

SPATIAL AND TEMPORAL PATTERNS IN THE DIET OF COMMON RAVENS IN SOUTHWESTERN IDAHO¹

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Abstract. From May to August 1984 and April 1985 to April 1986, we collected 574 Common Raven (*Corvus corax*) pellets from five communal roosts in southwestern Idaho. Results of pellet analyses differed from those of previous studies of the Common Raven diet. Cereal grains were the principal pellet constituent, followed by small mammals, grasshoppers, cattle carrion, and birds. Pellet composition differed significantly within years, between years, and among roosts. Insects were most numerous in summer and fall pellets, and cattle and bird remains were most abundant in spring pellets. Between years, amounts of insect and cattle remains differed significantly. Amounts of cattle remains also differed significantly among roosts. Our data suggest that the diet of Common Ravens in southwestern Idaho is closely associated with agricultural activities. We recommend intensive, year-round sampling from both raven nest sites and roosts to adequately describe the raven diet in a given area.

Key words: Common Raven; *Corvus corax*; diet; feeding; food habits; Idaho.

INTRODUCTION

There has been no year-round study of the diet of Common Ravens (*Corvus corax*) in North America. The raven diet has been studied primarily during the spring/early summer at nest sites (Nelson 1934; Murray 1945; Dorn 1972; Kochert 1973; Harlow et al. 1975; Kochert et al. 1975, 1976, 1979, 1980, 1981; Stiehl 1978), with little quantitative information collected from other times of year (Temple 1974, Harlow et al. 1975). No information on the diet of nonnesting ravens during the breeding season is available. The most comprehensive study of the Common Raven diet to date took place in the United Kingdom, where Marquiss and Booth (1986) analyzed 945 pellets collected year-round from both nest sites and roosts; all breeding season data therein were collected solely from nest sites. In this paper, we present year-round quantitative infor-

mation describing the diet of Common Ravens from communal roosts in southwestern Idaho and examine seasonal, annual, and spatial variation in diet.

STUDY AREA AND METHODS

We studied ravens along a 124-km segment of 500-kV electric transmission line in southwestern Idaho. Heavily grazed shrubsteppe vegetation (West 1983) and agriculture dominate this area. Both the topographic relief and amount of agriculture increase from east to west as the line crosses the Snake River Plain and enters the foothills of the Owyhee Mountains. Annual precipitation averages 20 cm, most of which occurs from late fall to early spring (U.S. Department of the Interior 1979).

From 1984 through 1986, Common Ravens roosted communally on transmission towers at eight locations in the study area. Ravens used the transmission line for roosting throughout the year; however, periods of occupancy varied among roosts (Young and Engel 1988). From May to August 1984 and April 1985 to April 1986, we collected pellets beneath towers at the five largest roosts. Maximum numbers of ravens using each of these roosts during this time ranged

¹ Received 29 July 1988. Final acceptance 6 February 1989.

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from 224 to 2,103. A 28- × 0.5-m transect was established beneath one occupied tower at each study roost. Each week that a roost was occupied, five pellets were collected at random intervals along the transect. The transect was then cleared of all remaining pellets.

We collected and analyzed 574 raven pellets: 204 from 1984 (one pellet was discarded) and 370 from 1985–1986. Pellets were air-dried for at least 6 months and weighed to the nearest 0.01 g using an analytical balance. Pellets were dissected and the contents identified to genus, if possible, by comparison with reference guides and specimens. Vegetation, animal (major taxa only), and inorganic remains were weighed to the nearest 0.01 g. Numbers of animals were estimated by determining the minimum number of individuals per taxon possible in each pellet (Mollhagen et al. 1972).

Pellet contents were quantified by three methods: % of total pellet weight (% of the total weight of pellets comprised of a specified food item), % of total number (animals only; % of the total number of either vertebrates or invertebrates in pellets comprised of a certain prey species), and frequency of occurrence (% of the total number of pellets containing a specified food item). For analysis and description of trends in use of major food items, we chose the measures that were most sensitive to change in the amounts of each pellet constituent; weight data were used to describe vegetation trends, and count data were used to describe animal component trends.

