

des Moissons *Anser fabalis fabalis* et *Anser f. rossicus*. Le Gerfaut 70:499–558.

WRIGHT, G., AND H. BOYD. 1983. Numbers, age and sex of Greylag and Pink-footed geese shot at Loch

Leven National Reserve, 1966–1981. Wildfowl 34: 163–167.

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## Does the Early Common Raven Get (and Show) the Meat?

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In the forests of western Maine, Common Ravens (*Corvus corax*) aggregate in large crowds at feeding bonanzas such as carcasses (Heinrich 1988a). A variety of evidence from field observations (Heinrich 1988b, 1989, Marzluff et al. 1994) indicates that the large crowds are primarily the result of recruitment from nocturnal communal roosts, although local enhancement by vocalizations also plays a role in short-range recruitment (Heinrich 1988b, 1989, Marzluff and Heinrich 1991, Heinrich and Marzluff 1991).

While build-up of large numbers is associated with recruitment from roosts, the mechanism whereby this occurs is unknown. There is no obvious vocal signal that birds give when leaving their roosts (Marzluff and Heinrich unpubl. data), so it seems unlikely that knowledgeable birds draw the rest of the roost behind them by way of a vocal display. One hypothesis is that, given a roost containing many hungry individuals that have no knowledge of food, the birds knowledgeable of a bonanza will leave first and the rest follow (Ward and Zahavi 1973). This hypothesis predicts that at new food bonanzas the birds (such as ravens, which can go many days without food; Heinrich 1994a) that have not previously fed should arrive early and in a crowd. Subsequently, after most of the birds are knowledgeable concerning the food source and have become satiated, they no longer have need to follow the early bird, and they should then arrive later and in smaller groups. I here test these predictions.

*Methods.*—My studies on group numbers and recruitment were conducted in the two winters (November–March) of 1991–1993 in western Maine (see Heinrich 1988b, 1989). Feeding stations of primarily cattle carcasses were provided in the forest. Throughout most of the study, night temperatures were below  $-15^{\circ}\text{C}$  and the meat was “rock” hard. Although ravens cache much food when they can tear off chunks (Heinrich 1989), at subzero temperatures the birds can only remove the meat in small chips, and no caching occurred. Flights of birds to the meat were observed every morning from approximately 30 min prior to sunrise until an hour after. Observations of arrivals were made from the tops of spruce trees located at

least 200 m away from the bait. Observations of crowd composition were conducted from blinds constructed of conifer branches within 5 to 10 m of the bait. Additional data on flock sizes from 1987 are also included.

The raven groups were often diffuse and “strung out” at the later stages of a feeding cycle at a bait. This leaves room for interpretation as to what constitutes a group or a “flock.” To be conservative, I defined as a group those birds that arrived approximately within no more than 10 s of each other. In level flight, ravens fly at approximately 50 km/h (as determined by car odometer of birds patrolling along roadsides). Thus, birds as far apart as 150 m were considered to arrive together because they were potentially (and likely) in visual contact of each other. Generally, however, most groups were separated by at least a minute (nearly 1 km).

Known individuals were observed at food patches to determine residence times for estimating the total numbers of birds that may arrive at a bait, as well as the effect of dominance on residence times. The individuals were identified primarily by patagial wing tags (see Heinrich 1988b), although previously unmarked birds were also identified by obvious physical features (e.g. a white wing feather, an unusual bill shape). Twelve of the patagial-marked birds that were observed at the bait came from a pool of 419 released near the site over the previous six years. Seventeen other individuals that earlier had been marked and released near the bait in the current studies were sited at the feeding stations. These birds came from two groups, A and B. All of the birds of group B were first-year birds (for method of identification, see Heinrich 1994a), and all of the birds in group A had molted to adult plumage. Birds of groups A and B were released on 17 January 1993, after having been held in an aviary complex within 1 km of the release site for 12 and 3 months, respectively. The dominance status of these birds had been determined (as described by Marzluff and Heinrich 1991) prior to release and assigned as D (dominant), S (subordinate), or M (intermediate) through a total of 517 dominance interactions. Dominance of the previously uncaged

