

DAILY AND SEASONAL ACTIVITY PATTERNS OF COMMON RAVENS IN SOUTHWESTERN IDAHO

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ABSTRACT.—From May 1985 through February 1987, we recorded the diurnal activity budgets of 26 radio-marked Common Ravens (*Corvus corax*) in southwestern Idaho. Resting (63% of observations) was the predominant diurnal activity, followed by feeding (13%), flying (13%), and moving along the ground (11%). Raven activity budgets differed significantly among seasons, times of day, and habitat types but not among age classes. Although seasonal times spent in locomotory activities were similar, during spring the proportion of time spent feeding nearly tripled and resting decreased. Ravens exhibited no distinct hourly pattern in feeding during winter; however, ravens fed primarily in the morning during spring and crepuscularly during summer and fall. Ravens mainly fed while in agricultural land and rested while in shrub- or grass-dominated rangeland. Our data suggest that seasonal activity budgets of ravens in southwestern Idaho are influenced by characteristics of the food supply and preparation for reproduction, and that daily patterns of activity are influenced by ambient temperature and food availability. Received 8 May 1991, accepted 15 Jan. 1992.

Verner (1965) suggested that every species has an optimal activity budget specifically adapted to local environmental conditions. The ability to vary time and energy budgets is a “potent means of coping with a changing environment and retaining some degree of adaptation to it” (Pianka 1974). Reproductive activities (Verner 1965), food availability (Boxall and Lein 1989), ambient temperature (Verbeek 1964, 1972), day length (Gibb 1956), and habitat (Eberhardt et al. 1989) can vary temporally, and all have been found to influence avian activity budgets. The degree to which activity budgets are influenced by daily and seasonal changes in the environment can provide important insight into the mechanisms by which an animal adapts to its environment.

The Common Raven (*Corvus corax*) is non-migratory and occurs across a wide variety of habitats throughout the northern hemisphere, ranging from the high Arctic tundra to the desert communities of Mexico (Goodwin 1976). Little is known about how ravens cope with such environmental extremes (Schwan and Williams 1978). Although basic to understanding the ecology of an animal, the activity budget of Common Ravens has not been described. We report the daily and seasonal diurnal activity budgets of Common Ravens in southwestern Idaho and examine

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the effects of time of year, time of day, ambient temperature, day length, age, and habitat on raven activity budgets. Assuming the most important activity of an animal is to obtain sufficient energy to exist, we focus particularly on the amount of time devoted to feeding.

STUDY AREA AND METHODS

We observed ravens from communal roosts located on towers of a 500-kV transmission line in southwestern Idaho (Engel et al. 1992). Livestock-grazed shrub-steppe vegetation (West 1983) and agriculture dominate this area. Major vegetation includes big sagebrush (*Artemisia tridentata*), grasses (*Poa* and *Bromus* spp.), black greasewood (*Sarcobatus vermiculatus*), and shadscale (*Atriplex confertifolia*). A more detailed description of the vegetation and topography can be found in a U.S. Department of the Interior report (1979). From 1978–1987, mean annual temperature averaged $10.1 \pm 1.1^\circ\text{C}$, and annual precipitation averaged $36.4 \text{ cm} \pm 7.8 \text{ cm}$ (U.S. Department of Commerce, unpubl. data). Each year, about two-thirds of the annual precipitation fell from October to March.

We used padded leghold traps and a rocket net to capture ravens (Engel and Young 1989a). Ages of captured ravens were determined by palate color and classified as juveniles (<1 year old), subadults (≥ 1 year old and <3 years old), or adults (≥ 3 years old; Kerttu 1973). Juvenile ravens were also captured by hand as fledglings (35–40 days old) at nest sites in the vicinity of communal roosts. Captured ravens were fitted with a back-mounted radio transmitter weighing either ca 21 g (ravens ≤ 950 g) or ca 30–32 g (ravens >950 g), an aluminum U.S. Fish and Wildlife Service leg band, and a yellow, vinyl-coated nylon, piercing patagial marker on each wing. Patagial markers were numbered uniquely to facilitate identification of individual birds in the field.

