COMMON RAVENS ARE ATTRACTED BY APPEASEMENT CALLS OF FOOD DISCOVERERS WHEN ATTACKED

BERND HEINRICH[1], JOHN M. MARZLUFF[2], AND
COLLEEN S. MARZLUFF[2]

[1]*Department of Zoology, University of Vermont, Burlington, Vermont 05405, USA; and*
[2]*Greenfalk Consultants, 8210 Gantz, Boise, Idaho 83709, USA*

ABSTRACT.—When adult territorial Common Ravens (*Corvus corax*) aggressively defend carcasses from vagrant immatures, both dominant and subordinate immature birds respond with begging postures and vocalizations. We demonstrated through experiments in an aviary complex that these vocalizations attract other ravens that then learn of new feeding opportunities. Nearby free-ranging ravens also are attracted to begging vocalizations. Begging is most common when six or fewer immatures interact with adults. Typically, fewer than five birds are attracted locally to begging vocalizations, a number that is not sufficient to account for the large numbers of ravens that eventually assemble at a carcass. Most of the recruitment to carcasses, therefore, cannot be explained by attraction to local vocalizations alone. *Received 21 October 1991, accepted 19 November 1992.*

THE EVOLUTIONARY significance of bird aggregations has long been of interest (Pulliam 1973). Numerous advantages of flocking have been suggested, including increased vigilance (Caraco 1981), swamping of predators or competitors (Wallace and Temple 1987, Marzluff and Heinrich 1991), and diversion or protection from predators (Kenward 1978). However, despite the wealth of information and theory on the potential evolutionary significance or adaptiveness of bird aggregations, the proximate behavioral mechanisms causing birds to form groups have been little investigated.

There are numerous potential scenarios for how birds may aggregate. Solitary individuals may incidentally aggregate by using the resource itself as a cue. Numbers of birds could then gradually increase simply because no mechanism exists to disperse them. Group size could also increase as naive birds follow others already at or on their way to the resource. When the advantages of individuals that follow also accrue to those already in the group, then the originally "passive" cues that are given by birds in the group and that the followers decipher should evolve to become amplified and/or to be more frequently given. A still further step in the evolution of group formation could involve the giving of specific cues or calls (Elgar 1986, Chapman and Lefebvre 1990) if any of the above mechanisms of group formation are inadequate in generating groups. In the same way, when the signallers incur more costs than benefits, they should evolve to mute or alter those signals that potential followers could use.

If the actions associated with preexisting behaviors (flight patterns, vocalizations, etc.) function as adequate signals for attracting conspecifics, the gradual evolution of specific recruitment signals would depend, in part, on the perceptive limitations of the receivers. Thus, "passive" recruitment in highly perceptive animals would not always be functionally different from "active" recruitment involving such obvious signals like recruitment dances and trail pheromones of social insects.

We previously defined recruitment on functional grounds as an attraction of others that increases the signaller's fitness; proximate intent (conscious motivation) of the signaller need not be considered (Heinrich and Marzluff 1991). The loud "yell" vocalization that nonterritorial Common Ravens (*Corvus corax*) give near food and which strongly attracts others (Heinrich 1988) is a case in point. The call is proximally released by hunger and functionally related to expressing high status which is important in establishing feeding rights (Heinrich and Marzluff 1991). By expressing high status, others are attracted to the status signalling and then all are able to feed more and fight less. However, status signalling at food theoretically could be accomplished by gestures without vocalizations that carry for 1 to 2 km. We here examine through field and aviary experiments whether or not "begging" or appeasement calls

that Common Ravens give in addition to yells, especially when they are in the presence of territorial adults defending food, can function as attraction signals.

METHODS

Subjects and apparatus.—Immature Common Ravens were captured at carcasses in the field as described previously (Heinrich 1988) and housed in a large aviary complex (see Heinrich and Marzluff 1991). The complex consisted of a main aviary (ca. 40 × 70 m) with two side arms (ca. 90 m long) leading to smaller aviaries (25 m diameter). One of the smaller aviaries contained a mated territorial pair of adults that had also been captured in the wild at the site. Unless otherwise indicated, the immature ravens were kept in the main aviary during the experiments. Access to the peripheral side arms and their associated aviaries was controlled by raising or lowering gates by guy wires operated from an observation hut. Each side arm contained two gates, one at the arm's interface with the main aviary and another about 5 m down the arm. All observations were made through one-way glass from windows in an observation hut located to provide visual coverage of most of the aviary complex.