Data from roosts that were <5 km apart and between which ravens regularly interchanged were combined for interroost comparisons. Thus, data from the two easternmost and two westernmost roosts were combined, resulting in three roost areas: Initial Point, Wilson Creek, and Marsing. These roost areas were an average of 24 km apart.

Only the Marsing roost area was occupied year-round; therefore, year-round dietary trends were described only at this roost. We used one-way analysis-of-variance (ANOVA) to test for seasonal differences in pellet composition at this roost. Pellet collections from Marsing were grouped into four seasons: winter (November–January), spring (February–April), summer (May–July), and fall (August–October). If significant seasonal differences were found, Student-Newman-Keuls multiple comparison tests (SNK) were used to locate between which seasons significant differences existed.

Only from May through August were all three roost areas occupied simultaneously and sampled during both years; therefore, data from only these months were used for interroost and between-year comparisons. We used repeated-measures two-way ANOVA (Milliken and Johnson 1984) to test for roost and year effects, whether there was a May through August trend in the amounts of each pellet constituent, as well as roost and year influences on the May through August trend, if it existed. Amounts of each major pellet constituent were averaged by month for the three roost areas in 2 years. Count data were $\log(x + 1)$ transformed; percent data were arcsine \sqrt{x} transformed.

RESULTS

Cereal grains comprised the majority of vegetation remains and were the primary pellet constituent by weight and frequency of occurrence (Table 1). Corn (*Zea* sp.) and oats (*Avena* sp.) were the principal cereal grains, followed by wheat (*Triticum* sp.) and barley (*Hordeum* sp.).

Vertebrate remains, primarily mammals, were the second most prevalent pellet constituent by weight and occurrence (Table 1). Small (≤ 1.0 kg) and large (> 20.0 kg) mammals together represented the majority of mammals counted. A large proportion (41%) of the small mammals could not be identified; however, of the identifiable small mammals, montane voles (*Microtus montanus*) were most numerous, followed by mice (*Peromyscus* spp.), and then ground squirrels (*Spermophilus* spp.). Cattle (*Bos taurus*) were the only large mammals identified and comprised almost all of the large mammal remains. Medium-sized mammals (> 1.0 kg and ≤ 20.0 kg), none of which could be identified, were the least abundant size class of mammals represented in pellets. Bird remains contributed an average of only 1% to the total pellet weight, but accounted for over 23% of the vertebrates counted and occurred in over 30% of the pellets. Remains of fish and reptiles accounted for an average of less than 1% of the total pellet weight and less than 2% of the vertebrates counted.

Insect remains were the third most prevalent constituent by weight but the second most common constituent encountered (Table 1). Grasshoppers (Orthoptera) and beetles (Coleoptera) were the only insect orders identified, with grasshoppers representing the majority (86%) of the insects counted.

TABLE 1. Composition of 574 Common Raven pellets collected in southwestern Idaho, May–August 1984 and April 1985–April 1986.^a

