonbreeders, some breeders shared more space with the population of nonbreeders than they shared with their breeding neighbors. Some breeding ravens' territories encompassed point subsidies, at which radio-tagged nonbreeders were almost always present. Breeding ravens' UD's containing neither point subsidies nor food bonanzas did not attract unrelated radio-tagged nonbreeders. Breeding ravens' sharing space with the population of nonbreeders reinforces previous findings (Marzluff and Heinrich 1991) that nonbreeders gain access to resources through their numerical advantage rather than their competitive abilities.

Low space sharing by neighboring breeding ravens suggested that breeders maintained relatively sharp territorial



boundaries. One advantage to territoriality is priority access to resources (Newton 1998, Sunde and Bolstad 2004), and for ravens on the Olympic Peninsula, territoriality confers not only the opportunity to breed but also greater access to those resources associated with higher survivorship (Webb et al. 2011a). Although we do not know the mechanisms determining territorial boundaries, we sometimes observed radio-tagged breeders chasing their radio-tagged neighbors, untagged conspecifics, and raptors from their territories. Kin neighborhoods resulting in relaxed aggression represents one possible explanation for our limited observations of territorial aggression between breeding neighbors. Two records, one from our study and one in California (Webb et al. 2009) represent short-distance natal dispersal by two male ravens that moved widely as nonbreeders but eventually established breeding territories 4.9 and 2.6 km, respectively, from their natal nests. Although our data are anecdotal, genetically structured populations are widespread in non-cooperative species (Hatchwell 2009).

#### MATE FIDELITY

In socially monogamous birds, divorce rates between individuals that can re-pair with the previous year's mate vary greatly, from 0% in the Australian Raven (*Corvus coronoides*; Rowley 1973) and Wandering Albatross (*Diomedea exulans*; Tickell 1968), to almost 100% in the House Martin (*Delichon urbica*; Bryant 1979) and Great Blue Heron (*Ardea herodias*; Simpson et al. 1987). Ravens breeding on the Olympic Peninsula maintained long-term fidelity to their mates; we observed no instances of mate switching or divorce—the first empirical data supporting the long-held but previously unsubstantiated assertion (Heinrich 1988b) of life-long pair bonds in the Common Raven.

#### SITE FIDELITY

Site fidelity is widespread among birds (Newton and Marquiss 1982, Sedgwick 2004), and, as have previous studies (Marzluff and Neatherlin 2006, Roth et al 2004), we found that breeders rarely traveled outside their territories. Possible explanations for breeders' site fidelity included sufficient resources within defended territories, the potential costs of challenging defending ravens in other territories (Marzluff and Heinrich 1991), the risks of leaving their own territories undefended (Marzluff and Neatherlin 2006), and absence of knowledge of extraterritorial resources (Beletsky and Orians 1987). Although it is difficult to disentangle site fidelity and mate fidelity in a socially monogamous species such as the Common Raven that maintains a territory year round, the patterns of extraterritorial movements and territory abandonment suggested that site fidelity is weaker than mate fidelity. Access to food appeared to be an important driver of extraterritorial movements since most were made to food bonanzas in the late fall and winter, in some cases by radio-tagged mates traveling together. Access to potential mates appeared to motivate extraterritorial movements for at least two breeders (one male, one female) that wandered widely after their

mates died. The female wandered widely for several months before remating in a territory adjacent to her previous territory, and the male made similar movements before resettling in the same territory with a new mate. Females' slightly smaller size (Webb et al. 2011b) might have contributed to two females abandoning their territory after their mates died. One of these females (see above) bred again. The other moved widely through the remainder of the study while two unrelated and untagged breeders moved into her former territory.

#### KINSHIP AND SPACE SHARING DURING JUVENILES' DISPERSAL

Movements of parents and dependent offspring beyond the parents' normal range occur in several species (Nack and Anderson 2006, Matthysen et al. 2010, van Overveld et al. 2011). Our observations add to previous studies (Stiehl 1985, Webb et al. 2009) of the raven that reported broodmates and parents associating during initial movements outside the natal territory. In at least some instances (6/22 observations; 27%) juveniles' dependence dissolved over several weeks since some juveniles were observed back inside the natal territory after their initial dispersal. In some species, adults are less aggressive toward their offspring than toward unrelated juveniles even after offspring gain independence (Ekman et al. 1994, Pravosudova et al. 2001). After gaining independence, juvenile ravens did not share significantly more space with their broodmates or parents, thus providing no evidence for nepotism after juvenile dispersal and strong support that family cohesion dissolved during juvenile dispersal. Once independent, juveniles returned to their natal territories only as members of large groups attracted to a food bonanza.

