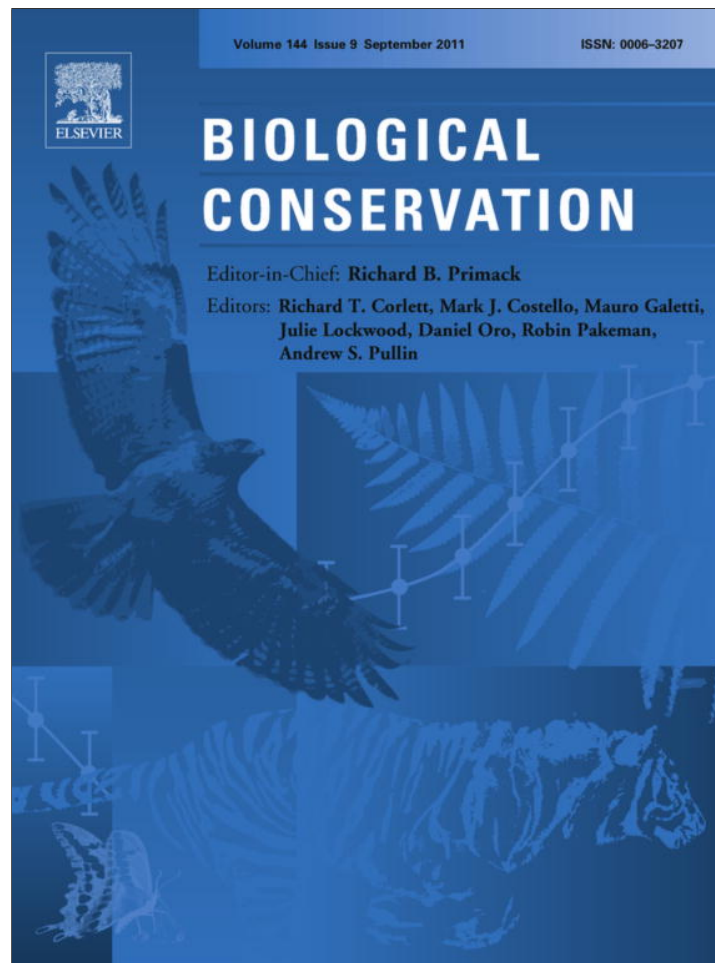


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## Linking resource use with demography in a synanthropic population of common ravens

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### ABSTRACT

A thorough understanding of a population's ecology requires knowledge of the relationship between habitat use, resource use and demographic parameters. We undertook an empirical investigation of habitat use, resource use and demography in a population of common ravens (*Corvus corax*), a species widely distributed throughout the Northern Hemisphere. The abundance of ravens is increasing in many parts of western North America, which represents a conservation concern since predation by ravens is thought to contribute to the decline of several sensitive species. We defined resources as the suite of physical and biological components in the environment that led to occupancy of a particular place by ravens. The home ranges of breeding and nonbreeding ravens contained similar proportions of resources, but breeding ravens used more edges, roads, forest, clearcuts, and towns than nonbreeders. We detected no differences in survival between the sexes, but breeding ravens survived at higher rates than nonbreeders, due to exclusion by breeding ravens from those resources positively associated with survival. Raven use of mature forests and anthropogenic land use types was positively associated with survival. Breeding raven use of clearcuts and patchy areas contributed to increased reproduction, but the use of clearcuts along with the use of roads was negatively associated with survival due to illegal shooting. Greater insight into the demography of synanthropic species such as the common raven will enable managers to make informed decisions for protecting biodiversity. This study is the first to consider the demographic consequences of habitat use and resource use for both nonbreeding and breeding common ravens.

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### 1. Introduction

As indigenous vegetation is destroyed and perforated on our increasingly human-dominated planet (Imhoff et al., 2004), an understanding of the relationship between habitat use, resource use and demography becomes all the more important for managing declining species as well as potential pest species that benefit from human activity (i.e., synanthropic; Marzluff, 2001). Human-modified landscapes especially provide opportunities for generalist species, including wide-ranging ones capable of exploiting both anthropogenic resources and those provided by surrounding, less disturbed landscapes (Hansson, 1997; Withey and Marzluff, 2009). An example of such a species is the common raven (*Corvus corax*), whose populations respond positively to anthropogenic resources (Webb et al., 2004; Marzluff and Neatherlin, 2006; Kristan and Boarman, 2007). In addition to scavenging on anthropogenic resources (Restani et al., 2001), ravens frequently hunt and are human-subsidized predators (Soulé et al., 1988). Raven

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abundance continues to grow in many parts of western North America, in concert with an expanding human presence (Sauer et al., 2008). The increasing abundance of ravens has raised concerns about raven predation of sensitive species, including the federally threatened marbled murrelet (*Brachyramphus marmoratus*) and other sensitive species (Boarman et al., 2006; Bui et al., 2010; Peery and Henry, 2010).

Individual variation in habitat use and the resources therein affect individual fitness and contribute to the regulation of avian populations (Clark and Shutler, 1999; Pulliam, 2000; Johnson, 2007). More specifically, individual variation in resource use can influence key demographic parameters such as survival and reproduction (Marzluff et al., 2004). Individual variation in resource use has been observed in numerous avian species in relation to age (Gustafsson, 1988; Sol et al., 2000) as well as sex (Marra, 2000; Safi and Konig, 2007). Resource specialization related to morphological differences (Bolnick et al., 2003; Phillips et al., 2004; Catry et al., 2005) or different nutritional requirements (Safi and Konig, 2007) represent alternative explanations for intraspecific variation in resource use.

Studies that link individual variation in resource use to avian demographic parameters, especially those that include multiple

classes within the same population, occur infrequently in the scientific literature (Moysey, 1997). In the case of the common raven, nonbreeding and breeding segments of raven populations have been studied separately (Marzluff and Neatherlin, 2006; Kristan and Boarman, 2007; Webb et al., 2004, 2009). However, the habitat use, resource use and demographic parameters of both nonbreeding and breeding common ravens has never been concurrently studied within the same population. Therefore, we undertook an empirical investigation relating individual variation in resource use to demographic parameters in a population of common ravens. We hypothesized that ravens would preferentially utilize anthropogenic resources providing supplemental food (Webb et al., 2009; Bui et al., 2010), and that raven demographic parameters would respond positively to their use (Webb et al., 2004; Marzluff and Neatherlin, 2006; Kristan and Boarman, 2007). Our objectives were (1) to quantify habitat and resource use by ravens of different sex and class, and (2) to relate resource use to survival and reproduction.