Food item	% of total weight	% of total no.	% occurrence
Vegetation			
Cereal grains	69.3	—	90.1
Corn	26.6	—	50.9
Oats	26.5	—	54.9
Wheat	11.2	—	22.0
Barley	4.5	—	10.7
Unidentified	0.5	—	0.7
Seed	2.4	—	24.9
Russian olive	2.2	—	5.3
Other	0.2	—	21.5
Unidentified	1.8	—	84.5
Total vegetation	73.5	—	96.5
Vertebrate			
Mammal	13.0	67.6	64.6
Small mammal	—	34.4	34.9
<i>Microtus montanus</i>	—	11.9	11.0
<i>Peromyscus</i> spp.	—	4.5	5.0
<i>Spermophilus</i> spp.	—	2.9	3.9
<i>Mus musculus</i>	—	0.6	0.2
<i>Perognathus parvus</i>	—	0.4	0.7
<i>Dipodomys</i> spp.	—	0.3	0.3
<i>Sorex</i> spp.	—	0.1	0.2
<i>Thomomys</i> spp.	—	0.1	0.1
Unidentified	—	13.7	17.2
Medium mammal	—	12.5	15.3
Unidentified	—	12.5	15.3
Large mammal	—	19.2	27.3
<i>Bos taurus</i>	—	18.2	26.1
Unidentified	—	1.0	3.2
Unidentified mammal	—	1.5	1.9
Bird	1.0	23.3	30.7
Egg	—	13.9	18.1
Unidentified	—	9.8	12.1
Reptile	0.2	0.4	0.5
Fish	0.2	1.8	2.1
Unidentified	0.3	6.0	9.1
Total vertebrate	14.6	100.0	80.8
Invertebrate			
Insect	7.0	100.0	72.9
Orthoptera	—	86.4	59.9
Coleoptera	—	13.4	31.7
Unidentified	—	0.3	3.8
Total invertebrate	7.0	100.0	72.9
Inorganic material	4.4	—	43.7

^a Percentages represent the averages of 12 monthly percentages for all three roosts combined.

WITHIN-YEAR VARIATION IN DIET

We found no significant seasonal differences in the amounts of vegetation (one-way ANOVA, $F = 2.19$, $df = 3,8$, $P = 0.17$), small mammals (one-way ANOVA, $F = 0.90$, $df = 3,8$, $P = 0.49$), or bird eggs (one-way ANOVA, $F = 2.46$, $df = 3,8$,

TABLE 2. Mean monthly compositions of 170 Common Raven pellets collected from the Marsing roost area, April 1985–April 1986.

Month	Vegetation ^a	Insects ^b	Mammals		Birds ^b	Bird eggs ^b
			Small ^b	Large ^b		
Jan	83.0	2.3	1.0	0.0	1.0	1.0
Feb	80.7	7.3	4.0	1.3	2.7	1.7
Mar	90.5	13.3	0.7	1.3	2.0	1.0
Apr	91.8	6.0	1.5	1.0	2.5	2.0
May	80.5	141.5	1.5	1.8	2.5	1.8
Jun	74.3	280.5	0.5	0.5	1.5	1.5
Jul	32.4	323.5	0.0	0.4	2.0	0.8
Aug	67.8	258.3	0.3	0.5	2.8	2.5
Sep	91.8	86.3	0.3	0.7	2.0	1.7
Oct	89.3	113.3	3.0	0.7	1.3	1.3
Nov	94.3	0.0	2.0	0.0	1.0	0.0
Dec	90.3	2.0	2.0	0.5	1.5	1.0

^a Means are expressed as % of total pellet weight per collection.

^b Means are expressed as numbers of individuals per collection.

$P = 0.14$) in Marsing pellets (Table 2). In contrast, numbers of insects, large mammals, and birds in pellets differed significantly among seasons (insects: one-way ANOVA, $F = 54.02$, $df = 3,8$, $P < 0.01$; large mammals: one-way ANOVA, $F = 4.46$, $df = 3,8$, $P = 0.04$; birds: one-way ANOVA, $F = 3.78$, $df = 3,8$, $P = 0.05$). Insects were most abundant in summer and fall pellets (SNK, $P \leq 0.05$), and spring pellets contained significantly more birds and large mammals than winter pellets (SNK, $P \leq 0.05$).

