Do common ravens yell because they want to attract others?

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Summary. The formation of groups at food bonanzas results from a variety of mechanism, which include recruitment by signalling and information parasitism. Recruitment is distinguished from information parasitism on functional grounds: attraction of a crowd is termed recruitment if the signaler's fitness is enhanced by the attraction of others but termed parasitism if the signaler's fitness is reduced by the attraction of others. We here show, however, that in Common Ravens, *Corvus corax*, the proximate reasons for giving recruitment signals are probably other than for attracting a crowd. In the forests of the northeastern United States, non-breeding, vagrant ravens commonly aggregate in large numbers at carcasses where they neutralize the defense of territorial adults. We attempted to mimic this situation with a captive flock of juveniles and a pair of resident adults in order to determine the proximate factors triggering "yells", vocalizations which attract nearby ravens to large animal carcasses. Our experiments indicate that yells are given primarily by hungry birds. However, yelling is strongly modified by status. Within the vagrant crowd, status is labile. When successive dominants were removed, replacements immediately took their place. Furthermore, when the dominants were re-introduced to the flock they always suffered significant losses of status and ceased yelling. The territorial male has, and constantly maintains, the highest status within (but not necessarily outside) his territory, and here he rarely yells. In sharp contrast, within the vagrant crowd of unmated birds it is the highest-status birds that are the most likely to yell when approaching food. Furthermore, the dominant vagrants (as well as adults) suppress yelling in subordinates. We conclude that ravens yell proximately to advertise their status at food, and that recruitment is only one of several ultimate advantages of the behavior.

Introduction

Many species of animals aggregate in large numbers at localized food bonanzas. Groups can be assembled by

a wide varietiy of mechanisms. For example, on the plains of Africa thousands of beetles are attracted to a single dung pile where they compete intensely (Heinrich and Bartholomew 1978). They are presumably attracted by the smell of the dung itself. Vultures are attracted to carcasses by seeing others spiralling down to them (König 1983). A food bonanza may also be discovered by a group, that then feeds as a group (Balda and Bateman 1971). In addition, and perhaps most interestingly, animals may be attracted by signals given by those discovering food. Specific attraction signals include the "chirrup" calls of House sparrows (Elgar 1986), the "whinny" calls of spider monkeys (Chapman and Lefebvre 1990), the undulating flights of ospreys (Greene 1987), and the "yells" of ravens (Heinrich 1988, 1989). Sometimes unsuccessful foragers also follow successful ones using subtle and largely unknown cues (Ward and Zhahavi 1973; Rabenold 1987a; Krebs 1974; Brown 1986). In the latter cases information may be withheld, and/or following may be suppressed (Waltz 1983; Rabenold 1987b).

Whether or not recruitment or information parasitism occurs is often a controversial topic, because to many it raises the question of whether the signallers try to call in others or whether instead they are being exploited. But part of the controversy is artificial because the distinction between proximate and ultimate causes of attraction signals have commonly not been made. Much confusion has arisen because it is generally assumed that the two coincide. In other words, it is usually assumed that when animals recruit they give signals "to" attract others. Likewise, if information is parasitized it is usually assumed that the signals are not given "to" attract others. It is not necessary to impart volition to animals giving recruitment signals and then use this as the basis for distinguishing recruitment from parasitism. Attraction of a crowd can yield a great variety of different costs and benefits. But the balance must be positive for attraction signals to evolve. Recruitment is distinguished from parasitism on this purely *functional* ground by investigating the ultimate consequences of group formation. Recruitment results when assembled groups increase the signaler's fitness. Parasitism results when assembled groups decrease the signaler's fitness.

By removing volition from the equation of whether or not recruitment occurs, we are faced with a second question: What is/are the proximate reason(s) for giving signal(s) that result in recruitment (or parasitism)? Presumably any of a number of signals originally used and perhaps still functional for other purposes can be used and even modified to function as recruitment signals. Therefore, the proximate reason a recruitment signal is given is not necessarily to attract others. Recruitment signals evolve because they enhance fitness and it is not necessary for a signaler to realize this function. Only when the proximate reasons for giving recruitment signals include the attraction of others is the signaler behaving in an apparently purposeful manner that previous workers implied was necessary for one to use the term "recruitment." Costa Rican spider monkeys provide a possible example of recruitment where proximate and ultimate reasons for signaling coincide. These monkeys adjust their group size to match resource availability by uttering "whinny" calls when groups are small relative to resource abundance and by withholding calls when enlarged group size results in heightened competition (Chapman and Lefebvre 1990). In the above and many other cases of documented recruitment, scenarios of kin selection or reciprocity could explain the attraction of others, where the animals may proximately "want" to recruit. However, as discussed elsewhere (Heinrich 1988, 1989), this ultimate adaptive advantage is unlikely for ravens because of their vagrancy.