#### NONBREEDERS' SPACE SHARING

Wandering flocks consisting of subordinate subadults are widespread among resident birds, especially those with a long life span and a population surplus (Newton 1998). After dispersing from their natal territories, we observed juvenile Common Ravens joining large flocks consisting primarily of other nonbreeders, as reported previously (Marzluff and Heinrich 1991, Webb et al. 2004). As a result, nonbreeders were significantly more gregarious than breeders and shared more space with other nonbreeders than they shared with breeders. These large groups of nonbreeders congregated at food bonanzas, both ephemeral ones like animal carcasses as well as permanent ones such as fish hatcheries and other point subsidies. Although some breeding ravens' home ranges included point subsidies, nonbreeders' UD's encompassed a greater proportion of communal point subsidies than did those of breeders.

#### SUMMARY

Our results provide new insight into the relationships between sex, kinship, breeding status, food bonanzas, and year-round space use by Common Ravens. We both added to the results of previous studies and contributed new information on the

patterns of space use within groups and between groups of breeding and nonbreeding ravens. Based upon our observations, worthwhile future questions to pursue include examining the role of kinship in natal dispersal, whether the degree of relatedness between neighboring breeders provides evidence for kin neighborhoods, and characterizing the frequency and magnitude of breeders' movements after the death of a mate. An improved understanding of the factors influencing space use by Common Ravens is important for managing the potential negative effects of this subsidized predator.

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## LITERATURE CITED

- AULÉN, G., AND A. LUNDBERG. 1991. Sexual dimorphism and patterns of territory use by the White-backed Woodpecker *Dendrocopos leucotos*. *Ornis Scandinavia* 22:60–64.
- BELETSKY, L. D., AND G. H. ORIANI. 1987. Territoriality among male Red-winged Blackbirds. *Behavioral Ecology and Sociobiology* 20:21–34.
- BLOCK, W. M., AND L. A. BRENNAN. 1993. The habitat concept in ornithology: theory and applications. *Current Ornithology* 11:35–91.
- BOARMAN, W. I. 2003. Managing a subsidized predator population: reducing Common Raven predation on Desert Tortoises. *Environmental Management* 32:205–207.
- BOARMAN, W. I., M. A. PATTEN, R. J. CAMP, AND S. J. COLLIS. 2006. Ecology of a population of subsidized predators: Common Ravens in the central Mojave Desert, California. *Journal of Arid Environments* 67:248–261.
- BOARMAN, W. I., AND B. HEINRICH. 1999. Common Raven (*Corvus corax*), no 476. In A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- BRYANT, D. M. 1979. Reproductive costs in the House Martin (*Delichon urbica*). *Journal of Animal Ecology* 48:655–675.
- BRUGGERS, D. J. 1988. The behavior and ecology of the Common Raven in northeastern Minnesota. Ph. D. dissertation, University of Minnesota, Minneapolis, MN.
- BUEHLER, D. A., J. D. FRASER, M. R. FULLER, L. S. McALLISTER, AND J. K. D. SEEGAR. 1995. Captive and field-tested radio transmitter attachments for Bald Eagles. *Journal of Field Ornithology* 66:173–180.
- CATTERALL, C. P., J. KIKKAWA, AND C. GRAY. 1989. Inter-related age-dependent patterns of ecology and behaviour in a population of Silvereyes (Aves: Zosteropidae). *Journal of Animal Ecology* 58:557–570.