Five groups of immatures were captured in the field for the experiments. They were marked with uniquely numbered and colored patagial tags (for details of study area and capture and marking techniques, see Heinrich 1988). The birds adapted quickly (within several hours) to their tags and their new surroundings. They fed together and roosted as a communal group in a covered shed. We determined dominance relationships among the immatures for a week or two during interactions at food in the main aviary as previously described (Marzluff and Heinrich 1991). The two wild-caught adults raised a brood of young to maturity in their side aviary during the winter and spring prior to when most of the experiments were conducted.

Experimental protocol.—The experiment testing whether or not ravens were attracted to the behavior of discoverers of defended food was replicated five times with 10 different immatures (nonbreeders of unspecified age but at least six months postfledging) comprising each group. Each replicate had four phases that were employed in random order with the stipulation that each phase occurred first and last at least once. In one phase of the experiment, no stimulus was applied. In the second and third phases, we had either dominant or subordinate birds discover food (40–60 kg of meat) in each aviary. In the fourth phase we broadcasted the appeasement vocalizations ("begging") of the discoverers from the undefended aviary so as to be only weakly audible to us from the main aviary.

We assured complete independence between subjects and between treatments, as emphasized by Kroodsma (1989), in three ways: (1) A new group of 10 immatures was used for each replicate. (2) Different subordinate and dominant birds from each group of 10 were allowed to discover defended and undefended food. (3) Different recordings of immatures begging were used as playback stimuli.

We followed the same protocol to initiate each phase of the experiment. First, prior to any experiment, the immatures were not fed for three days. Nevertheless, we assume they fed on at least some cached food. To initiate an experiment, the first of two doors closing each peripheral arm of the aviary complex was opened. This created a short (5–7 m deep) vestibule in each arm that the birds from the main aviary could enter. The experimenter, however, then walked down the full length of each arm of the aviary to place food (carried in bags) near the adult and undefended aviaries. Neither pile of meat was visible to the birds anywhere from the main aviary or from the vestibule then available to the birds. For playback experiments, the speaker instead of food was at this time placed into the undefended aviary, and the experimenter walked down to the defended aviary.

The immatures were next watched for a 30-min acclimation period to determine a pretreatment number of birds entering the now-opened vestibules leading to the side aviaries. After the 30-min period, the experimenter again walked down the entire arm of each aviary to move the food directly into each peripheral aviary and to release a "discoverer" into each aviary provided with the food bonanzas. At this time the last (third) gate near the discoverer and the territorial pair also was opened, so that the birds were free to interact and to move up and down the aviary arms. The next 30 min constituted the experimental or treatment period (i.e. when the control and stimuli were applied). The number of immatures (of the 10) entering the two vestibules again was tabulated.

We summarized the subjects' responses to each treatment by quantifying their preference for the right vestibule (that leading to food defended by the territorial pair) relative to the left vestibule by subtracting the number of birds entering the left vestibule from the number entering the right. Thus, we created a scale of −10 to 10, with −10 indicating exclusive preference for the left (undefended) side, 0 indicating no preference for either side, and 10 indicating exclusive preference for the right (defended) side. The same scales were calculated for both the pretreatment and treatment phases. We compared the preference for the right side in treatment versus acclimation periods for each type of stimulus using a Wilcoxen matched-pairs test (Wilkinson 1989) to find out if the immatures would show: (1) a preference for the right or defended side in the experimental phase when discoverers were present; (2) a preference for the left side during playbacks; and (3) no preference when

no stimulus was presented. In all cases one-tailed tests were done to test the predicted response.

We created a second response variable by subtracting the values obtained for the pretreatment from the treatment phases to create a scale from -20 to 20, with -20 indicating complete preference for the right side during pretreatment versus left side during treatment (avoidance of defended arm during treatment), 0 indicating no preference for either side in pretreatment relative to treatment, and 20 indicating complete preference for the left side during pretreatment and the right side during treatment (preference for defended arm during treatment). These responses were analyzed in a one-way repeated-measures ANOVA (Wilkinson 1989), where each of the four phases were repeated measures of the group's responses.