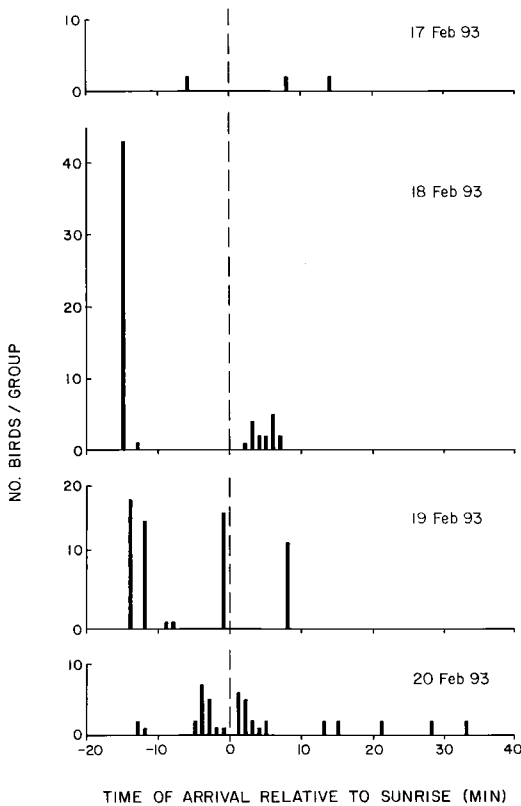


Fig. 1. Numbers and times of arrival (relative to sunrise) of ravens at a cow carcass on four successive days at beginning of a feeding cycle. Each group represented by one bar. A new bait was provided two days previously (15 February 1993).

birds at the bait was determined by feather posture (Gwinner 1964, Heinrich 1988b) in those cases where these postures were unambiguous.

The data of group sizes during late and early portions of the feeding cycle are derived from five separate food patches that were provided in 1987, 1992, and 1993. However, early and late groupings of birds were not all from the same baits. For example, there were no late groupings at a sheep and a deer carcass, because all the meat was consumed quickly. On the other hand, most of the data on late groupings refer to superbonanzas of whole, skinned Holstein cows (> 600 kg each), or piles of 10 to 12 calves (> 40 kg each calf).

**Results.**—A small number of birds typically fed on a carcass for one or several days, followed later by a tight flock of 40 or more arriving before sunrise (Fig. 1; see also Heinrich 1989:fig. 9). Over subsequent days, birds still arrived in groups, but these groups were always smaller. Furthermore, many birds arrived later.

Early in the feeding cycle at a new bait, most of the

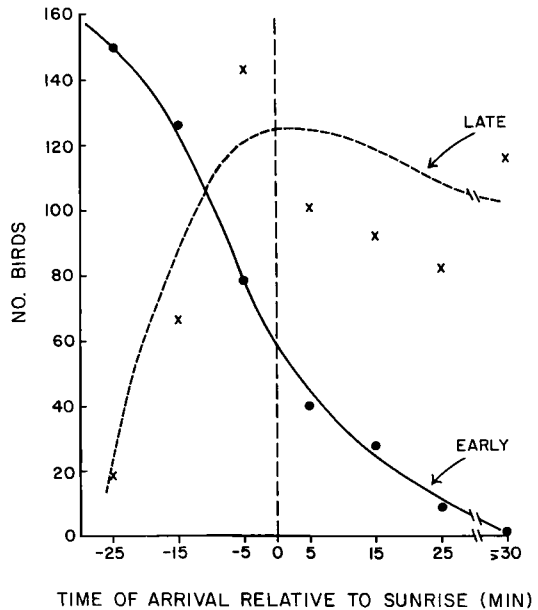


Fig. 2. Morning time of arrival of birds to carcasses early in feeding cycle (two to three days after feeding began) vs. later in cycle. Early in cycle most birds arrive about 15 to 25 min prior to sunrise, whereas later in cycle they arrive later and over a much greater time span. Lines showing general trends are drawn by eye.