Here we report on an experimental study designed to decipher the proximate factors eliciting the "yell" vocalization of Common Ravens (*Corvus corax*). This vocalization is given by immature vagrants near food which attracts other nearby vagrants (Heinrich 1988). Elsewhere we investigated the ultimate function of group formation and concluded that it increases the signaler's fitness because crowds are able to overpower territorial adults and access defended foods unavailable to single ravens (Heinrich 1988, 1989; Marzluff and Heinrich in prep.). Given our functional definitions, group formation by attraction to yells therefore constitutes recruitment, not parasitism. The results reported herein allow us to determine the motivation of the signaler thereby gaining a broader understanding of recruitment in this species.

Methods

Apparatus and subjects. On 29 and 31 December 1988 we captured 20 immature ravens (6 yearlings and 14 juveniles) and placed them in the main aviary of our aviary complex (Fig. 1). These immatures were part of a group of approximately 50 ravens that were foraging at a dead cow in the mountains of western Maine within 20 meters of the aviary. Birds were captured in a walk-in trap, aged by mouth and plumage coloration, and marked with uniquely numbered and colored patagial tags on both wings (see Heinrich, 1988 for details of the study area and capture and marking techniques). Laparotomies on December 8, 1989, indicated a sex ratio of 6♂/14♀.

Immatures quickly adapted to their new surroundings. They roosted as a communal group in a covered shed, fed as a group at liberally supplied carcasses and slaughter house offal (birds were
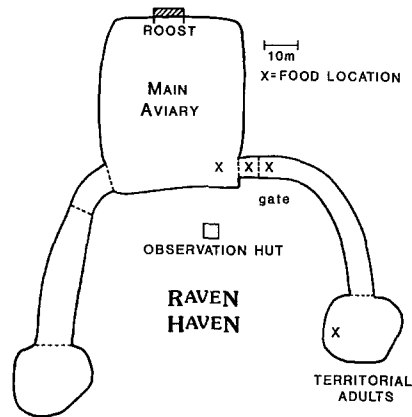
Fig. 1. Aviary complex where experiments were conducted. Twenty immatures resided in the main aviary and a pair of adults defended 1 peripheral aviary. The entire complex is interconnected and arms can be opened or shut off by raising or lowering gates with guy wires operated from inside the observation hut. Due to terrain (hut is at the apex of a knoll) and vegetation (a spruce thicket lies between 2 peripheral aviaries) birds in the peripheral aviaries can only see the lower quarter of the main aviary and vice versa. X's mark locations of food during experiments. The aviary complex is from 4–7 m in height and contains 50 vertical perches and 26 horizontal ones scattered throughout

never without food for more than 3 days during the first 3 months), bathed in the snow, allopreened and fought. Qualitatively, their behavior was identical to the behavior of free-living immatures we continued to monitor.

On 2 January we captured 3 adults and placed them in one of the peripheral aviaries of the complex (Fig. 1). 2 of these adults allopreened regularly, called in synchrony, and mirrored each other's actions suggesting to us (and another experienced with ravens, E. Gwinner) that they were an established pair. The third bird was released after 2 days of ostracism by the "pair". The pair was fed ad libitum in their aviary and quickly began to defend its boundaries from free-living wild birds and from juveniles wandering in the arm between the main aviary and the adult aviary. The adults asserted their dominant status by giving bowing ceremonies, thick-head postures, and ear-tuft intimidation displays (Gwinner 1964; Heinrich 1988) to any intruders.

We allowed our captive immatures to find food bonanzas (hunks of meat and carcasses ranging in size from squirrels to deer) randomly located throughout the aviary complex for 3 months prior to the experiment we discuss here. During this time we determined dominance-subordination relationships by ad libitum observations of dyads during foraging (Altman 1974). The dominant of an interaction was the bird that forced the other to back away from confrontation in the fuzzy-headed submission posture (Heinrich 1988).