With data from all roosts and both years combined, we found significant declines in small (two-way ANOVA, $F = 8.42$, $df = 3,6$, $P = 0.01$) and large mammal (two-way ANOVA, $F = 6.72$, $df = 3,6$, $P = 0.02$) remains from May through August. Likewise, the abundance of insects in pellets increased significantly during this time (two-way ANOVA, $F = 14.75$, $df = 3,6$, $P < 0.01$). In contrast, we found no significant overall trends in the amounts of vegetation (two-way ANOVA, $F = 0.53$, $df = 3,6$, $P = 0.68$), bird (two-way ANOVA, $F = 1.30$, $df = 3,6$, $P = 0.36$), or egg (two-way ANOVA, $F = 0.28$, $df = 3,6$, $P = 0.84$) remains from May through August.

ANNUAL VARIATION IN THE DIET

During May through August, there were no significant differences in the amounts of vegetation (two-way ANOVA, $F = 4.24$, $df = 1,2$, $P = 0.18$), small mammal (two-way ANOVA, $F = 6.76$, $df = 1,2$, $P = 0.12$), bird (two-way ANOVA, $F = 0.002$, $df = 1,2$, $P = 0.97$), or bird egg (two-way ANOVA, $F = 0.11$, $df = 1,2$, $P = 0.77$) remains between years; however, insects and large mam-

mals were significantly more abundant in 1985 pellets (insects: two-way ANOVA, $F = 163.74$, $df = 1,2$, $P = 0.01$; large mammals: two-way ANOVA, $F = 170.71$, $df = 1,2$, $P = 0.01$).

Whereas the abundance of large mammals in pellets differed between 1984 and 1985, May through August declines in the numbers of large and small mammals were statistically the same between years (large mammals: two-way ANOVA, $F = 0.11$, $df = 3,6$, $P = 0.95$; small mammals: two-way ANOVA, $F = 0.61$, $df = 3,6$, $P = 0.63$). In contrast, both the abundance and trends in insect numbers in pellets from May through August differed significantly between 1984 and 1985 (two-way ANOVA, $F = 7.40$, $df = 3,6$, $P = 0.02$).

INTERROOST VARIATION IN THE DIET

During May through August, there was no significant difference in the abundance of vegetation (two-way ANOVA, $F = 14.31$, $df = 2,2$, $P = 0.07$), insect (two-way ANOVA, $F = 4.22$, $df = 2,2$, $P = 0.19$), small mammal (two-way ANOVA, $F = 0.94$, $df = 2,2$, $P = 0.52$), bird (two-way ANOVA, $F = 4.39$, $df = 2,2$, $P = 0.19$), or bird egg (two-way ANOVA, $F = 9.66$, $df = 2,2$, $P = 0.09$) remains among roosts; however, numbers of large mammals in pellets differed significantly (two-way ANOVA, $F = 686.53$, $df = 2,2$, $P < 0.01$). Large mammal remains were most prevalent in pellets from Wilson Creek.

Although numbers of large mammals in pellets were not the same at all roosts, the decline in abundance of large mammal remains from May through August was consistent among roosts (two-way ANOVA, $F = 2.22$, $df = 6,6$, $P = 0.18$). Likewise, significant declines in small mammals and increases in insects from May through August were observed at all roosts (small mammals: two-way ANOVA, $F = 1.00$, $df = 6,6$, $P = 0.50$; insects: two-way ANOVA, $F = 0.51$, $df = 6,6$, $P = 0.79$).

DISCUSSION

ANALYSIS OF METHODS

Food items differ in digestibility, and thus the relative amounts of indigestible remains in pellets vary among food types. This limits the extent to which comparisons of use among different food types can be made from pellet analyses. However, for a given food type, amounts of remains should be proportional to amounts consumed, so pellet contents may serve as an accurate index to changes in use of a single item.