From May 1985 through February 1987, we followed radio-marked ravens during four randomly selected observation days each week. One raven was followed on each observation day, from the time the raven left its roost in the morning (ca 30 min before sunrise) until it returned to its roost in the evening (ca 30 min after sunset). Ravens to be tracked were selected sequentially from the sample pool of radio-marked birds and were not tracked more than once per week even if fewer than four birds were available for tracking. Ravens were included in the sample pool until they either died, left the study area, or their transmitters expired.

Ravens were observed from vehicles equipped with 15–60 \times spotting scopes and 7- to 10-power binoculars. We generally approached no closer than 400 m from the focal raven to avoid influencing its behavior. While the focal raven was in view, we recorded its activity every five min. Activities were classified as either feeding, flying, resting (sleeping, perching, standing, or preening), or moving (traveling along the ground). Maintenance activities, such as preening, occurred infrequently, thus we combined them with “resting” activities. Ravens were considered to be feeding if they were observed either swallowing or inserting their bills into the soil or a food item. In addition, habitat type was recorded for all non-flying observations and was classified as either shrub (i.e., shrub-dominated rangeland), grass (i.e., grass-dominated rangeland), pasture, mowed or stubble agricultural field, riparian, or other habitat. Pasture was distinguished from grass-dominated rangeland in that pasture was irrigated, and rangeland was not. Nine additional habitat categories were recorded initially, but each occurred so infrequently that we combined them into “other” habitat for analysis.

Ravens were considered the sample units for statistical analysis. The proportion of time spent engaged in each activity was summarized for individual ravens in each statistical subgroup and expressed as the number of observations in an activity category divided by the total number of observations for that bird. Proportions were arcsine transformed before

TABLE 1

PERCENTAGES OF MONTHLY OBSERVATIONS DURING WHICH COMMON RAVENS ENGAGED IN VARIOUS ACTIVITIES IN SOUTHWESTERN IDAHO, MAY 1985–FEBRUARY 1987

| Month | Feeding (SD)* | Flying (SD) | Resting (SD) | Moving (SD) | N |
|-------|---------------|-------------|--------------|-------------|----|
| Jan. | 16.9 (9.3) | 9.1 (4.5) | 52.8 (10.2) | 21.1 (8.5) | 5 |
| Feb. | 23.2 (22.0) | 9.5 (5.7) | 52.9 (20.2) | 14.4 (12.0) | 6 |
| Mar. | 39.6 (9.6) | 14.6 (15.0) | 34.5 (12.9) | 11.3 (8.9) | 3 |
| Apr. | 61.3 (54.7) | 8.1 (11.4) | 24.2 (34.2) | 6.5 (9.1) | 2 |
| May | 10.1 (9.8) | 19.5 (12.6) | 63.7 (17.7) | 6.8 (8.1) | 8 |
| June | 14.2 (5.4) | 15.0 (7.1) | 63.6 (10.9) | 7.2 (5.6) | 6 |
| July | 11.2 (7.1) | 9.1 (6.8) | 70.2 (12.8) | 9.4 (8.0) | 14 |
| Aug. | 10.5 (5.2) | 9.6 (4.2) | 68.0 (16.2) | 11.9 (10.7) | 11 |
| Sept. | 5.1 (7.0) | 7.6 (5.5) | 79.6 (17.2) | 7.7 (8.3) | 7 |
| Oct. | 10.7 (9.2) | 10.7 (8.0) | 69.1 (15.5) | 9.4 (11.5) | 6 |
| Nov. | 11.0 (9.0) | 13.8 (5.6) | 58.6 (15.5) | 16.7 (15.3) | 5 |
| Dec. | 14.1 (6.9) | 14.4 (10.1) | 55.3 (15.6) | 16.2 (18.0) | 6 |

*SD = standard deviation.

analysis (Zar 1974). Observations were grouped into four seasons: spring (February–April), summer (May–July), fall (August–October), and winter (November–January). Boundaries for these seasonal breaks were determined by gross changes in weather and raven diet (Engel and Young 1989b).