A stable dominance hierarchy quickly developed among our captive immatures. It was clear from the first few days of captivity that a few immatures consistently dominated all the other birds. Over a 3 month period (30 December–16 March) a hierarchy developed which we have broken into 4 categories: 1) 3 *dominants* who rarely deferred to others, 2) 6 *subdominants* who deferred to a minority of birds primarily dominants and other subdominants, 3) 5 *intermediates* who won roughly 40% of their encounters, and 4) 6 *subordinates* who rarely defeated any other bird. There was an obvious alpha male (RB) who only lost 2 encounters (both to the beta male) and had uncontested access to food at any time. Our method of determining the dominance hierarchy minimizes the number of times individuals lose to lower ranking birds (Appleby 1983), however some nonlinearity was evident as one subordinate consistently defeated an intermediate and a lower ranking
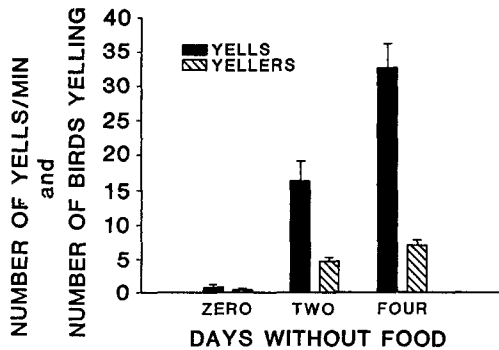
Fig. 2. The influence of increasing hunger on the number of yellers and yelling rates by immatures. Height of boxes indicate means. *Error bars* are 1 SEM. Means are derived from the total response of the group to each of 5 food locations during each of 8 group compositions ($N=40$ for 2 and 4 days without food, $N=39$ for zero days without food because of one missing observation)

subdominant defeated a higher ranking one. Despite the circular triads created by these reversals, Appleby's (1983) method indicates that this hierarchy was significantly linear (linearity coefficient, $K=0.93$, $X^2=157$, $df=27$, $P<0.001$).

Experimental protocol. From 23 March until 6 July 1989 we systematically varied composition of the immature group, the location of food, and the hunger level of immatures in order to determine how these three factors influenced yelling. Two observers watched birds through two-way mirrors with 10-power binoculars from an observation hut 10 meters from the main aviary (Fig. 2). We recorded the identity of yellers and their rate of yelling (number of yells in randomly selected 1 min intervals), who initially approached and contacted food, how long before food was contacted and consumed, and whether food was defended. Vocalizations were recorded on a Sony TCM-5000 cassette recorder using a Senheiser ME-88 microphone.

We could not accurately count yelling rates for all birds in an experiment. However, we could easily and unambiguously assign birds to primary or secondary yelling status. In an experiment there were usually 1 or 2 primary yellers who yelled nearly constantly and maintained consistently high rates of yelling throughout a majority of phases (different locations of food) of the experiment. Primary yellers accounted for a majority of the yells uttered. However, in most experiments 3–10 secondary yellers yelled 1 or a few times.

We employed a hierarchical experimental design to test the influence of the 3 factors. Group composition was the main blocking factor and consisted of 4 independent levels. Hunger was a three-level repeated measure nested within each group. Location was a five-level repeated measure within each hunger level. Each group was replicated twice resulting in 8 experiments. Each experiment consisted of 3 runs on 3 separate days (one for each hunger level) and on each day responses were measured in 5 phases (one for each food location). One phase was omitted from analysis ("Split Group" when birds were satiated and the alpha was removed) because birds could not be segregated in the aviary arm.

Group composition was modified by removing dominant birds from the immature group. The first group composition included all birds. Our first manipulation was to remove the alpha male and his consort. After 7–10 days of allowing the remaining immatures to establish a dominance hierarchy (all birds simply shifted up one position) we tested this new group and then removed its alpha male. Again 1 week was allowed for reshuffling (all shifted one position), birds were retested, and the alpha male removed. Thus by removing three alpha males in succession we created 4 group compositions. The response of birds in each composition

was replicated after a 14 day ad libitum feeding period by reintroducing each male in the reverse order from the order of removal.

Hunger level was repeated within each replicate of group composition. We modified hunger level by removing all food from satiated birds for varying lengths of time. Responses of satiated birds in each group were measured after they had fed ad libitum for 2–6 days and still had food left on the day of the test. This response was contrasted to the response of birds on the second and fourth day without food. The order of application of hunger level to groups was randomized. In order to reduce accumulation of carryover effects between hunger treatments on different groups we repeatedly satiated the birds during the 7–10 day period of reshuffling after an alpha male was removed.