birds arrived 20 or more minutes before sunrise, whereas at a well-established feeding site many birds continued to arrive 0.5 h after sunrise (Fig. 2). The large numbers of birds that arrived early in the morning came from one direction, primarily in one large flock, which on subsequent days became smaller and/or was broken up into smaller groups (Fig. 3). Late in the feeding cycle, most of the birds arrived by twos or one at a time (Fig. 3).

Group size of arriving birds also varied diurnally (Fig. 4). Most of the large groups (> 15 birds) came before sunrise. Small groups (2-5) and single birds also arrived before sunrise; however, these small groups continued to arrive long after the large groups (Fig. 4). Intermediate-sized groups (6-14 birds) showed intermediate response, with many arriving before sunrise, but others continuing to come even 35 min after sunrise.

There also were other differences between the birds' behavior early and late in the feeding cycle. Early in the cycle the birds were highly vocal (a great variety of calls) during their approach to the bait, and when coming near it they dove down to then feed. In contrast, late in the cycle most of the bird groups arrived silently or with little vocal behavior. They landed in the trees near the bait, often loitered there for 0.5 h or more. They sometimes left without feeding. Some

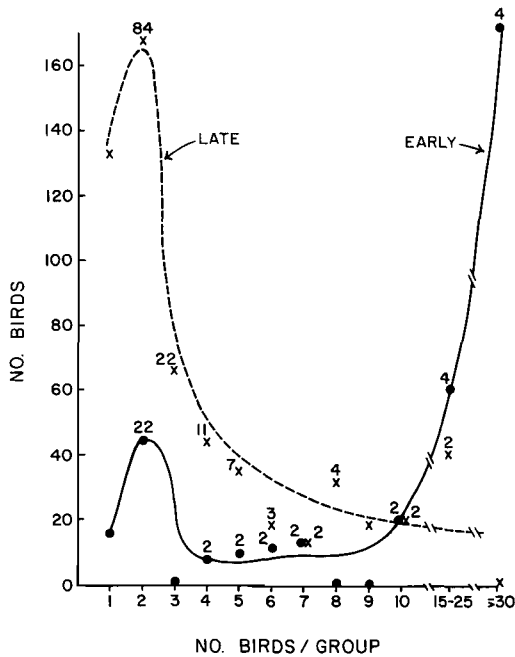


Fig. 3. Group size as function of time in feeding cycle at carcasses. Early in feeding cycle, most birds come as part of a large group, whereas later they come primarily as singles or pairs. Numbers refer to numbers of groups.

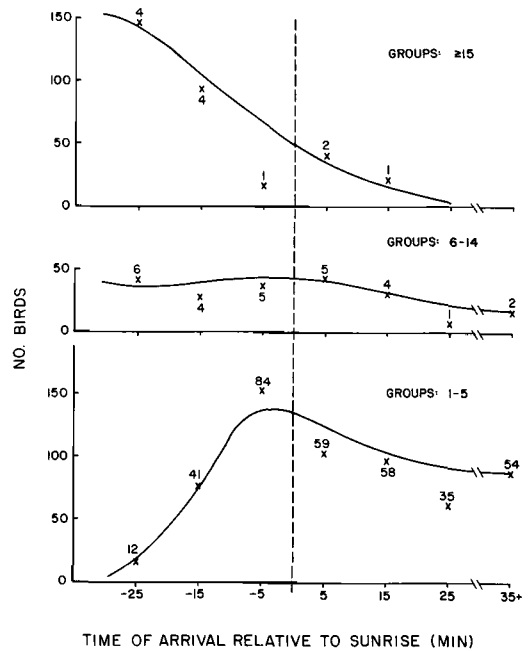


Fig. 4. Morning time of arrival of birds as function of group size. Birds travelling in largest groups arrive early (top) and later-arriving birds tend to come in smaller groups (bottom). Numbers refer to numbers of groups.

birds arriving from the distance flew over the bait, appearing to only inspect it from the air before flying on.