We used two-way analysis of variance (ANOVA) tests to examine seasonal differences in the proportion of the daytime spent engaged in each activity between years, among age classes, and among habitat types. If a significant difference was found with no significant interaction between treatments, one-way ANOVA was used to test for differences in the proportions of time devoted to each activity among seasons, ages, and/or habitat types, respectively. If significant differences were found, then Tukey's Honestly Significant Difference test (Tukey HSD) was used to locate between which seasons, age classes, or habitats differences existed. Analysis of covariance (ANCOVA) was used to test for a linear hourly trend (e.g., increase or decrease) in the proportion of time spent engaged in each activity and to test for seasonal differences in the hourly trend if it existed.

Due to continual addition and loss of marked ravens to and from the sample pool, sampling was not distributed evenly among all statistical subgroups. Thus, age-by-season comparisons could be made only for summer and fall when all three age classes were represented. All statistical tests were evaluated at the $P < 0.05$ level of significance.

RESULTS

We obtained 7753 5-min activity observations from 26 radio-marked ravens—14 adults, five subadults, and seven juveniles. Resting ($\bar{x} = 63\% \pm 14\%$ of observations) was by far the predominant diurnal activity of ravens, followed by feeding ($\bar{x} = 13\% \pm 10\%$), flying ($\bar{x} = 13\% \pm 9\%$), and moving ($\bar{x} = 11\% \pm 7\%$).

Seasonal activity budget.—The proportions of diurnal time spent flying and moving were similar throughout the year (one-way ANOVA, $P_s >$

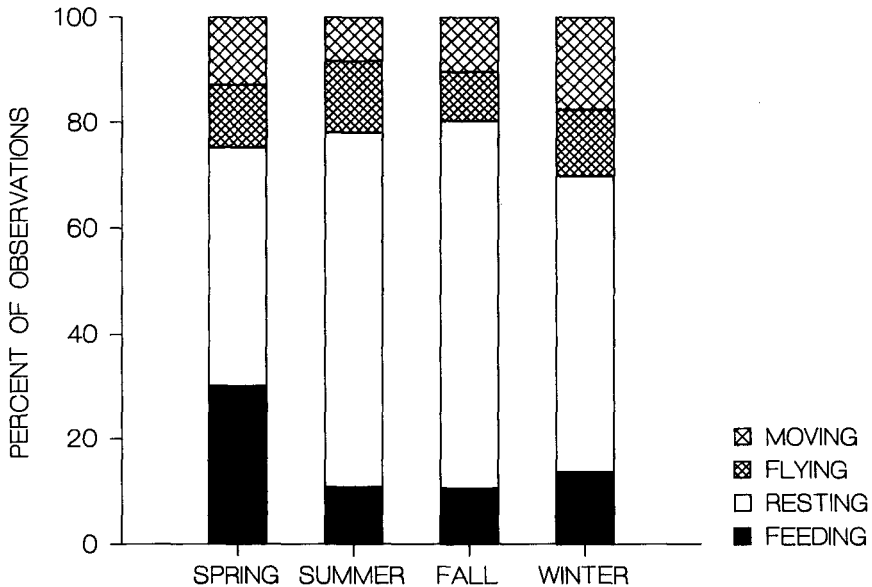


FIG. 1. Percentages of seasonal observations during which Common Ravens engaged in various activities, May 1985–February 1987.

0.30); in any given season, individual ravens spent 9–14% of the day flying and 8–18% of the day moving (Table 1; Fig. 1). The proportions of time ravens devoted to feeding and resting, however, differed significantly among seasons (one-way ANOVA, $P_s < 0.01$). Ravens spent similar proportions of time feeding from summer through winter (Tukey HSD, $P_s > 0.79$) but spent nearly three times as much time feeding during spring (Tukey HSD, $P_s < 0.02$). In addition, ravens spent more time resting during summer and fall than during spring (Tukey HSD, $P_s < 0.05$). Except for the proportion of time spent moving (two-way ANOVA, $P < 0.01$), these seasonal relationships were consistent between years (two-way ANOVA, $P_s > 0.15$).

We found no significant difference in the proportions of time ravens devoted to various activities among age classes (summer and fall only; two-way ANOVA, $P_s > 0.14$); this lack of difference was consistent between summer and fall (two-way ANOVA, $P_s > 0.31$).