Food (5–15 kg hunks of meat) location was a second repeated measure because the immatures were exposed to each food location on every day of the experiment. Each day we measured the calling response of immatures under 5 conditions. 1) *Baseline* = Before we placed food in the aviary. 2) *Group Approach* = As immatures approached freely accessible food in the main aviary or just inside the arm leading to the adult aviary. 3) *Behind Screen* = As they approached inaccessible food behind a lowered screen door separating the main aviary from the arm. 4) *With Adults* = As they approached inaccessible food in the adults' aviary behind a lowered screen door. 5) *Split Group* = We captured approximately half of the immatures in the arm of the complex by closing the screen door as the group began to enter. The rest of the group remained in the main aviary. Our intent was to separate the alpha male from the beta male. Food was placed in the main aviary or in the arm so that 1 group could get to it but the other group could only see the food. After the group with access approached and began to eat, the meat was removed and placed with the other group until they approached and began to eat. Behaviors of all birds as either group approached constituted the response for this treatment.

Additional observations, as indicated, were made on birds in the wild in the study area near the aviary, and on hand-reared birds.

Results

Overall ANOVA

Hunger and location of food significantly influenced yelling rate and the number of birds yelling (Table 1). Immatures yelled more frequently as their level of hunger increased (Fig. 2). Satiated birds rarely yelled. Only 50% of experiments with satiated birds produced any yelling. In contrast, after 4 days without food all experiments had yellers, over a third of the group yelled, and many of the birds yelled continuously. The rate of yelling increased 16-fold every 2 days immatures were without food. As soon as foraging began, even after 4 days without food, yelling subsided and was typically extinguished 10 min after the onset of eating. The major influence of food location on yelling was a decline in the number of yellers and their rate of yelling when food was located in the adults' aviary (Fig. 3). This food was approximately 0.5 m from the screen partition and when immatures approached it the adults flew up to meet them with ear-tuft intimidation displays and harsh calls that are often given by free-living adults when we trespass in their territories and when they fly over our captive adults. Yelling was most frequent when some or all birds had access to the food and adults were out of view (*Split Approach* and *Group Approach*). However, inaccessible

Table 1. Analysis of variance results for the influence of 3 factors on yelling rate and the number of yellers in an experiment

