Nest-Site Selection and Reproductive Success in Common Ravens

Jeffrey R. Dunk,[1] Roger N. Smith,[2] and Steven L. Cain
*Grand Teton National Park, Office of Science and Resource Management, P. O. Drawer 170,
Moose, Wyoming 83012, USA*

Studies of habitat selection by animals can be categorized in two ways: behavioral and evolutionary (Krebs 1994). Most studies of habitat selection consider the behavioral perspective whereby biotic and/or abiotic components of the environment that appear to influence habitat use are identified, generally by comparing used sites with random or available sites (e.g. Mosher et al. 1986, Seamans and Gutiérrez 1995). The evolutionary approach examines the effects of selecting particular habitats on an index of fitness, e.g. survivorship or reproduction (see Martin and Roper 1988, Petit and Petit 1996). If nest-site selection is a heritable trait, then natural selection should favor individuals that choose nest sites that confer greater reproductive success. Common Ravens (*Corvus corax*) are suitable subjects for examination of reproduction in relation to habitat characteristics owing to their variable clutch size, which ranges from three to seven eggs (Dunk et al. unpubl. data). Thus, in any one year, a relatively large range in number of young fledged is possible within a population, and it may be possible to detect a cline in reproductive success relative to nest-site characteristics. Common Ravens are widely distributed throughout North America and Europe. In western North America, ravens have been characterized as pests that easily adapt to human-modified landscapes (Butcko 1990, Boarman 1993, Marzluff et al. 1994). During the past 25 years, raven numbers have increased in many areas of the western United States (Boarman 1993, Dunk et al. 1994, Marzluff et al. 1994).

Despite their ubiquitous nature, large numbers, and broad geographic range, little is known about many aspects of the breeding biology of ravens. In particular, very little has been published on raven nest-site selection. Ravens nest on many substrates, including cliffs (Ratcliffe 1962, White and Cade 1971, Hooper 1977, Skarphédinsson et al. 1990), highway overpasses and billboards (White and Tanner-White 1988), churches (Heinrich 1989), power poles (Knight and Kawashima 1993), and trees (Dorn 1972, this study), but nest-site characteristics have been quantified only for cliff nests (White and Cade 1971, Hooper 1977).

---

[1] Present address: Department of Wildlife, Humboldt State University, Arcata, California 95521, USA. E-mail: jrd2@axe.humboldt.edu
[2] Present address: Teton Science School, P. O. Box 68, Kelly, Wyoming 83011, USA.

Furthermore, examination of forest nesting sites is lacking.

In 1990 and 1991 we recorded a high density of breeding ravens in our study area (Dunk et al. 1994), which had few breeding ravens 50 years previously (Craighead and Craighead 1956). Concomitantly, we documented a drastic decline in Red-tailed Hawk (*Buteo jamaicensis*) reproductive success relative to 50 years ago (Smith 1994; earlier estimates of reproductive success from Craighead and Craighead [1956]). To determine whether a relationship existed between the increase in ravens and the decrease in hawk reproductive success, we initiated studies on the breeding biology of both species. Herein, we report on the relationship between nest-site selection and reproductive success in Common Ravens nesting in forested habitats in Grand Teton National Park (GTNP).

Study area and methods.—The study area (ca. 225 km²) is in northwestern Wyoming within GTNP (43°91' N, 110°40' W). Elevations range from 1,890 to 2,500 m. GTNP is situated in a high mountain valley surrounded by the Teton Range to the west, the Gros Ventre Mountains to the east, and the Yellowstone plateau to the north. The valley floor is dominated by numerous river terraces (with little elevational relief), glacial moraines, and several isolated buttes. The Snake River bisects the valley and supports a large riparian/floodplain community. The core study area contains large areas of previously or currently grazed and irrigated hay lands.