## 2. Materials and methods

### 2.1. Study area

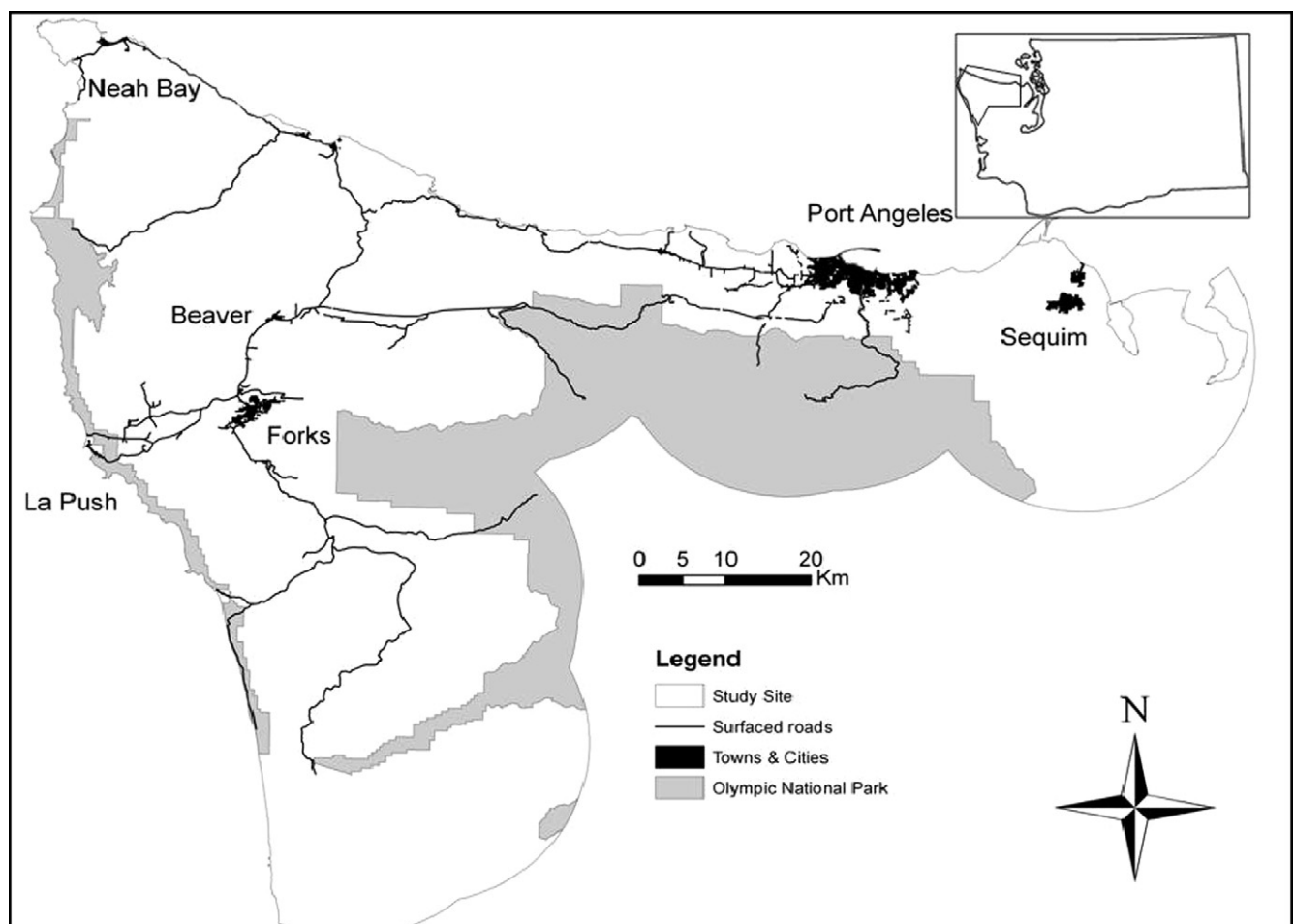
We conducted the study on the north and western portions of the Olympic Peninsula of Washington State (Fig. 1). Over the past 100 years, large tracts of old-growth temperate rainforest have been transformed, mostly by logging, into a heterogeneous patch-

work of relatively young seral stands (Franklin and Dyrness, 1988; Scott, 1999). These managed forests were 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).

We define resources as the suite of physical and biological components in the environment that lead to occupancy of a particular place by ravens. This definition includes the local physical characteristics that produce forest of varying seral development, as well as a variety of anthropogenic land uses (“habitat,” Block and Brennan, 1993; Jones, 2001). Resources within the study site include indigenous, ephemeral food bonanzas that attract 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 anthropogenic land use types in the region (e.g. livestock ranches, landfills) provide superabundant and dependable food for ravens. Unlike ephemeral food bonanzas, these spatially fixed anthropogenic subsidies provide consistently renewed food sources and are known as point subsidies (Webb et al., 2009).

### 2.2. Capture, sexing and monitoring reproductive success

Between December 2002 and August 2005, we captured 60 ravens (22 juveniles, 35 breeding adults, and 3 subadults) using a remote controlled portable net launcher (Coda Enterprises, Ltd.). We measured and color-banded each raven with a unique



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

combination of plastic color bands and an aluminum USFWS band. Each raven was outfitted with a backpack-mounted radio transmitter (Buehler et al., 1995) weighing 27 g (Advanced Telemetry Systems, Isanti, MN, USA) 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 social class of trapped ravens. Juveniles were birds of known age that had fledged from and were trapped within known territories during the 2003, 2004, or 2005 breeding season. Subadults were unpaired breeding-age individuals, as indicated by black mouth color (Heinrich and Marzluff, 1992). Adults were trapped in their breeding territories, and subadults were trapped opportunistically during efforts focused on trapping adults and their offspring. Since juveniles and subadults exhibit similar ranging behavior (Heinrich et al., 1994), we pooled these two groups into a nonbreeder class for statistical analyses. We used molecular techniques to identify the sex of individuals. Two small growing feathers were sampled from each raven, and we determined sex using a PCR reaction that amplifies the CHD gene fragments on the W and Z chromosomes (Griffiths et al., 1998).

We monitored reproductive success by observing nests and post-fledging family behavior at adult territories in which at least one adult was radio tagged. We returned to each territory at least once per week throughout the breeding season (March–July), and used the maximum number of fledglings observed during that period of time to represent a pair's reproductive success. For breeding pairs monitored for >1 year ( $n = 13$ ), we used the average of the maximum fledgling counts to represent their annual success.