	Yells/min			Number of birds yelling		
	F	DF	P	F	DF	P
Main effects						
Hunger	16.5	2.8	0.001	18.5	2.8	0.001
Placement of food	4.8	4,16	0.01	7.9	4,16	0.001
Group composition	0.1	3,4	0.98	0.3	3,4	0.80
Interactions						
Hunger × Group	0.3	6,8	0.90	0.2	6,8	0.96
Hunger × Placement	4.5	8,32	0.001	3.8	8.32	0.003
Group × Placement	0.2	12,16	0.99	0.3	12,16	0.96
Group × Hunger						
× Placement	0.9	24,32	0.57	0.7	24,32	0.80
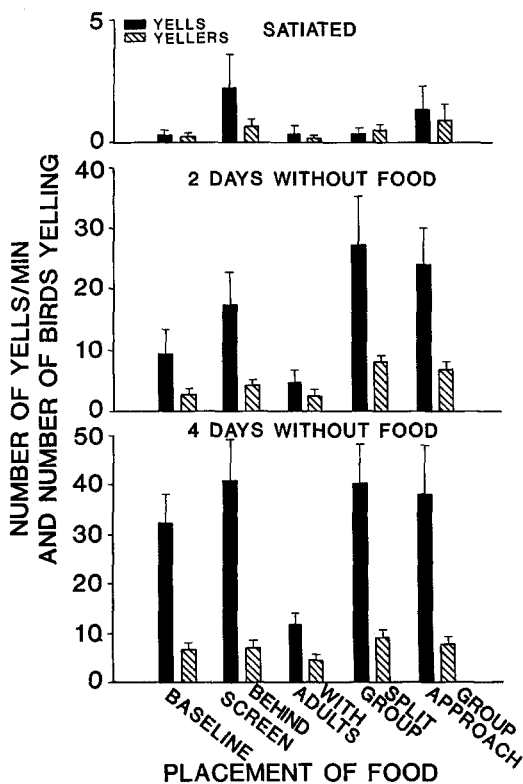
**Fig. 3.** The influence of food placement on yelling by immatures. Food placements are defined in Methods. Average response + 1 SEM are indicated at 3 hunger levels. Total responses of birds at each location for each level of hunger are averaged over $N = 8$ group compositions ($N = 7$ for split group, satiated because of missing observation)
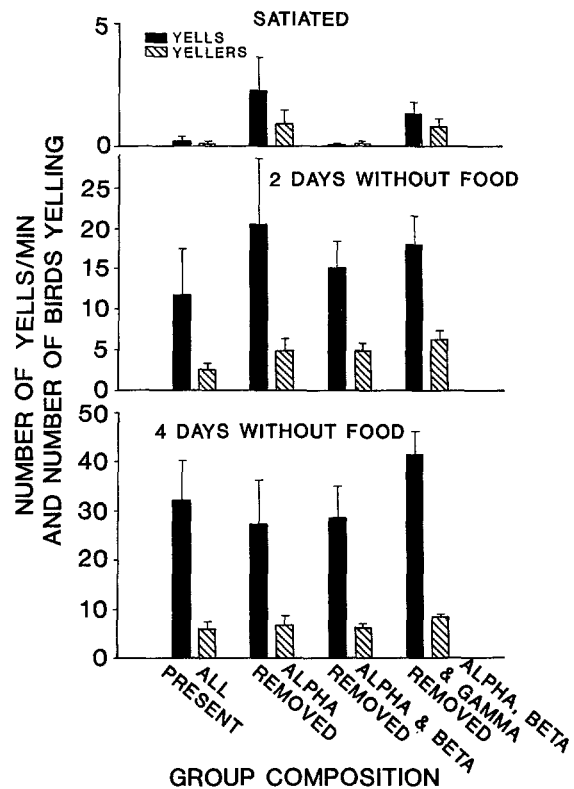
Fig. 4. Influence of group composition on yelling by immatures. (Responses of immatures are averaged over 5 food locations during 2 replicates of group composition to give $N = 10$ for each group at each of 3 hunger levels $N = 9$ for treatment with alpha removed and immatures satiated due to missing data). Means + 1 SEM are shown

food also elicited frequent yelling when adults were not present (compare *Behind Screen* to *With Adults*).

Hunger and placement of food had a significant interaction effect (Table 1). As hunger increased, yelling increased, in all locations. However, the relative reduction in yelling when food was placed with adults became more noticable as hunger increased (Fig. 3). After 4 days without food, yelling was even triggered by the sight

of the observers entering the observation hut without placing food in the aviary. (We suspect the birds were yelling in response to the *expectation* of food, inasmuch as fledged young yell when they see their parents approach.)

Group composition was not significantly related to yelling (Table 1, Fig. 4). However, dominance did influence yelling and hunger mediated this influence (Fig. 5).
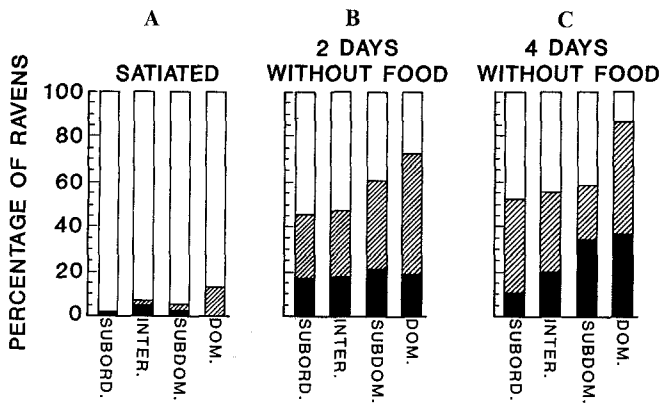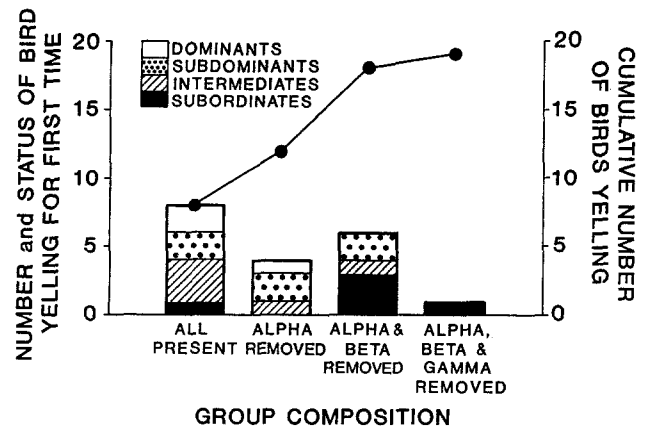
Fig. 5. Change in yelling and changing composition of yellers (with respect to dominance) as a function of hunger. The percentage of all birds in a given class that yelled or were silent at 3 hunger levels are shown. Percentages of yellers in each status class were determined by summing the number of yellers per dominance class across the 8 tests of group composition and dividing this sum by the total birds in each class summed across the 8 experiments. Changes in status through the course of experimentation were accounted for which resulted in a total of 144 subordinates, 120 intermediates, 114 subdominants, and 66 dominants across the 8 experiments. *Filled bars* primary yeller; *hatched bars* secondary yeller; *open bars* did not yell in experiment