Vegetation in the study area was described by Craighead and Craighead (1956). The principal plant community is sagebrush/bitterbrush (*Artemisia tridentata* and *A. arbuscula/Purshia tridentata*) interspersed with stands of aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*). Cottonwoods (*Populus angustifolia* and *P. balsamifera*), blue spruce (*Picea pungens*), and willow (*Salix* spp.) dominate the riparian forests. The climate is characterized by long, cold winters and short, cool summers. Approximately 67% of the annual precipitation occurs in the form of snow.

The study was conducted from March 1992 through August 1994. Raven nests were located by systematic searches of large areas (see Dunk et al. 1994); most of the searching occurred from April to May prior to leaf-out of deciduous trees. Nests were visited approximately once a week after an adult was observed in incubation position or young could be seen in the nest. Nests were periodically checked with a mirror-

TABLE 1. Univariate data ($\bar{x} \pm$ SE) and two-group discriminant function analysis comparing characteristics of Common Raven nest sites ($n = 35$) with random sites ($n = 33$), Grand Teton National Park.

Variable	Group		Structure coefficient
	Nest site	Random site	
Canopy cover (%)	51.63 (3.04)	30.38 (4.11)	0.72
Basal area (m²/0.04 ha)	0.79 (0.07)	0.52 (0.09)	0.39
Tree height (m)	13.73 (0.66)	12.04 (0.63)	0.32
Tree DBH (cm)	30.92 (3.08)	25.21 (1.76)	0.30
Ground cover (%)	72.57 (2.83)	65.30 (3.11)	0.28
Wilks' Lambda	0.622		
Approximate F-statistic	6.3	($P \leq 0.0001$)	
Correct classification (%)	77.94		
Cohen's Kappa	0.558 ($P \leq 0.0001$)		

and-pole device (Parker 1972) to determine number of eggs and young. When possible, laying dates were estimated by back-dating from time of hatching or fledging (21 and 42 days, respectively; Dorn 1972). Raven pairs were considered successful if they produced at least one fledgling (fledging defined as leaving the nest). We sampled vegetation structure and composition in 0.04-ha circular plots centered on nest trees and at one randomly located site for every raven nest. Random plots were selected using random compass directions and distances (25–200 m) from each nest tree and contained at least one tree >5 m tall; this excluded habitats in which ravens could not nest (e.g. sagebrush flats, roads, open water, and meadows). Sampling techniques followed James and Shugart (1970) and Noon (1981). Variables measured within each plot were: (1) number of trees; (2) number of snags; (3) diameter at breast height (DBH) of all trees and snags >5 m tall (by tree species); (4) basal area per plot (converting all DBH measurements to area); (5) percent canopy cover (>2 m); (6) percent shrub cover; (7) percent ground cover (<0.5 m); (8) understory foliage structure (estimated with a 3 × 1 m drop cloth marked with 10-cm grid squares; see Noon 1981); (9) tree height; (10) percent slope; (11) slope aspect; (12) height of nest in tree; and (13) distance from center of plot to nearest forest opening. Forest openings were boundaries between major changes in vegetation (e.g. trees vs. grass or sagebrush), not small openings or gaps created by single trees falling. Canopy, shrub, and ground cover were estimated using a modified point-intercept method on eight 10-m transects that began at the plot center and were 45° apart. Every 2 m on each transect we sighted through an ocular sighting tube and recorded presence or absence of vegetation in each of the three strata. Measurements were obtained in the year each nest was used but after the young had fledged. We also calculated the coefficient of variation (CV) of tree height and DBH. Weather data were obtained from the Moose, Wyoming weather station.