### 2.3. Radiotracking

We tracked ravens continuously from May 2003 to March 2007 (47 consecutive months) using ATS R2000 portable scanning radio receiver (ATS, Isanti, MN, USA) attached to 4-element Yagi antennas on a truck, 2- and 3-element Yagi antennas held by hand, and dual wing-mounted, 3-element Yagi antennas attached to an airplane 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 site. During the spring and summer (March–September), we tracked ravens several times per month and for one week per month during the rest of the year until each bird died or its transmitter stopped functioning (mean 2.44, range 0.77–5.11 locations/month). Thus, two surviving juveniles and one subadult from the 2003 cohort with functioning transmitters were followed into their fifth year, and juveniles from the 2004 ( $n = 3$ ) and 2005 ( $n = 3$ ) cohorts into their fourth and third years, respectively. We ascertained the cause of mortality from the location and timing of death, condition of the remains, and any markings left by predators.

We used homing techniques (White and Garrot, 1990) and triangulation to estimate raven locations (no more than once per bird per 24 h; Otis and White, 1999). Typically we saw the tagged bird and recorded its location using a handheld GPS unit. When this was not possible because of dense vegetation or the remote nature of parts of the study area, we triangulated (199 locations, or 6% of the total). Triangulation location estimates were based upon at least three compass bearings forming 45–110 angles, and 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 80 m radius) were omitted. Detectability of transmitter signals ranged from one 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 from the perimeter of the study site.

### 2.4. Home ranges analysis

We estimated home ranges based on point locations in ArcGIS 9.2 using 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 dispersal locations (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, 2010). We selected the smoothing parameter using an objective criterion that minimized the risk for oversmoothing or undersmoothing (Worton, 1989; Sain et al., 1994) 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 raven behavior and their sensory abilities. We then generated provisional home ranges using 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 utilization distribution (UD).

We compared average home range area across all data years between the sexes, classes, and their interaction using a two-factor ANOVA. We also compared the home range area with the percent composition of each resource within breeding raven home ranges. We used MANOVA to compare the percent composition of land cover types of home range between sexes and breeding status.

### 2.5. Geospatial analysis

To characterize resource use by ravens, we constructed geospatial layers combining land cover (vegetation types) and land use (anthropogenic elements) and quantified landscape structure (land cover composition, land use, and configuration). We created year-specific land cover using 1991 Landsat Thematic Mapper imagery (Green et al., 1993) 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 (TM) satellite imagery (2000, 2003, 2004). We used Washington State's Department of Natural Resources (DNR) forest practices geospatial data, which includes the date and extent of forest harvest to assist interpretation of forest harvest dates. We also introduced data layers of water and roads obtained from the DNR and digitized a layer of surface roads using the DNR roads layer, orthophotos, and our knowledge of the study site. We pooled several of the original forest classes delineated in the original data set, because of their hypothesized functional similarity for raven behavior, and to reduce the dimensionality of the set of predictor variables (Bergin et al., 2000, Table 1). We considered all land use and land cover classes as mutually exclusive in their spatial extent.

We quantified landscape structure (composition and configuration) within raven home ranges with Fragstats (v 3.3 build 5) (McGarigal et al., 2002) utilizing a moving windows analysis with a circular radius determined by each home range bandwidth. We reduced index redundancy (Riitters et al., 1995; Hargis et al., 1998) by selecting a few indices from the five unique aspects of spatial heterogeneity proposed by Li and Reynolds (1995): number of land cover types, proportion of each type on the landscape, spatial arrangement of patches, patch shape, and contrast between neighboring patches. All land cover and land use classes falling

**Table 1**

Categories and spatial extent of land use and land cover classes, and resources within the study site (20 km buffer around all raven locations, 9792 km<sup>2</sup>) and within home ranges for 59 common ravens with >10 locations on the Olympic Peninsula, May 2003–March 2007. The home range quantifies an animal's probability of occurrence at each point in space as determined by kernel analysis. We only included land use and land cover categories thought most important to Common Ravens in *a priori* models of resource utilization. Description and classes for forest classes reflect Hall et al. (1985) and anthropogenic land use classes follow Anderson et al. (1976).

Land use and land cover	RUF resource (abbreviation)	UDs	Total area (ha)	Within UD $\bar{X}$	Within UD $SD$	Description
Anthropogenic	AN	50	3757	33	32	
Gravel pits	AN	55	541	7	1	Shallow mining pits denuded of vegetation
Exurban	AN	40	1988	11	13	Low density residential outside towns
Rural	AN	47	1170	12	13	Isolated cabins, farms, and ranches
Waste facilities	AN	17	45	2	7	Landfills and waste transfer facilities
Fish hatcheries	AN	6	13	0.12	1	State or federal salmonid-rearing facilities
	CWED	59				Contrast-weighted edge density
	IJI	59				Interspersion and juxtaposition index
Logging roads	LR	59	37,223	81	74	Unpaved roads constructed for forest harvest
Mature forest	MF	59	289,787	215	248	
Old growth		58	107,598	12	16	Dominant DBH 30" or greater; ~135+ years
Large saw		59	49,981	63	82	Dominant DBH 20–30"; approx 90–135 years
Small saw		59	119,695	121	146	Dominant DBH 14–20"; 45–90 years
Pole		59	12,513	18	17	Dominant DBH 10–14"; 24–45 years
Recent clearcut	NEW	58	14,791	143	133	0–4 Years post-harvest; grass-forb dominated
High elevation	None	0	23,729	0.00	0.00	Forests above 4500 feet
Water	None	57	25,832	76	76	Lakes, ponds, streams, rivers, and salt water
Cloud/shadow	None	48	4440	10	12	Obscured during imaging by clouds and shadow
Open canopy mixed conifer	OC	59	82,680	124	143	At least 90% conifers and canopy closure <60%
Older clearcut	OLD	57	24,866	144	154	5–12 Years post-harvest; shrub dominated
	PD	59				Patch density
Pasture and prairie	PR	52	3305	82	87	Herbaceous rangeland
Surfaced roads	PRD	50	1787	23	20	Public roads layered with asphalt
Sapling	SA	59	168,330	268	263	Dominant DBH 4–10"; 12–30 years;
	SHAPE_AM_1	59				Shape index, mature forest, area-weighted mean
Towns and cities	TC	32	5140	33	60	Urban or built-up land
	TCA_1	59				Total core area mature forest

within home ranges were incorporated by Fragstats in the calculation of landscape metrics. The indices chosen for analysis of landscape structure in relation to all land cover and land use classes included: patch density (PD), contrast weighted edge density (CWED), and interspersion and juxtaposition index (IJI). Patch density is the number of patches in the landscape, divided by total landscape area (m<sup>2</sup>), multiplied by 10,000 and 100 (to convert to 100 ha). To calculate CWED, we defined edge contrast weights between 0 and 1 for each potential pair of edge types, with increasing weights representing greater edge contrast (Appendix A). We defined edge contrast based on ecological considerations and field observations of structural differences between adjacent land cover classes. IJI considers all patch types present on a landscape and computes the observed interspersion over the maximum possible interspersion for the given number of patch types. We also calculated two class-level metrics for the mature forest class, area-weighted mean for the shape index (SHAPE\_AM\_1), and total core area (TCA\_1). The shape index is the patch perimeter divided by the minimum perimeter possible for a maximally compact forest patch (a square) of the same patch area. The total core area quantified the amount of mature forest >25 m from any edge.