Observations of free-ranging birds.—We observed free-ranging ravens at naturally occurring carcasses and at carcasses and meat piles we placed in the field from 1989 through 1991. We watched ravens at these food bonanzas from blinds as previously described (Marzluff and Heinrich 1991) and recorded the number of ravens at these bonanzas periodically throughout the day, the presence or absence of defensive adults, and the repertoire of vocalizations used by adults and vagrant immatures.

We also assessed the attractive nature of vocalizations to free-ranging birds by counting the number of free-ranging ravens that came to the aviary while our captured birds fed. These "outsiders" were counted during 1- to 10-h watches on 218 days (from 1 October through 30 April of 1989, 1990, 1991). We analyzed the variation in the number of outsiders per day with a three-factor ANOVA (Wilkinson 1989). The factors were: (1) number of birds in aviary (10 or 20); (2) vocal activity of birds in aviary (quiet and not eating, occasionally fighting and calling, often vocalizing and fighting while feeding); and (3) proximity of a feeding site of wild birds to aviary (no feeding site known within 2 km, or a group feeding within 2 km). These wild birds usually fed at carcasses we placed in the field and regularly monitored. It is unlikely that a group was feeding within 2 km of the aviary unknown to us.

RESULTS

Aviary experiments.—Discoverers behaved differently when they encountered defended versus undefended food. Each of the 10 immatures that discovered defended food gave begging calls in submissive posture as the adults attacked them. Discoverers of undefended food were silent on seven occasions and uttered a mix of kaw, yell and trill vocalizations on the other three occasions. Discoverers of defended foods were never silent and, in addition to beg-

ging, gave kaws on two occasions and yells on one occasion. Begging calls were given more often in the presence of adults than in their absence ($X^2 = 20.0$, 1 df, $P < 0.001$).

One-half of the juveniles in the aviary with the adults defending food were able to feed briefly despite the adult defense. Six juveniles ate alone at undefended food. The other four did not go down to feed during the 0.5-h observation periods.

The relative preference for the right side during the experimental phase differed significantly across the four stimuli (repeated-measures ANOVA, $F = 9.5$, df = 3 and 12, $P = 0.001$). Contrasts of the response between each phase indicated that this was primarily due to the strong preference for the left side during the playback phase. Results from Tukey's HSD tests (Wilkinson 1989) were significant when comparing preference during playback phase to: (a) preference with no stimulus ($F = 5.1$, df = 1 and 4, $P = 0.05$), (b) preference with subordinate discoverers ($F = 49.9$, df = 1 and 4, $P = 0.001$), and (c) preference with dominant discoverers ($F = 114.4$, df = 1 and 4, $P < 0.001$). None of the contrasts between phases with discoverers and no stimulus were significant (Tukey's HSD, $P > 0.20$). However, this lack of significance is largely due to one replicate, where 10 birds wandered into the right vestibule almost at the very end of the 30-min acclimation period (Table 1).

The preference for the right vestibule in experimental and control responses differed between the four stimuli as predicted (Table 1). When no stimulus was present the number of birds entering the right or left vestibules was variable and not significantly different (Wilcoxon $T = 6$, $P > 0.05$). In contrast, the right side (with defending adults) was preferred in every trial when discoverers were present (Wilcoxon $T = 0$, $P < 0.05$ for dominant and subordinate discoverers). We observed that, as soon as the discoverers started to beg, the birds in the main aviary started to move in the direction of the sounds. Both dominant and subordinate juveniles begged in the presence of the adults. On the average, subordinate discoverers attracted $3.2 \pm$ SE of 0.97 more birds in the experimental versus control period, and dominants attracted 5.2 ± 0.86 (Fig. 1). In contrast, in every playback trial of begging calls, the birds preferentially entered the left vestibule (the one

TABLE 1. Numbers of juveniles entering right versus left vestibule of aviary during acclimation (Acclimation) and experimental (Experiment) portion of four phases of experiment in five replicates. Territorial adults defended right aviary from discoverers. Speaker placed in left wing during playback experiments.