To examine nest-site selection, we used discrimi-

nant function analysis (DFA) and multivariate matched-pairs analysis (paired Hotelling's T^2 test [BMDP 3D]; Dixon et al. 1990). For the DFA, we started with all variables and then sequentially reduced the model one variable at a time (dropping the variable with the lowest structure coefficient) until model correct classification fell below 75%. We sought to produce a model that was relatively accurate at distinguishing between nest sites and random sites using as few variables as possible. Although we had no *a priori* reason to expect that all of the variables we measured were relevant to raven nest-site selection, our intention was to elucidate biological reasons for our results while developing a model with high predictive power. Multivariate matched-pairs analysis offered a novel method for examining habitat selection at a scale that was relevant to individual animals because the random sites truly were available (i.e. they were within raven territories). We also calculated chance-corrected classification rates of DFA models using Cohen's Kappa statistic (Titus et al. 1984); DFA and Tukey-Krammer multiple comparisons tests were performed using NCSS 6.1.0 (Hintze 1995).

The relationships among reproductive success (i.e. number of young fledged), egg-laying date, and habitat variables were examined using all possible subsets in a regression analysis. We chose the model with the lowest root mean square error. Significance was assumed if $P \leq 0.05$.

Results.—Measurements were conducted at 35 raven nests and 33 random sites (two raven nests had no suitable random sites within 200 m). For distinguishing between nest sites and random sites, percent canopy cover, basal area, tree height, tree DBH, and percent ground cover were entered into the DFA model (Table 1); the discriminant function was significant (Wilks' lambda = 0.662, $P < 0.0001$). The DFA model classified 77.9% of the sites correctly, down 9.5% from the model containing all variables.

Univariate paired *t*-tests revealed significant differences between nest sites and random sites for five variables (Table 2). Among all differences, only CV

TABLE 2. Univariate and multivariate matched pairs analyses comparing Common Raven nest sites with associated random sites ($n = 33$).

Variable	$\bar{x}$ nest	$\bar{x}$ random	t-statistic	P-value	Power ($\alpha = 0.05$)
Canopy cover (%)	51.44	30.38	6.31	<0.0001	0.999
Basal area (m²/plot)	0.79	0.52	2.97	0.005	0.826
No. of snags	3.09	1.91	2.58	0.015	0.705
Ground cover (%)	72.07	65.30	2.17	0.036	0.558
Slope (%)	16.28	12.36	2.11	0.043	0.535
Tree height (m)	13.71	12.04	1.99	0.055	0.489
Tree DBH (cm)	31.57	25.21	1.17	0.107	0.363
CV Tree height	7.39	10.41	−1.31	0.199	0.247
Distance to edge (m)	11.88	9.36	1.27	0.213	0.234
CV DBH	10.19	13.18	−1.26	0.217	0.230
Shrub cover (%)	21.71	26.74	−1.24	0.225	0.224
No. of trees	13.51	11.85	1.20	0.240	0.213
Horizontal cover (%)	32.11	36.16	−0.65	0.261	0.155
Mahalanobis D^2			4.334		
Hotelling T^2			143.007		
F-value			4.748		
P-value			0.001		

of DBH, CV of tree height, percent horizontal cover, and percent shrub cover were greater at random sites than at nest sites (Table 2). Based on multivariate matched-pairs analysis, nest sites and random sites differed significantly, with percent canopy cover, basal area, number of snags, percent ground cover, and slope being the most important variables ($T^2 = 143.007$, $F = 4.748$, $P = 0.0013$; Table 2).

Clutch size ($n = 33$) ranged from one to seven eggs, with clutches of four and five being most frequent (70% of all clutches). Clutches of one and two may have been incomplete, although these nesting attempts were successful. Mean clutch size was 4.55 and did not differ significantly among years ($F = 2.04$, df $= 2$ and 30, $P = 0.148$; Table 3), although the power ($\alpha = 0.05$) of the test was only 0.387. The number of young fledged per nest ranged from zero to six, with zero and three being the most frequent (60% of all nests). The mean number of young fledged per nesting attempt was 2.39 and differed significantly between 1992 and 1993 ($F = 4.88$; df $= 2$ and 38, $P = 0.0129$; Table 3). The mean number of young fledged per successful nest was 4.11, 3.0, and 3.36 from 1992 to 1994, respectively and did not differ significantly among years ($F = 2.36$, df $= 2$ and 25, $P = 0.1148$, power [$\alpha = 0.05$] = 0.433). The proportion of nesting attempts that failed (eggs laid but no young fledged) was 0.18, 0.56, and 0.15 from 1992 to 1994, respectively

and varied significantly among years ($\chi^2 = 22.45$, df $= 2$, $P = 0.00001$).