A variety of techniques is available for quantifying food remains in regurgitated raptor pellets (Marti 1987). Each method has specific restrictions and biases, depending largely on the types of food involved. Given the wide diversity of the raven diet, we chose to quantify pellet contents by three methods. Composition by constituent numbers is relatively sensitive to changes in pellet composition, but it requires that food items be countable and is insensitive to discrepancies in the size and biomass of individuals consumed. Partially consumed items may be over-represented when compared with those that are eaten whole. Likewise, large food items (e.g., cattle) may be under-represented when compared to smaller items. If constituents are not countable (e.g., vegetation), then composition by constituent weight is an alternative; however, the bias from differential digestibility of food items is exacerbated by this measure. When quantified by weight, those items with relatively large amounts of indigestible parts (e.g., cereal grains) may be over-represented, and those with relatively small amounts of indigestible material (e.g., large mammal flesh, fruit, larvae, etc.) may be under-represented. When identification of remains is by hair, eggshell, or feather analysis, neither composition by constituent weights nor numbers is suitable, and frequency of occurrence may be employed (Marti 1987). However, this method is insensitive to differences in amounts of a given food item among individual pellets. Frequency of occurrence data may over-represent relatively minor food items which occur in pellets as often as major food items.

In our study, composition and frequency of occurrence data generally agreed, yet in some cases, they did not. For example, when quantified by number, small mammals appeared of much greater importance than birds and large mammals than when quantified by frequency of occurrence. Likewise, when quantified by weight, mammals appeared to be considerably more important than insects; however, when quantified by frequency of occurrence, the reverse appeared true. These discrepancies may be explained by the biases discussed above. When quantified by number, cattle and birds (i.e., items identified by hair or feather presence) were likely under-represented when compared with small mammals. Similarly, although insects contributed relatively little to pellets for approximately 6 months of the year, because at least one insect usually occurred in a collection throughout the year, the

importance of insects was greatly inflated when described solely in terms of occurrence. Thus, it is important to consider a variety of measures in describing the composition of food remains, and to keep these biases in mind when interpreting our summary table.

Finally, the two-way ANOVA tests we used have no replication. Consequently, no interaction between roost and year effects could be calculated. In a two-way ANOVA without replication, there is an increased chance for a Type II error, especially if it is assumed that there may be a significant interaction effect (Zar 1974). From visual inspection of the data, we observed no obvious interaction between roosts and years, but we do not rule out this possibility. Therefore, there is a possibility that some significant inter-roost or between-year differences were not detected, especially in cases of borderline *P*-values (i.e., inter-roost vegetation and bird egg comparisons).

VARIATION IN THE RAVEN DIET

Without detailed food availability data, many of the dietary trends we observed are unexplainable; however, some of the temporal and spatial differences in diet we found coincided with obvious differences in availability. For instance, grasshoppers were most abundant in pellets during May through October when grasshoppers were most numerous in our study area (U.S. Animal and Plant Health Inspection Service, unpubl. data). Bird remains were most prevalent in pellets during the spring nesting season when nestling birds and eggs were most abundant. Cattle carrion was most common in pellets during spring when cattle calves were most available to ravens.

Among roosts, our data indicate that cattle carrion was used most heavily at Wilson Creek. Wilson Creek was the only roost located immediately adjacent to a cattle feedlot, where ravens were frequently observed feeding on cattle carcasses. Inter-roost differences in use of vegetation and bird eggs, although not significant, are worth discussing. Vegetation was most prevalent in Wilson Creek pellets. Vegetation in pellets from this roost was primarily corn which was frequently included in the cattle feed used at the adjacent feedlot. We often observed ravens picking corn from feeding troughs and from cattle manure at this feedlot. Bird eggs were most abundant in pellets from Marsing. The Marsing roost area was located adjacent to a county landfill and

was also situated along a large irrigation canal where waterfowl and Long-billed Curlews (*Numenius americanus*) nested. We never observed ravens consuming young birds and eggs at this roost, but ravens are notorious for doing so (Stiehl 1978). Furthermore, ravens from the Marsing roost regularly foraged in the adjacent landfill, where they may have consumed eggshells. We observed captive ravens consume either entire domestic chicken eggs or the eggshells alone. This likely also explains the year-round presence of eggshell remains in pellets from Marsing.