Phase of experiment	Replicate									
	1		2		3		4		5	
	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left
No stimulus										
Acclimation	0	0	3	1	1	0	0	0	0	0
Experiment	10	0	2	4	0	0	0	2	0	0
Subordinate discoverers										
Acclimation	0	1	2	1	0	0	2	0	1	1
Experiment	6	0	5	2	6	4	7	2	4	2
Dominant discoverers										
Acclimation	2	0	0	0	0	0	0	1	0	4
Experiment	5	0	5	1	6	0	7	0	3	2
Playback										
Acclimation	0	0	1	1	1	0	1	2	1	1
Experiment	2	6	2	6	0	2	1	6	0	5

with the speaker); on average, 4.0 ± 0.30 more birds entered the left side relative to the right (Wilcoxon $T = 0$, $P < 0.05$). Thus, in all three experimental tests with stimuli, the birds preferentially entered the side aviary associated with sounds ravens make when attacked by dominant territory owners.

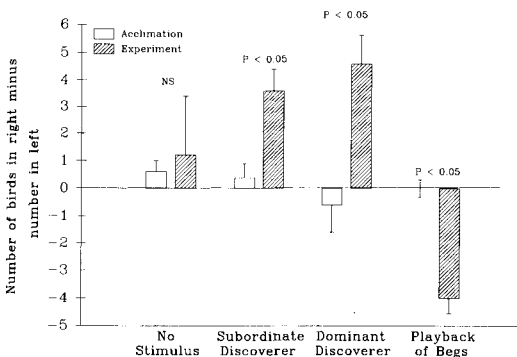As demonstrated above, by following vocalizations of discoverers, naive birds located new

Fig. 1. Number of birds entering right vs. left vestibule of aviary within 30 min. Right vestibule contained territorial pair of adults (and food) in a second aviary at the end. Left vestibule connected to aviary that contained food only. "Discoverers" refers to birds placed in adult aviary and that made appeasement begs to adults. Playbacks of appeasement begs made from left (unoccupied) aviary. Birds entered vestibules leading to other aviaries in response to appeasement begs made by both subordinate and dominant birds.

food sources within the right aviary containing the adults where they had never been before.

Field observations.—The behavior of discoverers in the aviary was confirmed in the field. One to six juveniles were seen at food defended by adults on 26 occasions and at food not defended by adults 24 times. Juveniles begged in the presence of adults on 21 of 26 times, but only begged in 2 of 24 times when no adults were in the area. The occurrence of begging calls in the field was significantly associated with the presence of adults ($X^2 = 26.4$, df = 1, $P < 0.001$).

The begging calls discoverers make in the presence of adults also attract others into the area. We released 21 marked juveniles (with patagial wing tags and with radio transmitters) as discoverers at 21 carcasses (single birds were released at 16 carcasses, and groups of five individuals [with one radiotagged] were released at 5 carcasses). In one case, the discoverer joined a nearby communal roost on the evening of its release and recruited roost mates to the bonanza. In 11 cases the discoverers remained in the area (within 1 km) and begged when adults approached them. In 10 of these 11 cases, other juveniles were attracted during the subsequent four days. In nine cases the discoverers left the area (no radio signals within at least 10 km) or did not beg and, in seven of these nine cases, no juvenile was attracted to the carcass during the subsequent four days. Juveniles were significantly more likely to be attracted when dis-
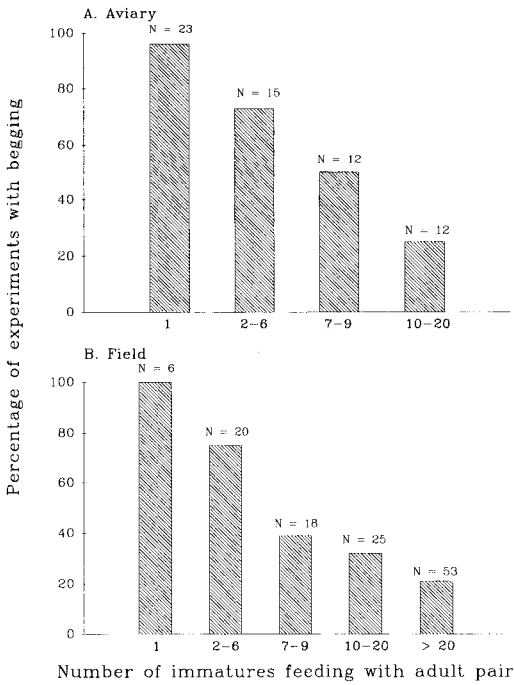
Fig. 2. Occurrence of begging in (A) aviary and (B) field by immatures as function of their numbers when feeding (B) or confined with and/or feeding with adult pair (in A). Occurrence of begging reflects the aggression of adults toward newcomers.
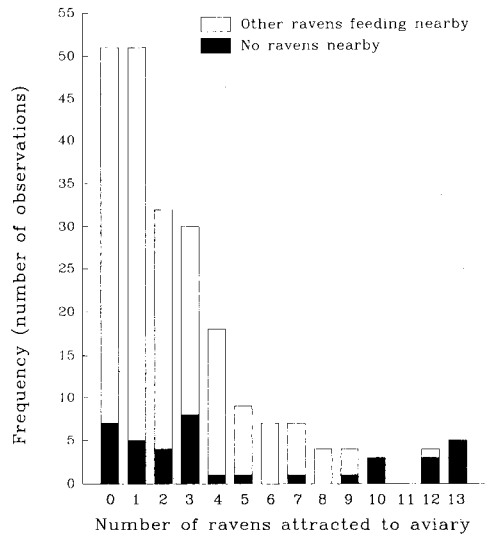