Mean egg laying dates differed among years ($F = 24.15$, $P < 0.00001$), with 1992 (Julian date; $\bar{x} = 93.9 \pm$ SD of 4.91) being significantly earlier than 1993 and 1994 (1993: $\bar{x} = 119 \pm 9.89$; 1994: $\bar{x} = 120 \pm 11.63$). Mean laying date appeared to be strongly influenced by cumulative winter snowfall (Fig. 1), with ravens laying earlier during the year with the least amount of snow.

Multiple regression analysis examining the relationship of number of young fledged to laying date and habitat variables revealed that ravens that fledged more young initiated laying earlier and nested in sites lower in basal area, CV of tree height, percentage ground cover, and percentage slope ($R^2 = 0.63$, $F = 7.72$, $P = 0.0003$, $n = 28$ nests).

Discussion.—Generally, ravens nested in isolated stands of trees or on the edges of larger stands. Twenty-six of 35 (74%) nest trees were the tallest trees within plots. Nesting in edge habitats and taller trees

TABLE 3. Reproductive success ($\bar{x} \pm$ SD) of Common Ravens in Grand Teton National Park, 1992 to 1994.

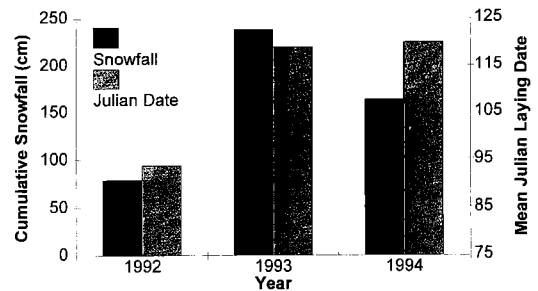| Year	No. eggs	n	No. fledged	n
1992	5.33 ± 1.03	6	3.36 ± 1.96	11
1993	4.56 ± 1.21	16	1.41 ± 1.73	17
1994	4.09 ± 1.30	11	2.85 ± 1.52	13
All years	4.55 ± 1.25	33	2.39 ± 1.90	41

Fig. 1. Relationship between cumulative winter snowfall (January to April) and mean egg laying date of Common Ravens, 1992–1994, Grand Teton National Park, Wyoming.

probably improved the accessibility of nests to ravens, as has been suggested for Red-tailed Hawks (Orians and Kuhlman 1956, Bednarz and Dinsmore 1982). These same properties also could provide ravens with better views of potential predators and/or food sources. Nests surrounded by other trees probably confer additional advantages, because areas with one or two trees, which were seldom used by ravens, would provide the same accessibility and visibility advantages. Larger trees also may be the only trees with an appropriate branch structure to hold nests.

We observed extreme variation (238%) in reproductive success (mean number of young fledged) among the three years of our study. Because clutch size did not vary significantly among years, egg and nestling mortality rates were greater in years of lower productivity. We did not locate nests early enough to detect potential breeding pairs that did not breed (i.e. all occupied territories; cf. Postupalsky 1974); thus, our estimates of reproductive success are probably slight overestimates. In a study area partly within and adjacent to ours, ravens fledged a mean of 3.3 young/pair ($n = 3$) in 1947 (Craighead and Craighead 1956) and 1.4 young/pair ($n = 11$) in 1975 (Craighead and Mindell 1981). Although the sample sizes were smaller than ours, the range of reproductive success values reported in these studies is nearly identical to ours.