## 2.6. Quantifying resource use

We used the resource utilization function (RUF) (Marzluff et al., 2004) using the RUFFIT package in R (R Development Core Team, 2009) to quantify raven resource use at the third-order, or within home range, scale (Johnson, 1980). This approach assumes that space use relates to resource use, and relates variation in the height of the UD to spatially-defined resources using multiple linear regression, while accounting for spatial autocorrelation in location data introduced by kernel analyses. The RUF uses a model from the Matern class where the correlation is a function of the distance between locations with the range set by the bandwidth from individ-

ual kernel density estimates (Marzluff et al., 2004). The RUF determines the resources at each grid cell in the UD and relates the height of the UD to resource values at each cell to produce coefficients of relative resource use. The coefficients in the RUF indicate the relative importance of each resource to each raven. The advantages of the RUF include reducing the impact of location error, treating the animal or group as the unit of observation, and using a response variable that is a continuous and probabilistic measure of space use (Marzluff et al., 2004).

We included in the RUF analysis adult and subadult ravens with >10 locations and juvenile ravens with >10 dispersal locations. We included 10 land cover and land use types along with five landscape structure indices as independent variables in the RUF analysis (Table 1). To incorporate temporal variation in resource use, we calculated separate RUFs (and associated UD's) between years for ravens whose home ranges encompassed areas of forest harvest since the previous year's imagery. For ravens with multiple RUF's, we took the average values of their standardized resource coefficients weighted by the proportion of locations in their separate, tracking-year specific UD's. Not all resources occurred within every home range (Table 1), so resources were omitted from analysis for individual birds if the resource did not occur within the home range for that individual. We used one sample *t*-tests to evaluate the null hypothesis that coefficient means for each group of ravens did not differ from a value of zero. We also compared standardized resource coefficients between the sexes and breeding status implementing MANOVA. To evaluate the relationship between resource use and productivity for breeding ravens, we regressed mean annual productivity with standardized resource coefficients, including only those resources whose values at the population level differed significantly from zero.

We generated RUF analyses for 59 individuals (21 nonbreeders, 38 breeding ravens; 30 males, 29 females); including those that moved their home ranges after changing mates or social class.

Changes in landscape structure and composition within individual home ranges due to forest harvest across years required multiple RUF analyses for 28 individuals, resulting in a total of 93 RUF analyses (mean RUF per individual = 1.58, range 1–3). As a consequence of this temporal data partitioning, 15 individuals had <10 locations ( $6 \pm 3\%$  of their data) in one of their data years, so we excluded these 38 locations (median excluded locations per individual = 2, range 1–4) from the RUF analyses.

### 2.7. Survival analysis

We used the R package RMark (Laake and Rexstad, 2008) to construct models for program MARK (White and Burnham, 1999) to estimate survival of groups of ravens and relate survivorship to standardized resource coefficients. We incorporated the data from radio tagged ravens in a Burnham joint live recaptures and dead recoveries analysis (Burnham, 1993). Because survival and recapture rates were our primary parameters of interest, we did not constrain recovery rate ( $r$ ) or site fidelity ( $F$ ). We tested global models and then constrained parameters according to *a priori* hypotheses concerning. We constrained parameters as functions sex (sex), social status (social), constancy ( $\sim 1$ ), and the standardized resource coefficients (Table 1). Model-weighted parameter estimates and standard errors were derived from the model with the lowest AICc value and all other models with  $\Delta AICc$  values <10 (Burnham and Anderson, 2002, p. 152). Model notation follows that of Lebreton et al. (1992) and Franklin et al. (2000).

Unless otherwise indicated, we used SPSS (SPSS 2004) to conduct analyses. We applied  $P < 0.05$  as the significance level along with two-tailed tests. We checked for normality using the Kolmogorov–Smirnov goodness-of-fit test, and tested for homogeneity of variance using 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 nonbreeder class. Data from the same ravens were analyzed separately when birds moved to new territories or transitioned between nonbreeding and breeding classes.

## 3. Results

### 3.1. Radiotracking and sources of mortality

We obtained 3215 locations by radio-tracking ravens from February 2003 until June 2007. Four juveniles perished before we obtained 10 locations outside their natal territories, and another disappeared before reaching an adequate sample size, and therefore these five individuals were excluded from relevant analyses. The number of individuals and the frequency of total locations for these 60 birds (including data from 4 ravens that were analyzed separately after these birds moved to new territories or transitioned between age classes) were 5 (1–9 locations), 12 (10–29), 17 (30–49), 20 (50–69), 10 (70+). The length of time that individual birds were followed after radio-tagging ranged between 67 and 1455 days (mean 678,  $SD$  365).

Through the end of the study, 25 ravens died, 4 ravens 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 site. The causes of mortality and their frequency included unknown causes (9), predation by owl or raptor (7), shooting (6), broken wing (1), crushed by falling tree (1), and one bird died when its transmitter harness became entangled in a tree canopy. Examination of mortality records revealed that carcasses from the six known shooting deaths were all recovered with 50 m of roads. In addition, recent timber harvest and resulting clearcuts occurred

within the home ranges of 8 out of 12 known deaths of breeding ravens. Recent changes to habitat structure creating more open habitat may have contributed to their deaths since four of these individuals were shot and two were killed by Great-horned Owls.

Search efforts by vehicle or plane covering a wider area probably would not have located the three missing breeding ravens given strong site fidelity exhibited by breeding ravens (Webb, 2010). It is most likely that three cases of breeding raven disappearances and the single missing juvenile were shootings that also destroyed the transmitters and precluded carcass recovery. If this juvenile evaded detection, it permanently and rapidly dispersed to the east or south (due to oceanic barriers), well beyond the extended area (up to 100 km outside the study site) periodically visited to look for missing birds. Furthermore, it would have been the only juvenile out of a combined total of 262 juveniles followed in Washington (present study) and California (Webb et al., 2009) to display such extreme movement behavior.