The number of birds arriving and feeding at baits at any one time was only a small portion of the total consumers of the bait. At one station I simultaneously provided two whole adult Holstein cows. The cows were skinned to provide easy access to the meat. An adult Holstein cow has a mass of 635 kg on average, and the two cows totalled at least 1,000 kg of meat. In 10 days at least three-fourths of the solidly frozen meat was gone, and only ravens had eaten the cows. No coyote (*Canis lutrans*) or other tracks were on the snow near the cows. How many ravens does it take to consume about 750 kg of meat in 10 days?

In order to find out how much meat ravens eat under comparable (subzero) weather conditions, I provided two aviary birds with frozen calf meat, weighing the frozen chunks every day to see how much was removed. Over a period of seven days, the two birds removed on the average 830 g per day or 415 g each. Thus, 750 kg of meat constitutes enough food for about 1,800 raven days ( $750,000/415$ ), or about 180 ravens for 10 days, if they fed only there.

An estimate of the minimum number of ravens that had eaten the two cows must include not only what a certain number could have eaten if they had been

feeding only there, but also an estimate of how many days they fed there (Fig. 5). Generally 50 or fewer birds were feeding at the carcasses at any one time. In 20 surveys at the meat (between 22 January and 4 February 1993), 785 birds were counted, and 12 individually identified birds that were among them were sighted 30 times. Thus, at any one time, 1 in 26.1 ( $785/30$ ) birds was marked, and the total population of birds feeding at that bait was estimated to be 314 ( $12 \times 26.1$ ). This is a minimum estimate because I likely missed seeing some marked birds.

The 12 known individuals were at the carcass only on 37% of the 25 days surveyed. If they consumed 415 g each per day but fed 63% of the time at other sites (Fig. 5), then they each consumed only 154 g at the one bonanza and the number of ravens that were involved in removing the 750 kg of meat could have been 490. This number represents an upper estimate. Therefore, the two estimates indicate that between 300 to 500 birds were feeding or had fed at this superbonanza.

To put these numbers into perspective relative to raven abundance, I tabulated the numbers of birds seen as a function of distance and time driving or walking in the Maine, New Hampshire, and Vermont area. During 52 h of wintertime travelling (driving and walking during December 1992–February 1993)