The mean laying date was approximately 25 days earlier in 1992 than in 1993 or 1994. Cumulative winter snowfall during 1992 was less than half that during 1993 or 1994 (Fig. 1). Cumulative snowfall probably is a reasonable index of winter severity and may influence individual birds' condition and/or the abundance or availability of food. Raven egg-laying dates in Iceland were later during a spring with record cold temperatures (Skarphédinsson et al. 1990). We found that laying date, basal area, CV of tree height, percentage ground cover, and percentage slope explained 63% of the variation in numbers of young fledged. Factors such as food abundance or availability, distance of nest to nests or dens of competitors or predators, and individual experience would probably explain much of the additional variation in reproductive success.

Ravens selected nest sites in a variety of forest types but generally in areas with characteristics of mature forests (i.e. larger and taller trees). Ravens that nested earliest experienced the highest reproductive success. This relationship mostly resulted from early laying dates and relatively high reproductive success during 1992. Earlier breeders may have had higher reproductive success for a variety of reasons, e.g. because they were older and more experienced, they obtained better territories, and/or the timing of nesting was optimal for the production of young. We have no way to distinguish among these factors, and our inferences are relevant only at the scale that habitat sampling was conducted. Analyses at the scale of the entire stand or landscape might reveal additional or different patterns.

LITERATURE CITED

BEDNARZ, J. C., AND J. J. DINSMORE. 1982. Nest-sites and habitat of Red-shouldered and Red-tailed hawks in Iowa. Wilson Bulletin 94:31–45.

BOARMAN, W. I. 1993. When a native predator becomes a pest: A case study. Pages 186–201 *in* Conservation and resource management (S. K. Majumdar, E. W. Miller, D. E. Miller, J. R. Pratt, R. F. Schmalz, and E. K. Brown, Eds.). The Pennsylvania Academy of Science, Easton.

BUTCHKO, P. H. 1990. Predator control for the protection of endangered species in California. Pages 237–240 *in* Proceedings of the 14th Vertebrate Pest Conference (L. R. Davis and R. E. Marsh, Eds.). University of California, Davis.

CRAIGHEAD, F. C., JR., AND D. MINDELL. 1981. Nesting raptors in western Wyoming, 1947 and 1975. Journal of Wildlife Management 45:865–872.

CRAIGHEAD, J. J., AND F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Stackpole, Harrisburg, Pennsylvania.

DIXON, W. J. (Ed.). 1990. BMDP statistical software. University of California Press, Berkeley.

DORN, J. L. 1972. The Common Raven in Jackson Hole, Wyoming. M.S. thesis, University of Wyoming, Laramie.

DUNK, J. R., S. L. CAIN, M. E. REID, AND R. N. SMITH. 1994. A high breeding density of Common Ravens in northwestern Wyoming. Northwestern Naturalist 75:70–73.

HEINRICH, B. 1989. Ravens in winter. Summit Books, New York.

HINTZE, J. L. 1995. NCSS 6.0.1 statistical system for windows. Number Cruncher Statistical Systems, Kaysville, Utah.

HOOPER, R. G. 1977. Nesting of Common Ravens in Virginia. Wilson Bulletin 89:233–242.

JAMES, F. C., AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

KNIGHT, R. L., AND J. Y. KAWASHIMA. 1993. Responses of Raven and Red-tailed Hawk populations to linear right-of ways. Journal of Wildlife Management 57:266–271.

KREBS, C. J. 1994. Ecology: The experimental analysis of distribution and abundance. Harper Collins College Publishers, New York.

MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

MARZLUFF, J. M., R. B. BOONE, AND G. W. COX. 1994. Historical changes in populations and perceptions of native pest bird species in the West. Pages 202–220 *in* A century of avifaunal change in western North America (J. R. Jehl, Jr. and N. K. Johnson, Eds.). Studies in Avian Biology No. 15.

MOSHER, J. A., K. TITUS, AND M. FULLER. 1986. Developing a practical model to predict nesting habitat of woodland hawks. Pages 31–35 *in* Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates (J. Verner, M. L. Morrison, and C.J. Ralph, Eds.). University of Wisconsin Press, Madison.