All 22 radio-tagged juveniles survived dispersal from their natal territory, although an accurate radio location was not obtained for one of the dispersed juveniles until after it had died. A radio signal from this juvenile was briefly detected in August 2005  $\sim 10$  km south of the natal territory which indicated the bird was flying rapidly which prevented a reliable radio tracking located to be obtained. The signal for this juvenile was not detected again until May 2006 when the carcass was recovered 48.6 km from the nest. The mean date when juveniles were first observed outside their natal territories in 2003–2005 was 9 August ( $n = 21$ ), range 9 July–25 September).

We radio-tagged both members of 15 mated pairs, and on 8 occasions, one member of a mated pair perished (3 males, 5 females). All 5 males remated by the following breeding season and remained in the same territory, although one male temporarily exhibited movement behavior suggestive of 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 floating that lasted 5 weeks during which she was located up to 16 km from her original trapping location. After her mate perished in August 2005, one female left her territory in which she fledged four offspring earlier that season. This female remained a nonbreeder through the end of the study, and did not breed, while two untagged breeding ravens took residence in her former territory.

### 3.2. Home range size and resource use

Nonbreeders maintained larger home ranges than breeding ravens (two-way ANOVA,  $F_{3,55} = 39.44$ ,  $P < .01$ ), but home range size did not differ between the sexes ( $F_{1,55} = 0.11$ ,  $P = 0.74$ ), nor was there a significant interaction for home range area between class and sex ( $F_{1,55} = 0.44$ ,  $P = 0.62$ , Table 2). Breeding and nonbreeding raven home ranges encompassed similar proportions of all land cover types, except nonbreeder home ranges contained more prairie (MANOVA:  $F_{1,55} = 14.44$   $P < 0.01$ ). There was no significant relationship between home range area and the proportion of different land cover types within breeding raven home ranges ( $R^2 = 0.328$ ,  $P = 0.270$ ).

We found no differences in resource use associated with landscape metrics between groups, but breeding ravens and nonbreeders differed in their use of all land cover classes (all  $P < 0.05$ , Fig. 2). Males and females did not differ in their use of land cover classes except the sapling class, which was used more by males (standardized resource coefficients: ♂ mean 0.55,  $SD$  2.44; ♀ mean  $-0.96$ ,  $SD$  4.14;  $P = 0.04$ ). Standardized resource coefficients that

**Table 2**

Sample size, home range size, and standardized resource coefficients derived from the RUF analysis for breeding and nonbreeding ravens on the Olympic Peninsula. Values are explicitly compared between individuals with >30 locations in all data analysis years with individuals located between 10 and 30 times within one or more data analysis years. To incorporate temporal variation in resource use, we calculated separate RUFs (and associated UD's) between years for ravens whose home ranges encompassed areas of forest harvest since the previous year's imagery. For ravens with multiple RUF's, we took the average values of their standardized resource coefficients weighted by the proportion of locations in their separate, tracking-year specific UD's. We found no relationship between the number of locations and home range size ( $R^2 = 0.01$ ,  $P = 0.49$ ). Abbreviations for RUF standardized resource coefficients include AN (anthropogenic land use), CWED (contrast weighted edge density), IJI (interspersed and juxtaposition index), LR (logging roads), MF (mature forest), NEW (new clearcut), OC (open canopy mixed conifer), OLD (old clearcut), PD (patch density), PRD (paved road), SA (sapling), SHAPE\_AM\_1 (shape index, mature forest, area weighted mean), TC (town and city), and TCA\_1 (total core area, mature forest).

	≥30 (n = 27)		<30 (n = 32)	
	n = 20		n = 15	
Nonbreeding ravens	n = 7		n = 17	
Movement metrics	Mean	SE	Mean	SE
Tracking years	2	0.15	3	0.21
Data analysis years	1	0.10	2	0.12
Total dispersal locations	54	3.61	48	5.17
Locations in data analysis years	47	2.74	36	5.02
Home range (ha)	1503	327	1050	73
<i>RUF standardized coefficients</i>				
AN	0.15	0.49	1.16	0.45
CWED	-0.39	1.01	-0.23	0.54
IJI	0.37	0.28	1.09	0.43
LR	0.28	0.61	0.64	0.36
MF	0.62	0.76	0.26	0.58
NEW	1.54	0.75	2.10	0.57
OC	0.21	0.56	-0.20	0.46
OLD	0.38	0.90	-0.02	0.54
PD	2.70	0.87	2.48	0.62
PR	0.44	0.61	0.99	0.51
PRD	0.35	0.44	0.38	0.29
SA	-0.08	0.77	-0.28	0.52
SHAPE_AM_1	0.99	0.52	-0.35	0.35
TC	0.34	0.78	-0.42	0.30
TCA_1	0.72	0.80	0.23	0.50

differed significantly from zero for the breeding population included anthropogenic resources (+), interspersed and juxtaposition index (IJI)(+), logging roads (+), mature forest (+), new clearcuts (+), old clearcuts (+), patch density (PD)(+), prairie(+), and paved roads (+) (one sample *t*-tests,  $n = 38$ , all  $P < 0.05$ , Fig. 2). Standardized resource coefficients for the nonbreeder population that differed from zero included contrast-weighted edge density (-), interspersed and juxtaposition index (IJI)(+), and patch density (PD)(+) (one sample *t*-test,  $n = 21$ , all  $P < 0.05$ , Fig. 2).

Considering only those resources that were important to either nonbreeders or breeding ravens, individuals that transitioned between social classes changed their resource use to reflect their new class. For the three individuals that transitioned between classes, the difference between their own standardized resource coefficients before and after transitioning between social classes (mean 2.11,  $SD$  1.84) was greater than the difference between their new standardized resource coefficients and the mean values for the individuals' new social class (Wilcoxon's matched-pairs test, mean 1.34,  $SD$  1.14,  $Z = -2.04$ ,  $P = 0.04$ ). In other words, after transitioning into new social classes, these birds exhibited resource use more similar to their new social classes than to their previous patterns of resource use.

### 3.3. Reproduction and survival

Twenty-five breeding pairs produced  $1.46 \pm 1.06$  (mean  $\pm$   $SD$ , range 0–5) fledglings per year in 52 nesting attempts during

2003–2007. Reproductive success varied with resource use ( $R^2 = 0.46$ ,  $P = 0.03$ ; including only those resources which differed significantly from zero for the breeding population). Breeding raven standardized resource coefficients explaining a significant amount of variation in nest productivity included interspersed and juxtaposition index (IJI) ( $B = -0.40$ ,  $P = 0.04$ ), new clearcuts ( $B = 0.77$ ,  $P < 0.01$ ), and PD ( $B = -0.39$ ,  $P = 0.04$ ).