Fig. 3. Frequency of different numbers of outsiders attracted to aviary while 10 to 20 juveniles were feeding inside. Filled bars refer to instances when feeding crowds were in vicinity (<2 km) outside aviary.

coverers begged than when they did not ($X^2 = 7.1$ with Yate's correction, df $= 1$, $P < 0.001$). Results during experiments when discoverers did not beg and when discoverers left the area were lumped in the previous analysis to increase sample size. However, both reactions by discoverers were equally ineffective at attracting other ravens (ravens were attracted in one of five cases when the discoverer stayed but did not beg, and in one of four cases when the discoverer left the release site).

Begging signals the location of defended foods when one or a few immatures try to feed with adults. Adult defense is intense at this time and begging was observed more commonly in small groups than in larger groups of immatures, both in the aviary and in the field (Fig. 2). As group size increases, adult defense declines (Marzluff and Heinrich 1991) and, accordingly, begging becomes less frequent.

Few birds were attracted to the aviary complex. It was common for only a single or no birds to visit the aviary, but up to 13 visitors were observed. On the average, only 2.6 ± 0.18

birds were outside the aviary at one time while our birds were feeding inside (Fig. 3). The only significant factor influencing the number of birds gathered outside our aviary was whether or not a crowd was already at a nearby food source ($F = 19.1$, df $= 1$ and 208, $P < 0.001$). On average, 3.7 ± 0.27 birds were attracted when birds were near, in contrast to 1.7 ± 0.24 when no crowd was known to be nearby. On 9 of 10 days during which 10 or more birds came to our aviary, we also were aware of another feeding site nearby where a raven crowd was gathered.

We observed a similar pattern of attraction to food outside of the aviary. Rarely did numbers of birds at a carcass in nature increase by more than 10 throughout the course of the day (Fig. 4). For 9 of 11 cases where 10 or more birds were attracted throughout the day, we knew of another feeding site within 2 km. More birds were attracted to carcasses when the feeding groups already there were small than when they were larger (groups of 1–5 birds, $\bar{x} = 4.16 ± 0.92$, $n = 50$; groups of 6–10, $\bar{x} = 2.78 ± 1.33$, $n = 23$; groups > 10, $\bar{x} = 2.64 ± 0.93$, $n = 11$). As in the aviary, the trend for more birds to be attracted to small groups is correlated with the increased frequency of begging within small groups when adults are very defensive (Fig. 3).
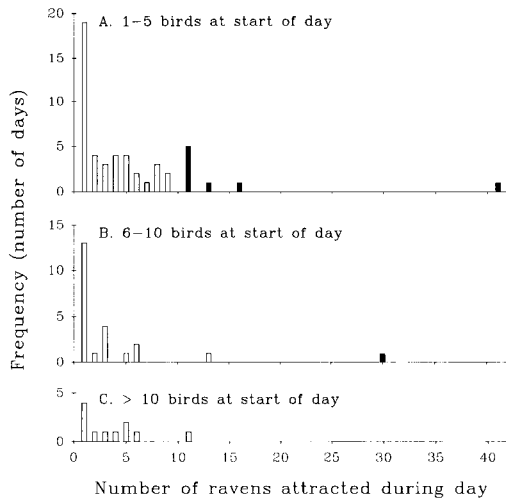
Fig. 4. Increase in numbers of Common Ravens throughout day at defended carcasses in field involving (A) 1–5, (B) 6–10, and (C) >10 birds at the start of day. Generally, numbers were stable throughout day. Smaller groups tended to attract more additional birds than larger feeding groups. Filled bars represent instances when feeding crowds were in vicinity (<2 km) at other food bonanzas.