NOON, B. R. 1981. Techniques for sampling avian habitats. Pages 42–52 *in* The use of multivariate statistics in studies of wildlife habitat (D. E. Capen, Ed.). General Technical Report RM-87, U. S. Forest Service, Fort Collins, Colorado.

ORIANS, G., AND F. KUHLMAN. 1956. Red-tailed Hawks and Horned Owl populations in Wisconsin. Condor 58:371–385.

PARKER, J. W. 1972. A mirror pole device for examining high nests. Bird-Banding 43:216–218.

PETIT, L. J., AND D. R. PETIT. 1996. Factors governing habitat selection by Prothonotary Warblers: Field tests of the Fretwell-Lucas models. Ecological Monographs 66:367–387.

POSTUPALSKY, S. 1974. Raptor reproductive success: Some problems with methods, criteria, and terminology. Pages 21–31 *in* Management of raptors

(F. N. Hamerstrom, Jr., B. E. Harrell, and R. R. Olendorff, Eds.). Raptor Research Report No. 2. Raptor Research Foundation, Inc. Vermillion, South Dakota.

RATCLIFFE, D. A. 1962. Breeding density in the Peregrine (*Falco peregrinus*) and Raven (*Corvus corax*). Ibis 104:13–39.

SEAMANS, M. E., AND R. J. GUTIÉRREZ. 1995. Breeding habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. Condor 97:944: 952.

SKARPHÉDINSSON, K. H., O. K NIELSEN, S. THÓRISSON, S. THORSTENSEN, AND S. A. TEMPLE. 1990. Breeding biology, movements, and persecution of Ravens in Iceland. Acta Naturalia Islandica 33:1–45.

SMITH, R. N. 1994. Factors affecting Red-tailed Hawk reproductive success in Grand Teton National Park, Wyoming. M. S. thesis, University of Wyoming, Laramie.

TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: Ecological applications. American Midland Naturalist 107:1–7.

WHITE, C. M., AND T. J. CADE. 1971. Cliff-nesting raptors and Ravens along the Colville River in Arctic Alaska. Living Bird 10:107–149.

WHITE, C. M., AND M. TANNER-WHITE. 1988. Use of interstate highway overpasses and billboards for nesting by the Common Raven (*Corvus corax*). Great Basin Naturalist 48:64–67.

Social and Sexual Monogamy in Translocated New Zealand Robin Populations Detected Using Minisatellite DNA

SIMONE L. ARDERN,[1,3] WEI MA,[2] JOHN G. EWEN,[2]
DOUG P. ARMSTRONG,[1,2] AND DAVID M. LAMBERT[1,2,4]
[1]*Ecology and Evolution, School of Biological Sciences, University of Auckland,
Private Bag 92019, Auckland, New Zealand; and*
[2]*Department of Ecology, Massey University, Private Bag 11-222, Palmerston North, New Zealand*

Most bird species are characterized as monogamous (Lack 1968, McKinney et al. 1984). However, recent research using genetic techniques has shown that social monogamy does not necessarily imply genetic

[3] Present address: School of Medicine, University of Auckland, Private Bag 92019, Auckland, New Zealand.

[4] Address correspondence to this author at Department of Ecology, Massey University, Private Bag 11-222, Palmerston North, New Zealand.
E-mail: d.m.lambert@massey.ac.nz

monogamy. Although monogamous relationships involve social associations and often parental care shared by a male and female, they do not necessarily reflect the genetic contributions of attending adults to future generations (Davies 1991). Extrapair copulation (McKinney et al. 1984) and intraspecific brood parasitism (Yom-Tov 1980) cause discrepancies between apparent and realized reproductive success that are commonly missed in field observations.

Extrapair paternity is common in some species of socially monogamous birds (e.g. Westneat 1990, Yamagishi et al. 1992, Lifjeld et al. 1993), but uncommon in others (e.g. Burke et al. 1989, 1990; Decker et al.