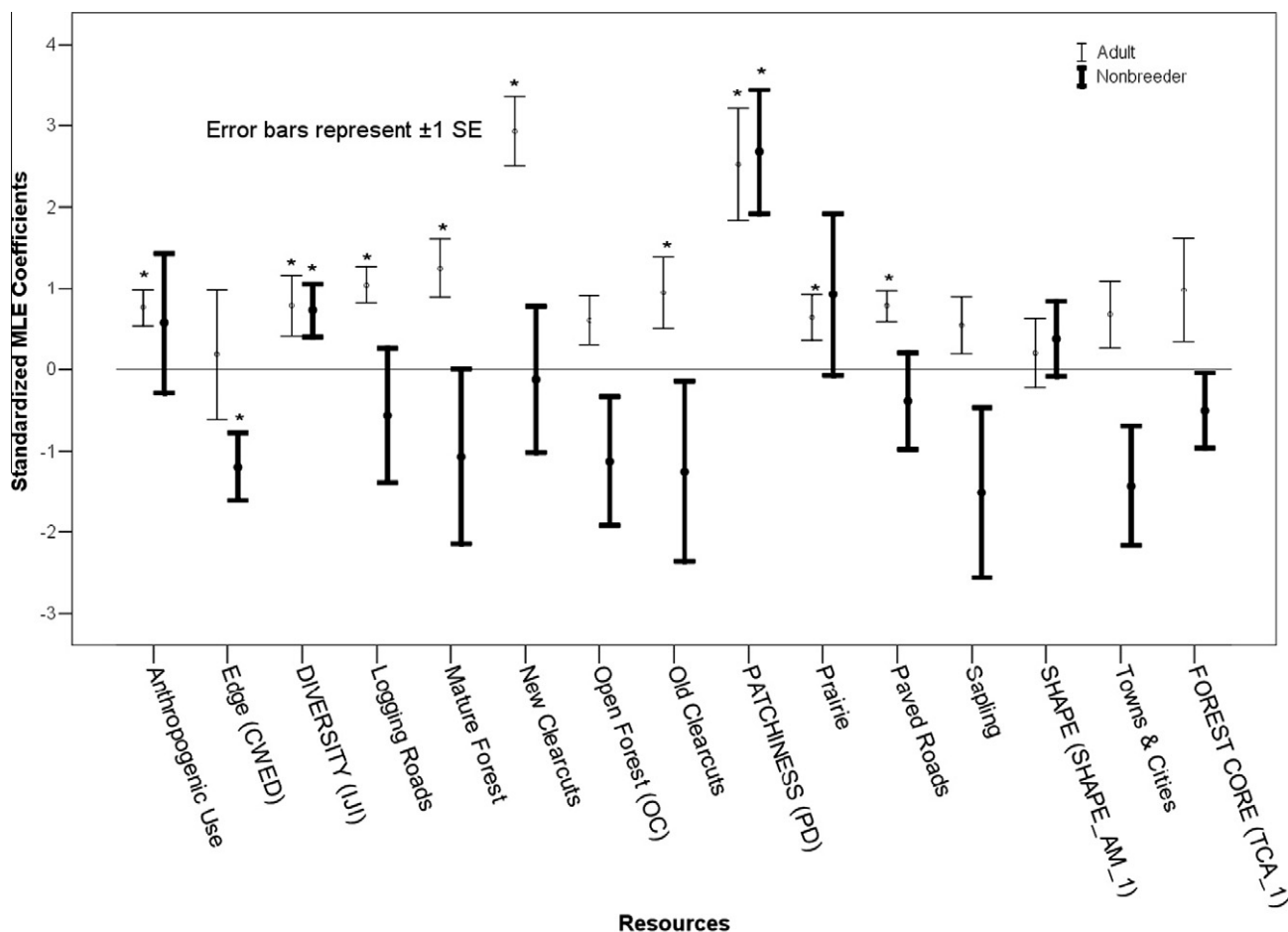
Survival did not vary with the sex of breeding ravens (model-weighted survival estimate for males and females = 0.86,  $SE$  0.05) or nonbreeders (both 0.79,  $SE$  0.08). Model-weighted parameter estimates and  $SE$ 's revealed that the resources most positively associated with survival include mature forest, anthropogenic land use, and towns and cities (Fig. 3). In order of decreasing absolute magnitude, the variables with the largest relationship with survival included nonbreeders status (-), logging roads (-), paved roads (-), mature forest (+), anthropogenic land use (+), new clearcuts (-), and towns and cities (+) (Table 3, Fig. 3).

## 4. Discussion

In this study, we examined the relationship between habitat use, resource use and demographic parameters across different classes within the same population. In particular, we demonstrated that breeding and nonbreeding ravens used resources differently; that resources varied in their demographic effects; and that demographic tradeoffs occurred in the use of some resources. We also expanded upon previous research of a more limited scope that correlated demographic parameters with raven access to anthropogenic resources (juvenile survival; Webb et al., 2004; reproduction; Marzluff and Neatherlin, 2006; Kristan and Boarman, 2007; movements; Webb et al., 2009). As anticipated, we found that raven use of anthropogenic land use and towns contributed to increased survival. However, the use of roads and clearcuts was also associated with reduced survival due to illegal shooting. Overall, raven use of anthropogenic resources contributed positively to demographic parameters, which helps explain their increasing abundance on the Olympic Peninsula and elsewhere (Sauer et al., 2008). In addition, raven use of anthropogenic resources indirectly contributes to raven predation of sensitive species such as the marbled murrelet (*Brachyramphus marmoratus*).

The resources used most by breeding ravens included roads, clearcuts, mature forest, prairies, and anthropogenic land use. Logging roads and paved roads present supplemental foraging opportunities for ravens in the form of refuse and road-killed carrion. Breeding ravens use mature forest for nesting, and most prairies in the study site host livestock ranches where ravens forage for small mammals, invertebrates, and feed on the occasional livestock carcass. Anthropogenic land uses includes low density residential, waste facilities, and fish hatcheries which all present supplemental food for ravens. Although survival was positively associated with towns and cities, most raven home ranges did not contain this land use type, and therefore it was not significantly used by the population.

Breeding and nonbreeding ravens utilized all land cover types differently even though their home ranges encompassed similar proportions of land cover types. On the other hand, both breeding and nonbreeding ravens preferentially used areas of complex landscape configurations: patch density (PD) and interspersed and juxtaposition index (IJI). Breeding and nonbreeding raven use of complex landscape configurations reflects an attraction to disturbed habitats such as anthropogenic land use which perforates and replaces contiguous forest tract with anthropogenic land uses and early seral vegetation. Based upon our observations of raven behavior, an abundance of perches for the purposes of display and observation also attracts ravens to these heterogeneous areas.