- CATRY, P., R. A. PHILLIPS, AND J. P. CROXALL. 2005. Sexual segregation in birds: patterns, processes and implications for conservation, p. 351–429. In K. E. Ruckstuhl and P. Neuhaus [EDS.], *Sexual segregation: ecology of the two sexes*. Cambridge University Press, New York.
- DEL MAR DELGADO, M., V. PENTERIANI, V. O. NAMS, AND L. CAMPIONI. 2009. Changes of movement patterns from early dispersal to settlement. *Behavioral Ecology and Sociobiology* 64:35–43.
- EKMAN, J., B. SKLEPKOVYCH, AND H. TEGELSTROM. 1994. Offspring retention in the Siberian Jay (*Perisoreus infaustus*): the prolonged brood care hypothesis. *Behavioral Ecology* 5:245–253.
- FRANKLIN, J. F., AND C. T. DYRNESS. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, OR.
- GARTON, E. O., M. J. WISDOM, F. A. LEBAN, AND B. K. JOHNSON. 2001. Experimental design for radiotelemetry studies, p. 15–42. In J. J. Millsaugh and J. M. Marzluff [EDS.], *Radio tracking and animal populations*. Academic Press, San Diego.
- GAUTHREAUX, S. A. JR. 1978. The ecological significance of behavioural dominance. *Perspectives in Ethology* 3:17–54.
- GREEN, K., S. BERNATH, L. LACKEY, M. BRUNEGO, AND S. SMITH. 1993. Analyzing the cumulative effects of forest practices: where do we start? *Geographic Information Systems* 3:31–41.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–62.
- GRIESSER, M., M. NYSTRAND, S. EGGERS, AND J. EKMAN. 2007. Social constraints limit dispersal and settlement decisions in a group-living bird species. *Behavioral Ecology* 19:317–324.
- GRIFFITHS, R., M. DOUBLE, K. ORR, AND J. G. ROBERT. 1998. A DNA test to sex most birds. *Molecular Ecology* 7:1071–1075.
- GUSTAFSSON, L. 1988. Foraging behaviour of individual Coal Tits, *Parus ater*, in relation to their age, sex, and morphology. *Animal Behavior* 36:696–704.
- HATCHWELL, B. J. 2009. The evolution of cooperatively breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society B* 364:3217–3227.
- HEINRICH, B. 1988a. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*. *Behavioral Ecology and Sociobiology* 23:141–156.
- HEINRICH, B. 1988b. Why do ravens fear their food? *Condor* 90:950–952.
- HEINRICH, B., D. DAYE, T. KNIGHT, AND K. SCHAUMBURG. 1994. Dispersal and association among Common Ravens. *Condor* 96:545–551.
- HEINRICH, B., AND J. M. MARZLUFF. 1992. Age and mouth color in Common Ravens. *Condor* 94:549–550.
- JONES, J. 2001. Habitat selection studies in avian ecology: a critical review. *Auk* 118:557–562.
- KERNOHAN, B. J., R. A. GITZEN, AND J. J. MILLSAUGH. 2001. Analysis of animal space use and movements, p. 126–164. In J. J. Millsaugh and J. M. Marzluff [EDS.], *Radiotelemetry and animal populations*. Academic Press, San Diego.
- MARRA, P. P. 2000. The role of behavioral dominance in structuring patterns of occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11:299–308.
- MARZLUFF, J. M., AND B. HEINRICH. 1991. Foraging by Common Ravens in the presence and absence of territory holders: an experimental analysis of social foraging. *Animal Behaviour* 42:755–770.
- MARZLUFF, J. M., B. HEINRICH, AND C. S. MARZLUFF. 1996. Raven roosts are mobile information centres. *Animal Behaviour* 51:89–103.
- MARZLUFF, J. M., J. J. MILLSAUGH, P. HURVITZ, AND M. HANDCOCK. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- MARZLUFF, J. M., AND E. NEATHERLIN. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation* 130:301–314.
- MATTHYSEN, E. 1999. Foraging behaviour of Nuthatches (*Sitta europaea*) in relation to the presence of mates and mixed flocks. *Journal of Ornithology* 140:443–451.