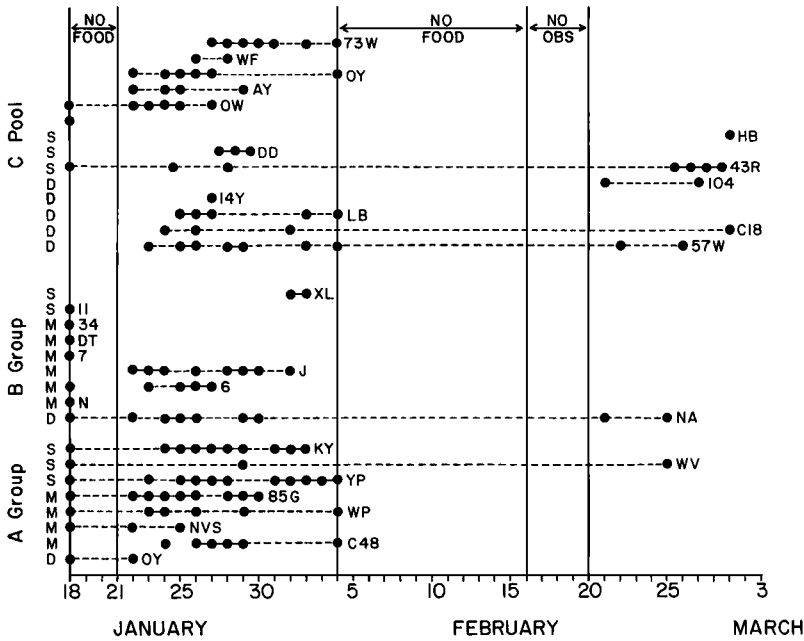


Fig. 5. Visitations of known individuals (identified by letters and/or numbers) at a superbonanza bait. Each large dot represents numerous sightings of the same individual bird. Birds of groups A and B were released on 17 Jan after having been held in aviary for 12 and 3 months, respectively. Birds of group C were of a pool of 419 marked birds released near site over previous six years. Status where known refers to D (dominant), S (subordinate) or M (intermediate). Solid lines connect consecutive days of residence, and broken lines indicate presence at the same bait, but with no sighting on intervening days.

covering approximately 1,760 km, I saw five pairs of ravens and seven singles. Thus, on the average, I covered 100 km to see one raven, and many of these birds were seen at a distance of at least 0.5 km. Furthermore, it is likely that the birds are more common along highways (where I was on the lookout) than away from them. My conclusion is that ravens are sparsely distributed even though large numbers may gather at a large food bonanza.

As indicated, the ravens did not stay at a feeding site even though the food there remained abundant. However, when they were absent, or when attempts were made to disperse them by removing the bait, they did not necessarily leave the area entirely. For example, although removal of the superbonanza for three days resulted in 4 of 17 previously identified individuals not showing up again (Fig. 5), a fifth (34R) was seen at that site on several occasions two months later (in late March). Many other birds were absent for a few days or weeks and, as individuals left, new ones were continually arriving (Fig. 5). Even after the bait was removed for 12 days, I saw two new birds (HB and 104) not seen previously in 25 days of monitoring, in addition to five of the previously seen birds.

Since only a portion of the ravens that know the location of a bait is found there on any one day, what

determines which ones stay and which ones leave? One hypothesis is that dominant individuals maintain a long residence, while subordinates are evicted and forced to wander. If so, long versus short residence times of dominants versus subordinates should be evident. The data, however, do not support this idea. For example, bird 43R was one of the most subordinate ones at the bait, yet it had the longest residence times (Fig. 5), being seen into late March. A very dominant bird (14y) was seen only once. Of those birds whose dominance was established for three or more months within groups in the aviary prior to release, there also was no trend. For example, birds OY and NA (the most dominant birds) stayed four days and over a month, respectively, whereas highly subordinate individuals also stayed for equally variable lengths of time (Fig. 5).

If one considers residence time on consecutive days at the bait, the longest residence time (six days) was that of a subordinate bird (Ky) and three days for dominants (birds LB and WA). Mean residence times ( $n = 16$ ) of subordinates was 2.25 days, whereas it was 1.24 days ( $n = 25$ ) and 1.61 days ( $n = 26$ ) for dominants and intermediates, respectively. Similarly, the total duration of longest intervals between sightings of individuals at a bait are highly erratic. Means were 19.6 days ( $n = 6$ ) and 17.6 days ( $n = 7$ ) for dominants

and subordinates, respectively, with a range of 1 to 43 days for each.

*Discussion.*—As first pointed out by Ward and Zahavi (1973), communal bird roosts may serve as information centers from where naive birds are led to food. A literature of hundreds of papers on the information-center hypothesis (ICH) has accumulated and some authors find confirmation of the idea (Waltz 1982, 1985, Rabenold 1987), while others suggest that roosts may be merely convenient resting places near food (Caccamise and Morrison 1986, Morrison and Caccamise 1990). As pointed out by Rabenold (1987), "Part of the problem lies in the reluctance by some authors to accept anything short of a waggle-dance or a detailed map as information." Since information is that which reduces the uncertainty of the recipient, Rabenold reasoned that any cue that increases a bird's foraging success that is obtained at the roost or colony qualifies as information exchange because it reduces the recipient's uncertainty. Waltz (1982) also agreed that active communication is not essential for the information-center hypothesis to apply. Thus, the problem is whether or not birds do in fact follow others to food. Mock et al. (1988) do not think that they do, stating "widespread acceptance of the ICH is still premature. We do not know if any birds regularly reap the proposed benefits through information exchange at the assembly. . . ."