DISCUSSION

Common Ravens in western Maine forage by flying singly or in pairs over the forest but in the winter they commonly aggregate (Mylne 1961) in large numbers at animal carcasses, provided the carcasses are opened for them (Heinrich 1988, 1989). The immatures consist primarily of vagrant birds that require a crowd of some 8 to 10 individuals before access is gained to the food bonanzas that, otherwise, are highly defended by the resident territorial adults (Heinrich 1988, 1989, Marzluff and Heinrich 1991). Only the immatures attract others, and the mechanism of crowd formation involves both vocalizations near the food and recruitment from communal nocturnal roosts (Heinrich 1988, 1989, Marzluff et al. in prep.).

Feeding crowds at deer or moose carcasses commonly range up to 20 and 60 birds, respectively, and two major interactions occur within such feeding crowds at defended carcasses. First, at least before a crowd has assembled, the adults attempt to repel all other birds in the vicinity both by chasing them in the air and by attacking them when they are perched near the bait on the ground or on trees. The attacked immatures

bow, fluff their feathers, spread and quiver their wings in a submissive display (Heinrich 1988, 1989), and give begging vocalizations. The second major social contests at feeding crowds are among the immatures themselves for access to often limited feeding spots. The most dominant among the immatures gains the choice feeding spot, and these birds signal their dominance by yell vocalizations (Heinrich and Marzluff 1991), which are one of the cues used by other hungry ravens in the vicinity (<2 km) to locate the contested food (Heinrich 1988, 1989).

We sought to answer two questions: (1) Do the beg vocalizations also serve as an attractant cue as does the yell? (2) Can local cues (such as yells, begs, and all other potential sorts of local enhancement) alone account for the attraction of sufficiently large crowds to neutralize the defenses of the territorial adult pair?

Our experiments in the aviary indicate that the begs given during agonistic encounters do attract hungry immatures. The encounters occur primarily at food worth defending. Thus, the calls then given are a reliable indicator of the presence of a food bonanza. In our experiments in the aviary, immatures following such begs were led to new food. Similarly, our field results show that ravens are attracted to new food by such calls in the wild. When discoverers feed quietly at a carcass or leave the area other vagrant ravens rarely find the bonanza. However, when discoverers cower, beg and flee from defensive adults, recruits are quickly assembled.

Both in the aviary and in the field (Fig. 2), the probability of begging decreased greatly as the numbers of immatures feeding with the adults increased. For example, begging always occurred with only one immature present, but when about 20 individuals were present, then begging occurred at only 20 to 25% of the observation, which reflects a very substantial reduction in begging per individual. The reduction in begging in the presence of a defending adult pair was probably due to the reduction in aggression by the adults, which also decreases as crowd size increases (Marzluff and Heinrich 1991).

Despite the great reduction in the beg signal at larger group sizes, the number of birds attracted to carcasses throughout any one day when the begs (and many other signals) are given decreases only marginally, from a mean of 4.2 at one to five birds at the start of the day

to 2.6 when more than 10 birds were at the start of the day (Fig. 4). That is, a decrease of about 55% (from about 80 to 35%) in the incidence of begging resulted in a decrease of only 39% (from 4.2 to 2.6 birds) in the number of birds attracted. In only seven instances did we observe 10 or more birds attracted throughout the day and, in five of these, we knew of another nearby food bonanza from which they could have come.

The above results from the field do not distinguish between numbers of birds attracted by begs versus those attracted by some other cue(s). The lack of correspondence between numbers of birds attracted versus amount of begging calls could indicate either that a few begs are alone sufficient to attract the local birds and/or, since the incidence of yelling increases rather than decreases as competition at the bait increases, this second signal may compensate as the begs decrease.