**Fig. 2.** Standardized maximum likelihood estimators (MLE) of resource coefficients for breeding and nonbreeding Common Ravens on the Olympic Peninsula. Standardized resource coefficients were generated using the resource utilization function (RUF). Error bars represent  $\pm 1$  SE. Asterisks identify coefficients that differ significantly from zero at  $P < 0.05$ .

Utilization by nonbreeders of food bonanzas and point subsidies explained the large negative coefficient for nonbreeder use of contrast-weighted edge density (CWED). Food bonanzas and point subsidies in our study area which attract large numbers of nonbreeders generally occur in anthropogenic land use and clearcuts, respectively. Anthropogenic land use and clearcuts replace indigenous land cover classes such as mature forest. Since mature forest forms the largest contrast with other land cover classes (Webb, 2010), nonbreeder affinity for point subsidies and food bonanzas contributed to the large negative coefficient for nonbreeder use of contrast-weighted edge density (CWED).

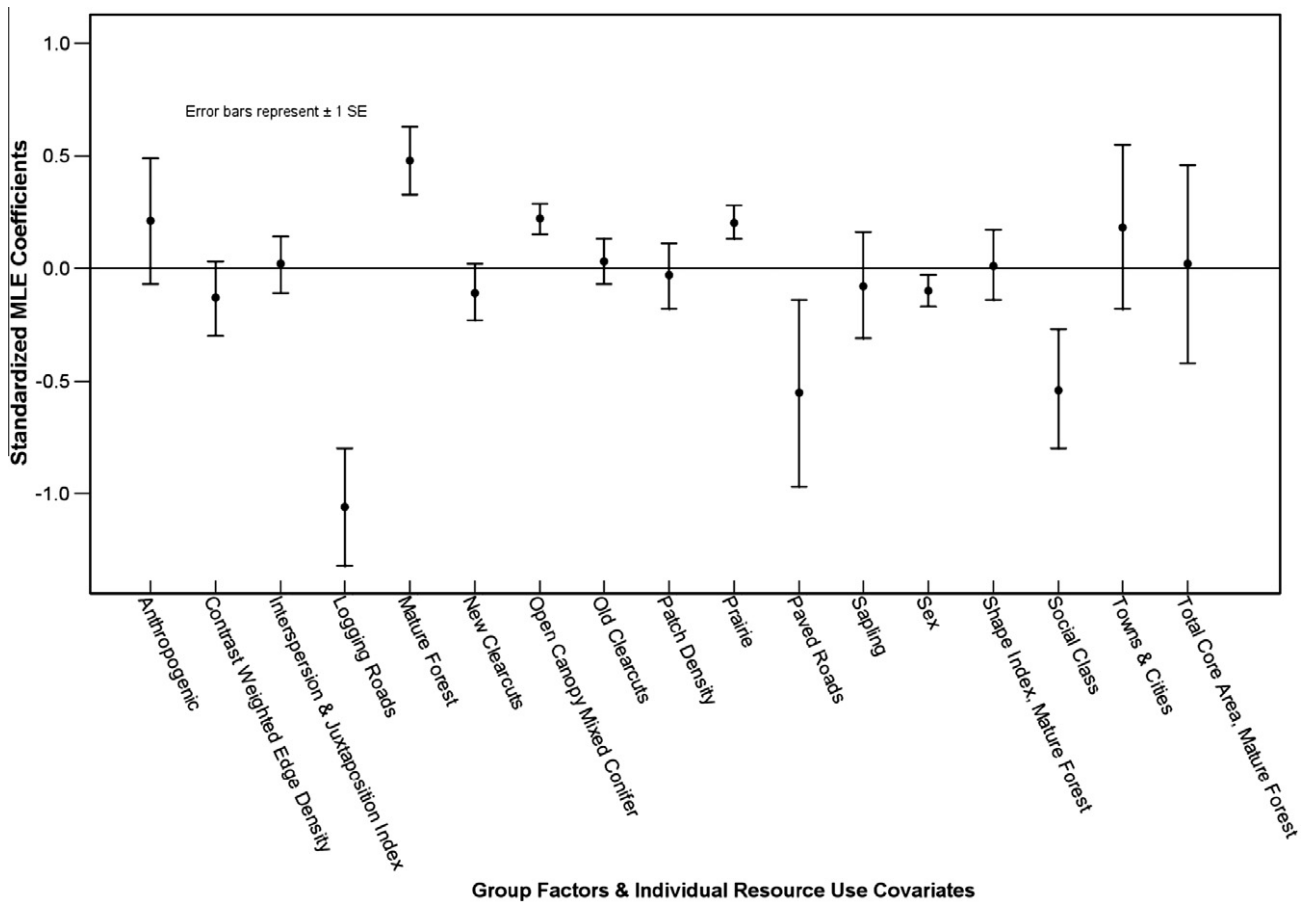
The large variance of resource coefficients for nonbreeders reflected territorial exclusion of nonbreeders by breeding ravens as well as the transience of nonbreeders as they tracked ephemeral food bonanzas. Although the results should be viewed with caution due to the small sample size, the differences in resource use by three individuals that transitioned between classes also supported the hypothesis that territorial exclusion by breeding ravens influenced resource use by nonbreeders. Resource use for two nonbreeders after they established breeding territories resembled the mean resource use for breeding ravens and differed from the prior resources utilized by these birds as nonbreeders. Likewise, resource use for a breeding female after she became a nonbreeder resembled the mean resource use for nonbreeders and differed from her resource use as a breeding raven.

Breeding ravens that used new clearcuts raised a greater number of offspring, probably due to increased foraging efficiency as well as an abundance of both indigenous and anthropogenic foods. In addition

to providing a frequent location for hunter-killed carcasses and refuse disposal, new clearcuts present indigenous foraging opportunities for ravens. New clearcuts support a high density of small mammals (Gunther et al., 1983; Songer et al., 1997) and arthropods (Niemela, 1997; Marra and Edmonds, 1998) as well as open habitat conducive to foraging by visual species. In our study site, ravens used intact, relatively homogeneous mature forest tracts for nesting which explains why the resources least associated with raven reproduction included measures of configuration complexity: interspersed and juxtaposition index (IJI) and patch density (PD).

Within-population differences in survival between sexes and social classes have been previously reported for many species (Newton, 1998). Male and female ravens exhibited similar survivorship, but the acquisition of a territory probably contributed to the higher survival of breeding ravens compared to nonbreeders. Lower survival rates of nonbreeding ravens was due in part to exclusion by breeding ravens from those resources positively associated with survival: mature forest (MF), anthropogenic land use (AN), and town and city (TC), which is a pattern observed in other species as well (Winker et al., 1990; Marra, 2000). Mature forest confers higher survival because of increased protection from sources of mortality, such as shooting and predation. Anthropogenic land use (AN) as well as town and city (TC) confer higher survival because of supplemental food. Although logging roads, paved roads, and new clearcuts present supplemental foods for ravens, their use was negatively associated with survival. These land use types represent a significant hazard to ravens since most shooting deaths occurred near these land use types.