GROUP COMPOSITION

Fig. 6. Number and status of birds yelling for the first time when we varied group composition in the first replicate (experiments 1–4). The line graph gives the cumulative number of birds that had yelled at some point during experimentation. The *bar graph* indicates the composition of the new yellers accumulated in the line graph each time an alpha was removed. (Status categories refer to status prior to the experiment)

During experiments with satiated birds there were few primary yellers and these were usually low ranking birds and never dominants (Fig. 5A). The few dominants that did yell did so only occasionally. As hunger increased nearly all dominants yelled and after four days without food most primary yellers were high ranking birds (Fig. 5B, C).

Dominant immatures suppress yelling by subordinates

During the first replicate of the group composition manipulations subordinates yelled more frequently as dominants were removed (Fig. 6). When the alpha was removed, 4 new birds yelled for the first time including the new dominant who did not yell in experiment 1 and 2 intermediates who, after the alpha's removal, had risen in status. After removing the beta in addition to the alpha, 6 additional birds yelled for the first time. These were primarily subordinates. Lastly, after the gamma was removed still 1 more subordinate yelled. In total, 19 of 20 birds yelled, but over half of these did not yell until 1 or more of their superiors were removed from the group. One subordinate never yelled.

It appears that alpha birds actively suppress the yelling of other dominants. A dramatic example of suppression occurred in experiment 2. The birds headed down the arm toward the adults' aviary and the beta male yelled 8 times during the first minute. The alpha, who had been silent, then attacked the beta, pinned him to the snow and jabbed him with his bill. For the remainder of the experiment the beta was silent and the alpha yelled an average of 18.4 times/min. More typically, suppression by the alpha was not physically forced upon other dominants and was only obvious when the dominants were separated as we did in our *Split Group* treatment.

During this phase of experiment 1 we succeeded in getting the alpha and beta on opposite sides of the screen door. Although these birds were in visual and vocal contact within a few meters of each other the beta's behavior immediately shifted when he was protected from the alpha and assumed the top position within his subgroup. Instead of waiting for the alpha to lead the way to food, the beta was the first to eat and he yelled and attacked others as he approached the food (Fig. 7A). However, he never yelled when in the same subgroup with the alpha.

In experiment 2, the alpha was removed leaving the beta in charge and he yelled regardless of who was in his presence (Fig. 7B). We were not able to isolate the gamma in this experiment and he remained silent in the presence of the beta. We did succeed in isolating the delta and he took charge of his subgroup and yelled only when isolated from the beta and gamma.