In the winter, ravens in the northern New England forests feed from carcasses, a highly patchy rich food resource. As argued elsewhere (Heinrich 1988b, 1989, Marzluff et al. 1994), the use of these carcasses by large groups that accumulate is best explained by recruitment from communal roosts. These roosts serve as overnight resting places near food (Caccamise and Morrison 1986, Morrison and Caccamise 1990). However, they are formed there (apparently because they reduce commuting costs) only after recruitment from a distant location. That is, without the information exchange occurring at a distant roost, there would be no large build-up of birds at the food and, subsequently, no roost near it. Communal roosting may be a conditional strategy, used primarily when food is temporarily abundant in patches (Davies 1986). Presumably, if food were less patchy, birds could always remain in the same roost and feed at the closest feeding site(s).

Like Rabenold (1987), I argue that recruitment could be demonstrated by large numbers of birds arriving in groups shortly after the bait was discovered. Furthermore, the data suggest a mechanism: following the early bird to leave the roost.

Almost all of the large groups of ravens came early in the feeding cycle. Furthermore, they only came prior to sunrise. The data are consistent with the idea that birds anxious to feed, yet not knowledgeable of food, follow those leaving early. Those leaving early likely have a predetermined destination. However, the meat at a very large carcass lasts a number of days

and, after the birds know of its location, they no longer need to arrive before dawn. They can now leave on their own at any time. In accordance with this prediction I found that although the size of the feeding group soon stabilizes, the times of arrival of the individuals get spread out, and birds begin to arrive as individuals, pairs, or in small groups.

Counter to the above expectation, it could also be reasoned that as more birds become knowledgeable of a carcass, the more the distribution of arrivals becomes skewed to earlier in the morning. However, satiation likely mitigates against this. As already indicated, late in the feeding cycle birds often pass by in the morning or loiter nearby for hours without feeding at all. The more well-fed a bird is (i.e. the more it has knowledge of food bonanzas), the less likely it may be inclined to head directly to a food source 0.5 h before daylight. Adult ravens under the weather conditions of my study (concurrently examined) have an average mass loss of only 45 g (or 3.5% body mass) per day under food deprivation, and they regain all of this mass in 5 h or less of feeding (Heinrich 1994a). Thus, ravens that have fed all day or until late in the evening are presumably not as highly motivated to feed the next morning as those that have not fed for a week or more.

One unanswered question is how it is possible that several hundred birds can learn of the bait, whereas roost size in the study area is almost always less than 100, and usually less than 50 (pers. obs.; pers. comm. from Frank Oatman, George Lisi, Brett Engstrom and Clarence Nutting, Marzluff et al. 1994). Therefore, over 300 birds feeding at a carcass cannot be accounted for by recruitment from the local roost alone. More than one roost may then be consolidated, or several roosts may partake of the same bait.

Our radio-tracking data (Heinrich et al. 1994) show that birds wander widely, visiting many roosts. They may visit several different roosts in succession, staying at each for varying amounts of time. The present data show birds feeding at a bait for a day, or a week, and also being absent for a day, or even over a week. These birds could not have cached food from the rock-hard frozen carcasses, as they never removed food of sufficient size for caching. All of their food in this midwinter study was eaten on site. The varying lengths of residency, therefore, indicate that birds spent possibly weeks feeding at other sites, and/or that they have a strong tendency to leave after being satiated. The residency data combined with the radio-tagging data indicate that the birds use their reserves gained at any carcass to travel (i.e. to be "vagrant"). If so, how can so many birds be recruited to one site?