**Fig. 3.** Model-weighted parameter estimates of individual covariates generated from the survival analysis. Error bars represent  $\pm 1$  SE. Individual standardized beta coefficients for RUF resources (see Table 1) in addition to sex and social status were entered as individual covariates in the survival analysis.

**Table 3**

Ranking of models for raven survival and recapture, comparing parameters between sexes, social status, and relating to raven resource use as individual covariates. We used the Akaike information criterion (Akaike, 1973) corrected for small sample size to rank the models from the list of *a priori* models. Models with  $\Delta AICc$  values  $< 10.00$  were used for model-weighted parameter estimation.  $\Delta AICc$  is the numerical difference between each model and the model with the lowest AICc. The likelihood of any model is the AICc Weight for the model of interest divided by the AICc Weight of the best model. The top model predicted survival as a function of social status, and raven use of high-contrast edges, mature forest, clearcuts, and paved roads. Notation explanation: S = survival; p = recapture; r = recovery rate; F = site fidelity; an = anthropogenic land use; cwed = contrast-weighted edge density; IJI = interspersion and juxtaposition index; lr = logging roads; mf = mature forest; new = recent clearcuts; old = older clearcuts; oc = open forest; pd = patch density; pr = prairie; prd = surfaced roads; sa = sapling; shape\_am\_1 = shape index for mature forests, area-weighted mean; tc = towns and cities; tca\_1 = total core area of mature forest, (~1) = constancy.

Model	AICc	$\Delta AICc$	AICc Weight	# Param.
$S(\sim cwed + mf + new + old + prd + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1297.56	0.00	0.14	12
$S(\sim mf + oc + sa + new + old + lr + tc + an + pr + prd)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1297.77	0.21	0.13	16
$S(\sim cwed + mf + new + old + prd)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1298.20	0.64	0.10	11
$S(\sim mf + oc + sa + new + old + lr + tc + an + pr + prd + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1299.15	1.59	0.06	17
$S(\sim tca_1 + shape\_am\_1 + mf + sa + new + old + lr + tc + an + prd)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1299.19	1.64	0.06	16
$S(\sim social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1299.75	2.19	0.05	7
$S(\sim cwed + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1299.81	2.25	0.05	8
$S(\sim oc + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1300.81	3.26	0.03	8
$S(\sim prd + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1301.13	3.57	0.02	8
$S(\sim tca_1 + shape\_am\_1 + mf + sa + new + old + lr + tc + an + prd + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1301.25	3.69	0.02	17
$S(\sim mf + oc + sa + new + old)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1301.33	3.78	0.02	11
$S(\sim lr + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1301.38	3.82	0.02	8
$S(\sim mf + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1301.46	3.90	0.02	8
$S(\sim new + social)p(\sim sex + social)r(\sim 1)F(\sim 1)$	1301.56	4.00	0.02	8

Variation in external factors including resources influence demographic parameters differently (Franklin et al., 2000; Bears et al., 2009). For common ravens on the Olympic Peninsula, breeding ravens increased their reproduction using supplemental foods associated with clearcuts and roads, but they also experienced de-

creased survival associated with these resources. Trade offs between survival and reproduction have also been observed in several other terrestrial avian species, including the red-breasted nuthatch (Ghalambor and Martin, 2000), pied flycatcher (Dale et al., 1996), and white-crowned sparrow (Morton et al., 2004).

## 5. Conclusions

Greater insight into demography of synanthropic species such as the common raven will enable managers to make informed decisions for reducing the negative impacts of these species on biodiversity. However, despite decades of ecological research, basic natural history and life history information still remains lacking for most species, even those presenting management concerns (Villard and Nudds, 2009). Although limited aspects of raven distribution and demography have been studied before, we present the first intrapopulation examination of multiple demographic parameters, and the first quantification of demographic consequences of habitat use and resource use for the common raven.

Managers seeking to reduce the potential impacts of ravens on sensitive species could enact a variety of approaches that would negatively effect demographic parameters. The primary areas of management focus for reducing anthropogenic supplementation of raven survival and reproduction should address public roads, anthropogenic land use, and outdoor users. Road-kill and refuse food subsidies for ravens could be reduced by lowering speed limits, erecting wildlife fencing, building wildlife crossing culverts, and discouraging roadside dumping with warning signage at problem locations. Altering land use practices at both public and private properties would reduce food subsidies for ravens. Landfills and waste transfer stations should keep all refuse covered as much as possible, and police their facilities for escaped trash. Hatcheries and waste treatment facilities should cover all ponds, and eliminate the practice of discarding fish carcasses in the open at hatcheries. Ranchers and hobby farmers should bury all animal carcasses and cover livestock feed to reduce raven access. Timber harvesting practices such as selective logging which reduce the number and extent of clearcuts should be encouraged. Outdoor users such as park visitors, hikers, fishers and hunters can be informed through educational campaigns to increase proper disposal of refuse and discontinue the practice of leaving animal remains from hunting and fishing in the open.

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**Table A1**

Contrast weighted edge density matrix. We defined edge contrast weights between 0 and 1 for each potential pair of edge types, with increasing weights representing greater edge contrast. We defined edge contrast based on ecological considerations and field experience of structural differences between adjacent land cover classes. Notation explanation: mf = mature forest; oc = open forest; sa = sapling; wa = water; cs = cloud and shadow; he = high elevation forest; cc = old and new clearcuts; lr = logging roads; an = anthropogenic land use; gp = gravel pits.

	mf	oc	sa	wa	cs	he	cc	lr	an	gp
Mature forest	0	0	0.5	0.5	0	0	1	1	0.9	1
Open forest	0	0	0.5	0.5	0	0	1	1	0.9	1
Sapling	0.5	0.5	0	0.5	0	0.2	0.7	0.7	0.3	0.7
Water	0.5	0.5	0.5	0	0	0.5	0.8	0.8	0.8	0.8
Clouds and shadow	0	0	0	0	0	0	0	0	0	0
High elevation	0	0	0.2	0.5	0	0	1	1	0.8	0.8
Clearcut	1	1	0.7	0.8	0	1	0	0	0.1	0.2
Logging roads	1	1	0.7	0.8	0	1	0	0	0.1	0
Anthropogenic	0.9	0.9	0.3	0.8	0	0.8	0.1	0.1	0	0
Gravel pits	1	1	0.7	0.8	0	0.8	0.2	0	0	0

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## Appendix A

See Table A1.

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