Daily activity budget.—Hourly patterns in both the percentages of time spent feeding and flying differed significantly among seasons (ANCOVA, $P_s < 0.04$; Fig. 2). During spring, the proportion of each hour devoted to feeding decreased throughout the day, while during summer and fall, feeding maxima appeared bimodally distributed. No distinct hourly pat-

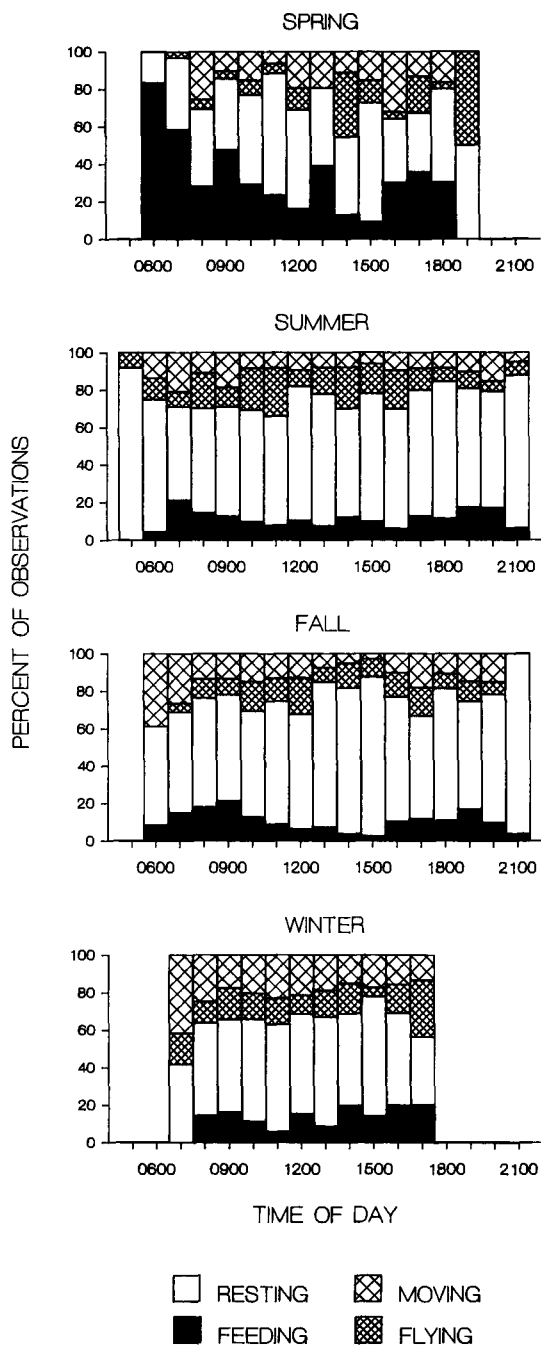


FIG. 2. Percentages of observations during which Common Ravens engaged in various activities in different seasons and times of day, May 1985–February 1987.