- MATTHYSEN, E., T. VAN DE CASTEELE, AND F. ADRIAENSEN. 2005. Do sibling tits (*Parus major*, *P. caeruleus*) disperse over similar distances and in similar directions? *Oecologia* 143:301–307.
- MATTHYSEN, E., T. VAN OVERVELD, T. VAN DE CASTEELE, AND F. ADRIAENSEN. 2010. Family movements before independence influence natal dispersal in a territorial songbird. *Oecologia* 162:591–597.
- NACK, R. R., AND D. E. ANDERSEN. 2006. Brood movements of eastern prairie population Canada Geese: potential influence of light goose abundance. *Journal of Wildlife Management* 70:435–442.
- NAMS, V. O. 1990. *Locate II user's guide*. Pacer Software, Truro, Nova Scotia, Canada.
- NEWTON, I., AND M. MARQUISS. 1982. Fidelity to breeding area and mate in Sparrowhawks *Accipiter nisus*. *Journal of Animal Ecology* 51:327–341.
- NEWTON, I. 1998. *Population limitation in birds*. Academic Press, San Diego.
- NICE, M. M. 1941. The role of territory in bird life. *American Midland Naturalist* 26:441–487.
- NICE, M. M. 1943. Nesting success in altricial birds. *Auk* 74:305–321.
- OTIS, D. L., AND G. C. WHITE. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* 63:1039–1044.
- PARTRIDGE, L., AND P. GREEN. 1985. Intraspecific feeding specializations and populations dynamics, p. 207–226. *In* R. M. Sibly and R. H. Smith [EDS.], *Behavioural ecology: ecological consequences of adaptive behavior*. Blackwell Scientific, Oxford, England.
- PHILLIPS, R. A., J. R. D SILK, B. PHALAN, P. CATRY, AND J. P. CROXALL. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization, or foraging niche divergence? *Proceedings of the Royal Society of London B* 271:1283–1291.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1997. *Identification guide to North American passerines*. Slate Creek Press, Bolinas, CA.
- PRAVOSUDOVA, E. V., T. C. GRUBB JR., AND P. G. PARKER. 2001. The influence of kinship on nutritional condition and aggression levels in winter social groups of Tufted Titmice. *Condor* 103:821–828.
- RESTANI, M., J. M. MARZLUFF, AND R. E. YATES. 2001. Effects of anthropogenic food sources on movements, survivorship, and sociality of Common Ravens in the Arctic. *Condor* 103:399–404.
- RODGERS, A. R., A. P. CARR, L. SMITH, AND J. G. KIE. 2005. HRT: Home range tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
- ROTH, J. E., J. P. KELLY, W. J. SYDEMAN, AND M. A. COLWELL. 2004. Sex differences in space use of breeding Common Ravens in western Marin County, California. *Condor* 106:529–539.
- ROWLEY, I. 1973. The comparative ecology of Australian corvids II. Social organization and behaviour. *Wildlife Research* 18:25–65.
- SAFI, K., B. KÖNIG, AND G. KERTH. 2007. Sex differences in population genetics, home range size and habitat use of the parti-colored bat (*Vespertilio murinus*, Linnaeus 1758) in Switzerland and their consequences for conservation. *Biological Conservation* 137:8–36.
- SAIN, S. R., K. A. BAGGERLY, AND D. W. SCOTT. 1994. Cross-validation of multivariate densities. *Journal of the American Statistical Association* 89:807–817.
- SCOTT, J. M. 1999. Vulnerability of forested ecosystems in the Pacific Northwest to loss of area. *Forest fragmentation: wildlife and management implications*, p. 33–43. *In* J. A. Rochell and J. Wisniewski [EDS.], *Forest fragmentation: wildlife and management implications*. Brill, Leiden, the Netherlands.
- SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, G. C. KENNETH, J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- SEDGWICK, J. A. 2004. Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). *Auk* 121:1103–1121.
- SEIDEL, K. S. 1992. *Statistical properties and applications of a new measure of joint space use for wildlife*. M.Sc. thesis, University of Washington, Seattle, WA.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113–151.
- SIMPSON, K., J. N. M. SMITH, AND J. P. KELSALL. 1987. Correlates and consequences of coloniality in Great Blue Herons. *Canadian Journal of Zoology* 65:327–340.
- SOL, D., D. M. SANTOS, AND M. CUADRADO. 2000. Age-related feeding site selection in urban pigeons (*Columba livia*): experimental evidence of the competition hypothesis. *Canadian Journal of Zoology* 78:144–149.
- SPSS, INC. 2004. *Release 13.0 for Windows*. SPSS, Inc., Chicago.
- STAHLER, D., B. HEINRICH, AND D. SMITH. 2002. Common Ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Animal Behaviour* 64:283–290.
- STAMPS, J. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior* 23:173–232.
- STIEHL, R. B. 1985. Brood chronology of the Common Raven. *Wilson Bulletin* 97:78–87.
- SUNDE, P., AND M. S. BOLSTAD. 2004. A telemetry study of the social organization of a Tawny Owl (*Strix aluco*) population. *Journal of Zoology* 263:65–76.
- TICKELL, W. L. N. 1968. The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora*. *Antarctic Bird Studies* 12:191–212.
- VAN OVERVELD, T., F. ADRIAENSEN, AND E. MATTHYSEN. 2011. Postfledging family space use in Great Tits in relation to environmental and parental characteristics. *Behavioral Ecology* 22:899–907.
- WEBB, W. C., W. I. BOARMAN, AND J. T. ROTENBERRY. 2004. Common Raven juvenile survival in a human-augmented landscape. *Condor* 106:517–528.
- WEBB, W. C., W. I. BOARMAN, AND J. T. ROTENBERRY. 2009. Movements of juvenile Common Ravens in an arid landscape. *Journal of Wildlife Management* 73:72–82.
- WEBB, W. C. 2010. *Common Raven demography, nest predatory behavior, and gene flow in a temperate rainforest*. Ph.D. dissertation, University of Washington, Seattle, WA.
- WEBB, W. C., J. M. MARZLUFF, AND J. HEPINSTALL-CYMERMAN. 2011a. Linking resource use with demographic parameters in a synanthropic population of Common Ravens. *Biological Conservation* 144:2264–2273.
- WEBB, W. C., J. M. MARZLUFF, AND K. E. OMLAND. 2011b. Interbreeding between cryptic lineages of the Common Raven: evidence for speciation in reverse. *Molecular Ecology* 20:2390–2402.
- WHITE, G. C., AND R. A. GARROT. 1990. *Analysis of wildlife radiotracking data*. Academic Press, San Diego.
- WILSON, E. O. 1975. *Sociobiology*. Harvard University Press, Cambridge, MA.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- WRIGHT, J., R. E. STONE, AND N. BROWN. 2003. Communal roosts as structured information centres in the raven, *Corvus corax*. *Journal of Animal Ecology* 72:1003–1014.
- WUNDERLE, J. M. JR. 1991. Age-specific foraging proficiency in birds. *Current Ornithology* 8:273–324.