The fact that the May–August trends in use of many of the food items were repeated consistently among roosts and between years suggests that our year-round data from the Marsing roost are fairly representative of within-year changes in the raven diet in our study area. However, it is important to note that during 1984 and 1985, grasshopper numbers in southwestern Idaho and southeastern Oregon were the highest recorded in 50 years, with densities of up to 100 grasshoppers/m² in our study area (U.S. Bureau of Land Management, unpubl. data). Thus, use of grasshoppers by ravens during our study may have been much higher than normal.

The diet of ravens in our study area appears to be closely associated with agriculture. Our data suggest that cereal grains and cattle carrion comprise significant portions of the raven diet in southwestern Idaho. This conclusion is further supported by observations of transmitter-equipped ravens; we often observed ravens feeding on cattle carcasses and consuming grain in cattle feedlots and cattle manure, and picking salvage grain from plowed or stubble fields. In addition, montane voles, which are common to cereal grain fields (Palmer 1954), were the most prevalent small mammals represented in pellets. Transmitter-equipped ravens commonly followed harvesting machinery and captured voles that were injured or exposed.

Our findings differ considerably from those of previous studies of the Common Raven diet. Vegetation has never been reported as a significant food for ravens, and insects have been a significant food in only two studies (Nelson 1934, Dorn 1972). Mammals were reported as the principal food item in the stomachs of ravens collected in Oregon (Nelson 1934) and in raven pellets collected in Virginia (Murray 1945, Harlow et al. 1975), Wyoming (Dorn 1972), Alaska (Temple 1974), southwestern Idaho (Kochert 1973; Kochert et al. 1975, 1976, 1979, 1980,

1981), and the United Kingdom (Marquiss and Booth 1986). Bird remains (primarily waterfowl eggs) were the principal food item in raven pellets from Malheur National Wildlife Refuge in south-eastern Oregon (Stiehl 1978).

Based on our findings, considerable local, seasonal, and annual variation in the raven diet may explain the differences between this study and previous studies. Our study used dietary information collected year-round, whereas 12 of 13 previous studies used data collected during only part of a year. Marquiss and Booth (1986) collected dietary information year-round, yet their findings still strongly differ from ours, suggesting that local differences in food availability likely account for these differences. As mentioned above, we sampled raven diets during a grasshopper infestation, which may account for the high use of insects we observed relative to other studies. Furthermore, in 10 of the 13 studies, food remains were collected solely from nest sites. Not only are there biases in analyzing food remains from nest sites (Nelson 1934), but the diet of nesting birds and their young may differ considerably from that of non-nesting birds during the breeding season. This may partially explain the differences between results of our study and those of Kochert (1973) and Kochert et al. (1975, 1976, 1979, 1980, 1981), in which data were collected from nest sites within and adjacent to our study area.

Our data and those of previous studies indicate that Common Ravens are omnivorous generalists that exploit a wide variety of food sources. We found the diet of ravens to be variable among areas, and within and between years. Consequently, dietary sampling during only 1 year or portion of a year, or extrapolating data between years or between nesting and non-nesting birds may be misleading. We recommend intensive, year-round sampling from both nest sites and roosts to adequately describe the raven diet in a given area.

ACKNOWLEDGMENTS

This research was part of a cooperative effort between Pacific Power and Light Company's Environmental Services Department and the U.S. Bureau of Land Management's Snake River Birds of Prey Research Project. We thank W. Kell, C. Johnson, and J. Putera for analyzing raven pellets for this study. C. Baker, A. DeBolt, B. Keller, J. Marks, and P. Olmstead voluntarily assisted in identification of pellet contents. J. Cary, K. Steenhof, and A. Holthuijzen provided statistical advice. We appreciate the helpful comments

and suggestions from J. Coleman, R. Conner, M. Kochert, J. Marks, J. Marzluff, K. Steenhof, and S. Temple which improved the quality of this manuscript.

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