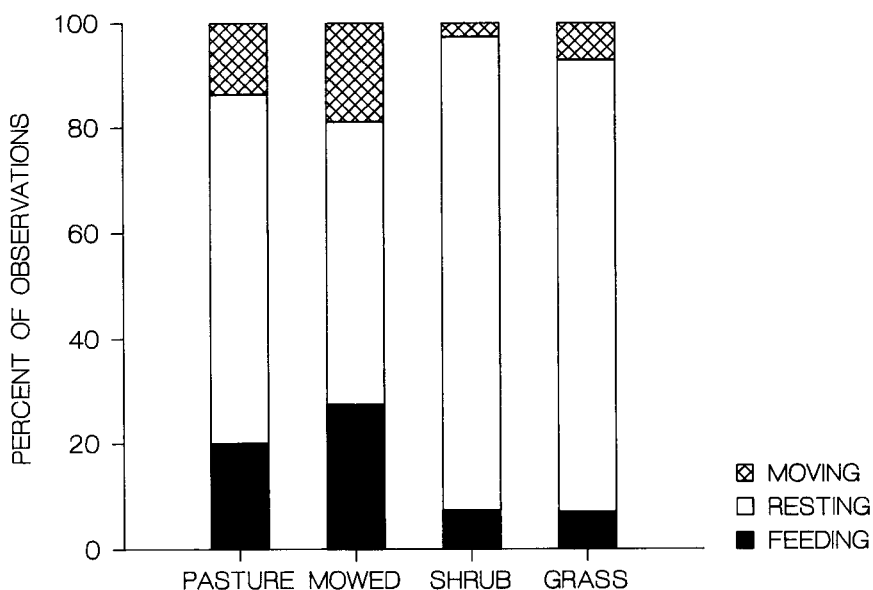


FIG. 3. Percentages of observations during which Common Ravens engaged in various activities in different habitat types, May 1985–February 1987.

tern in feeding was apparent during winter. The proportion of each hour devoted to flying appeared greatest in the late afternoon during spring and in the middle of the day during summer and fall. In contrast, no significant linear trends were apparent in the proportions of hours spent either resting or moving (ANCOVA, $P_s > 0.14$), and these patterns did not differ significantly among seasons (ANCOVA, $P_s > 0.12$).

Habitat effects on activity.—The percentages of time ravens devoted to feeding, resting, and moving differed among habitat types (two-way ANOVA, $P_s < 0.001$; Fig. 3). These differences were similar among seasons (two-way ANOVA, $P_s > 0.75$): in any given season, ravens spent a higher proportion of the daytime feeding, and less time resting, while in mowed or stubble agricultural fields and pastures than when they were in either shrub or grass habitats (Tukey HSD, $P_s < 0.02$).

DISCUSSION

Passerine birds have extremely high weight-specific metabolic rates among vertebrates (Lasiewski and Dawson 1967), thus feeding is typically a dominant daytime activity (Schartz and Zimmerman 1971, Fischer 1981). In ravens, however, resting was the predominant daytime activity during all times of year. This difference may be due to the relatively large

body size of the raven and/or the abundant food supply in our study area. The Common Raven is the largest passerine bird (Goodwin 1976), and larger birds tend to spend less time feeding than do smaller ones (Gibb 1954). In addition, the abundant food supply for ravens in our study area (Engel and Young 1989b) may have enabled ravens to devote relatively little time to acquiring food. Food density has been known to influence negatively the amount of time spent feeding by an animal (Pianka 1974).

Seasonal activity budget.—Similar to other passerine birds (Gibb 1956, Verner 1965, Verbeek 1972), ravens exhibited prominent seasonal changes in their activity budgets, the most obvious of which was a dramatic increase in feeding during spring. This springtime hyperphagia was likely due to increased energy demands of breeding activities. Increased day lengths in spring stimulate gonad development in a variety of birds, and the concomitant energy demands are often met by increased feeding (Ken-deigh 1941).

Lack of seasonal variation in time engaged in locomotory activities (i.e., flying and moving) may further reflect the perennially abundant concentration of food for ravens in our study area (Engel and Young 1989b). Year-round, ravens in our study area tended to fly to a single foraging area (e.g., cattle feedlot, landfill, or stubble corn field) where they spent the majority of the day before returning to the roost in the evening (Engel 1990). Furthermore, with seasonal times devoted to locomotory activities remaining stable, the springtime decrease in resting suggests an inverse relationship between feeding and resting as observed in Rock Pipits (*Anthus spinoletta*; Gibb 1956).

Although feeding rates and gross energy intake in passerine birds are typically influenced directly by ambient temperature (Seibert 1949) and day length (Gibb 1956), raven feeding rates appeared unaffected by either. Below the thermoneutral zone, temperature regulation in birds requires an increase in metabolism and energy consumption (Calder and King 1974). The lower critical temperature of winter-acclimatized ravens is below -20°C (Schwan and Williams 1978). Mean daily temperatures in our study area, however, were never below -15°C (U.S. Department of Commerce, unpubl. data) and were thus within the lower bounds of the thermoneutral zone for ravens. Similarly, although relatively few daylight hours were available for feeding during winter, ravens spent virtually the same proportion of the daytime feeding during winter as during summer. This apparent lack of influence of day length on raven feeding reflects the ability of ravens to obtain adequate amounts of food on a daily basis in our study area (Engel and Young 1989a, b).