Consistent with the data so far, suppose now a hypothetical example where 50 birds become satiated at a cow carcass and then leave it and the local roost. Within a few days they may be hungry again and join another roost, then joining their new roost mates at their local food bonanzas and, therefore, not return-

ing to the old, still-ample food bonanza. However, if these other roosts are not tapping into good food, then the raven that joined them is now instead forced to return to the food site it had fed from previously. Meanwhile, the new, hungry roost mates will follow. In this way information of the bonanza becomes spread between all of the roosts over hundreds of kilometers and, thus, a superbonanza should draw hundreds of visitors from afar. As previously indicated, the individual sharers gain benefit because they gain access to food otherwise defended by territorial adults (Heinrich 1988b, 1989, Marzluff and Heinrich 1991).

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#### LITERATURE CITED

- CACCAMISE, D. F., AND D. W. MORRISON. 1986. Avian communal roosting: Implications of diurnal activity centers. *Am. Nat.* 128:191-198.
- DAVIES, N. B. 1986. Food, flocking and terrestrial behaviour of the Pied Wagtail (*Motacilla alba yar-ellii* Gould) in winter. *J. Anim. Ecol.* 45:235-254.
- GWINNER, E. 1964. Untersuchungen über das Ausdrucks- und Sozialverhalten des Kolkraben (*Corvus corax* L.). *Z. Tierpsychol.* 21:657-748.
- HEINRICH, B. 1988a. Foodsharing in the raven, *Corvus corax*. Pages 285-311 in *The ecology of social behavior*. (C. N. Slobodchikoff, Ed.). Academic Press, New York.
- HEINRICH, B. 1988b. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*. *Behav. Ecol. Sociobiol.* 23:141-156.
- HEINRICH, B. 1989. Ravens in winter. Simon and Schuster, New York.
- HEINRICH, B. 1994a. Dominance and weight-changes in the Common Raven, *Corvus corax*. *Anim. Behav.* In press.
- HEINRICH, B. 1994b. When is the Common Raven black? *Wilson Bull.* In press.
- HEINRICH, B., AND J. MARZLUFF. 1991. Do Common Ravens yell because they want to attract others? *Behav. Ecol. Sociobiol.* 28:13-21.
- HEINRICH, B., D. KAYE, T. KNIGHT, AND K. SCHAUMBURG. 1994. Dispersal and associations among a "flock" of Common Ravens, *Corvus corax*. *Condor*. In press.
- MARZLUFF, J. M., AND B. HEINRICH. 1991. Foraging by Common Ravens in the presence and absence of territory holders: An experimental analysis of social foraging. *Anim. Behav.* 42:755-770.
- MARZLUFF, J. M., B. HEINRICH, AND C. MARZLUFF. 1994. Raven roosts are mobile information centers. *Anim. Behav.* In press.
- MOCK, D. W., T. C. LAMEY, AND D. B. A. THOMPSON. 1988. Falsifiability and the information centre hypothesis. *Ornis Scand.* 19:231-248.
- MORRISON, D. W., AND D. F. CACCAMISE. 1990. Comparison of roost use by three species of communal roostmates. *Condor* 92:405-412.
- RABENOLD, P. P. 1987. Recruitment to food in Black Vultures: Evidence for following from communal roosts. *Anim. Behav.* 35:1775-1785.
- WALTZ, E. C. 1982. Resource characteristics and the evolution of information centers. *Am. Nat.* 119:73-90.
- WALTZ, E. C. 1985. On tolerating followers in information-centers, with comments on testing the adaptive significance of coloniality. *Waterbirds* 6:51-56.
- WARD, P., AND Z. ZAHAVI. 1973. The importance of certain assemblages of birds as "information-centres" for food finding. *Ibis* 15:517-534.

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