Throughout three winters we seldom saw more than three to four ravens attracted near the aviary complex containing both captive birds and exposed meat piles. There were usually different meat piles in different portions of the aviary. Furthermore, in the main portion of the aviary there was no tree cover, making both the birds and the meat highly visible. Birds potentially could have been attracted to the aviary by calls of the inhabitants and by any of a variety of other possible cues. However, since there were seldom more than 8 to 10 birds around the aviary, the local cues that the inhabitants were restricted to giving were not sufficient to attract the crowds observed at carcasses and/or meat piles located nearby in the forest. Furthermore, our results also indicate that when birds see meat, but are unable to reach it, they do not recruit. When more than nine birds were attracted to the vicinity of the aviary, we always knew of another nearby feeding bonanza from which these birds probably came, because birds in any one area move freely between different locally available food bonanzas (Heinrich 1988, 1989). As indicated for previous studies (Heinrich 1988, 1989), the observations reported here support the idea that cues given near the bait act only locally, and that the large numbers of ravens assembled at carcasses can only be explained by recruitment from a nocturnal roost (Marzluff et al. in prep.).

Given that the begs seldom result in the attraction of sufficient numbers of immatures to overcome the defenses of the resident territorial adults, and since they are not given at food bonanzas in the absence of adults, it seems likely that they function proximally in reducing aggression. Nevertheless, the attraction of even one other nearby raven could be important, even if locally attracted birds are hardly ever likely to be numerous enough to overpower the territory holders. The initial vagrant discoverer that is attacked may or may not have access to a roost to recruit others, but by attracting even one bird that does have access to a roost, the local attraction in effect could draw in a distant crowd (Marzluff et al. in prep.) that then can gain access to the bonanza (Marzluff and Heinrich 1991). We observed single individuals released near baits (hence, out of contact with roosts) to remain in the bait vicinity for days. Eventually, all of these baits were eaten by crowds of birds, despite their defense by territorial pairs.

Since the begging attracts others who could bring in a crowd, immatures responding with begs, in effect, exert a penalty on the adults' aggression. Therefore, if the adults could be certain that an intruder would not recruit then it should be advantageous for them to tolerate it. However, if any of the attracted birds ultimately bring in a crowd from a roost, they should be vigorously repelled despite the small risk involved of altering others during the eviction process. Since the adults have no assurance that a stranger will not recruit, perhaps the best strategy for an adult is to always attempt an immediate eviction, but to become tolerant if the vagrant shows itself to be very dominant and resistant to eviction. Indeed, we find (unpubl. data) that the subordinate birds are the first to leave feeding aggregations where they are challenged.

There is greater relative cost to sharing a small rather than a large carcass with a crowd (Marzluff and Heinrich 1991). Therefore, a territorial bird should have more confidence that a vagrant would not recruit to a small carcass and, hence, it could be more tolerant of it. However, the greater cost of sharing a small carcass applies to the adult and the vagrant as well. The adult should not share a small food item it can consume itself. Thus, the opposite effects of carcass size could cancel out.

LITERATURE CITED

CARACO, T. 1981. Energy budgets, risk and foraging preferences in Dark-eyed Juncos (*Junco hyemalis*). Behav. Ecol. Sociobiol. 8:213–217.

CHAPMAN, C. A., AND L. LEFEBVRE. 1990. Manipulating foraging group size: Spider monkey food calls at fruiting trees. Anim. Behav. 39:891–896.

ELGAR, M. A. 1986. House Sparrows establish foraging flocks by giving chirrup calls if the resource is divisible. Anim. Behav. 34:169–174.

HEINRICH, B. 1988. 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. Summit Books, Simon & Schuster, New York.

HEINRICH, B., AND J. MARZLUFF. 1991. Do Common Ravens yell because they want to attract others? Behav. Ecol. Sociobiol. 28:13–21.

KENWARD, R. E. 1978. Hawks and doves: Factors affecting success and selection in Goshawk attacks on Woodpigeons. J. Anim. Ecol. 47:449–460.

KROODSMA, D. E. 1989. Suggested experimental designs for song playbacks. Anim. Behav. 37:600–609.

MARZLUFF, J., AND B. HEINRICH. 1991. Foraging by Common Ravens in the presence or absence of territory holders: An experimental analysis of social foraging. Anim. Behav. 42:755–770.

MYLNE, C. K. 1961. Large flocks of Ravens at food. Br. Birds 54:206–207.

PULLIAM, H. R. 1973. On the advantage of flocking. J. Theor. Biol. 38:419–422.

WALLACE, M. P., AND S. A. TEMPLE. 1987. Competitive interactions within and between a guild of avian scavengers. Auk 104:290–295.

WILKINSON, L. 1989. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.