Daily activity budget.—Seasonal variation in daily feeding patterns such as we observed has been described in a variety of birds and is thought to

relate to changes in daily patterns of food availability (Fischer 1981, Boxall and Lein 1989) and ambient temperature (Gibb 1956, Verbeek 1972). Bimodal feeding patterns, in particular, are common in both migratory and non-migratory birds (Baldwin and Kendeigh 1938, Lees 1948, Gibb 1956, Boxall and Lein 1989) and are apparently adaptive for accumulating overnight energy reserves immediately before roosting and then replenishing depleted reserves the following morning (Murton and Westwood 1977).

The bimodal foraging pattern of ravens may have been influenced by crepuscular activity maxima of their main prey species as observed in Snowy Owls (*Nyctea scandiaca*; Boxall and Lein 1989). Grasshoppers (Orthoptera) were one of the main food sources for ravens in summer and fall (Engel and Young 1989b), and during the heat of the day, grasshoppers were likely less active and thus less obvious to foraging ravens. Uvarov (1977) found that grasshopper activity became depressed at temperatures $\geq 41^{\circ}\text{C}$, which are not uncommon during summer and fall in our study area.

Bimodal feeding patterns of ravens were also likely influenced by relatively high ambient temperatures during mid-day in summer and fall as observed in White-crowned Sparrows (*Zonotrichia leucophrys*; Morton 1967). When ambient temperatures exceed the upper limits of a bird's thermoneutral zone, active regulation of body temperature can become more crucial than foraging (Calder and King 1974); consequently, birds may become less active, seek shade, or fly to higher, cooler altitudes to decrease or maintain acceptable body temperatures. This phenomenon may also explain the increase in flying we observed during mid-day in summer and fall.

Lack of any distinct feeding pattern during winter may have been due to a need to accumulate energy more evenly throughout the day during cold weather. Morton (1967) observed a loss of the bimodal feeding pattern in White-crowned Sparrows during stressful weather.

Habitat effects on activity.—During any given season, ravens primarily fed while on agricultural land and rested while in shrub- or grass-dominated rangelands. These patterns of habitat use were reflected in the composition of the raven diet, a large proportion of which was comprised of food items obtained from agricultural land (Engel and Young 1989b). Food sources for ravens may have been more concentrated or of higher quality in agricultural habitats than in "natural" (i.e., shrub and grass) habitats. Eberhardt et al. (1989) found that Canada Geese (*Branta canadensis*) foraged most often in habitats where food was more concentrated or of higher protein content than in other habitats.

Ravens may have used shrub- or grass-dominated rangelands primarily

for resting because of the protective cover the taller, denser vegetation provides from both the weather and predators. Caraco et al. (1980) found that flocks of the Yellow-eyed Junco (*Junco phaeonotus*) were able to spend less time watching for predators the closer they were to cover.

Overall, raven activity budgets appeared to be strongly influenced by characteristics of food sources in our study area and preparation for reproduction, rather than by age of bird or changes in ambient temperature and day length. Ambient temperature may have influenced daily patterns of activity but not the overall percentages of time devoted to various activities. Therefore, we expect raven activity budgets may differ significantly in areas with less abundant and more dispersed food supplies than in our study area, but that dramatic springtime increases in feeding should occur regardless of locale.

ACKNOWLEDGMENTS

This research was part of a cooperative study by Pacific Power's Environmental Services Department and the U.S. Bureau of Land Management's Snake River Birds of Prey Research Project. Financial support was provided by the study cooperators and the Univ. of Wisconsin-Madison, Dept. of Wildlife Ecology. We extend our deepest thanks to J. Roppe, M. Kochert, K. Steenhof, and S. Temple for guidance and support during this study. We greatly appreciate the efforts of A. Brody, R. Bowman, and W. Kell for enduring long, strenuous days of radio-tracking and trapping ravens, and to D. Ames, K. Gonzalez, and K. Hegstad for their assistance in trapping. J. Cary provided invaluable statistical advice. The helpful comments and suggestions of J. Botero, M. Kochert, R. Small, K. Steenhof, and S. Temple greatly improved the quality of this manuscript.

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