In experiment 3, the alpha and beta were removed and the gamma finally yelled as he assumed the alpha role in the group (Fig. 7C). As in experiment 2, the delta yelled only when isolated from the gamma. The delta continued yelling after the alpha, beta, and gamma were removed (Fig. 7D). In this last experiment, however, the delta and epsilon both yelled and even yelled without conflict when perched side by side.
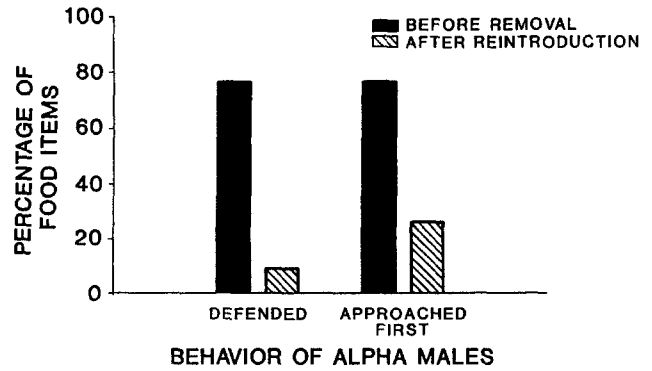
In the first 3 experiments we can make 6 independent comparisons of yelling by dominants when in the alpha's group versus when not in his group. 3 of these are comparisons of yelling within an experiment when dominants never yelled unless they were out of the alpha's group (then they averaged 8 yells/min, SD = 5). Yelling by dominants in the experiments following removal of the current alpha versus yelling in the previous experiment with the alpha provide three more comparisons. Dominants did not yell with the alpha, but averaged
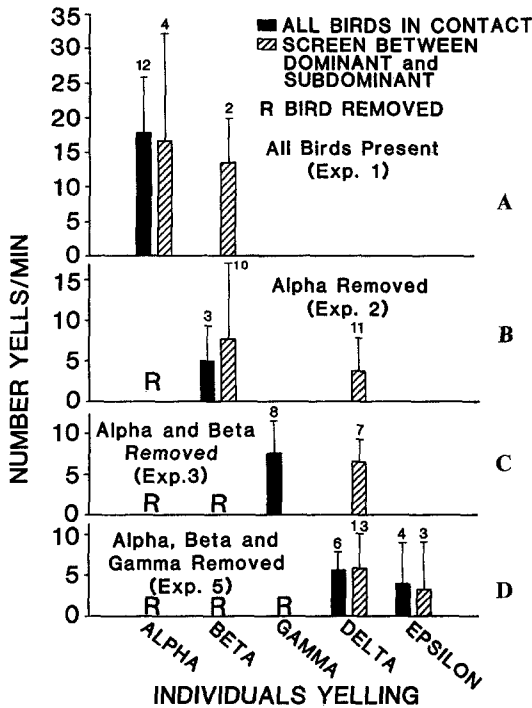
Fig. 7. Yelling by (5) most dominant immatures as a function of days without food and who they are in contact with. Lower ranking dominants begin to yell as top ranking dominants are removed or when they are prevented from contact with the dominant when they are behind screen doors (*shaded bars*). Yell rates for each male are averages +1SD for 1 min samples during focal observations of each male. Number of such samples for each male is given above error bar
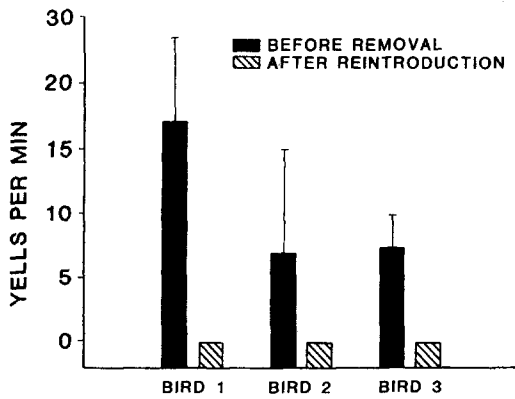

Fig. 8. Defense and first approach to food items by alpha males (3) while in the group (*filled bars*) and when reintroduced (*hatched bars*). Only approaches to food by hungry birds (3–4 days without food) are included. Samples are derived from $N=13$ approaches before removal and $N=46$ after reintroduction. Note apparent loss of both status (defense) and "bravery" (willingness to approach first)

6.1 yells/min (SD=1.9) in the subsequent experiment. Together these 6 comparisons allow us to conclude that alphas suppress yelling by the other dominants (Wilcoxon T=0, P=0.031).

Given the significant suppression of yelling by alphas we were surprised by the lack of a significant increase in the *number* of yellers as successive dominants were

removed (Table 1, Fig. 4). In the first replicate of group composition the percentage of immatures yelling increased from 40% when all birds were present, to 50% after the alpha was removed, to 88% after the beta was removed, and it remained at 88% after the gamma was removed. However, when the dominant birds were reintroduced the percentage of the group yelling remained high varying only between 75% and 83%, rather than returning to previous levels.

The continued yelling of many birds after the dominants were reintroduced was likely due to status shifts. The moment we placed previous dominants back into the main aviary they were chased and attacked by the new alpha and beta birds. Evidently, the returnees were recognized as intruders and not as formerly dominant group members (free-living vagrants that visit the aviary are also responded to with threatening postures). Returning dominants did not reclaim their prior status. Each dropped at least 3 places in the hierarchy (Table 2).

Table 2. Changes in the status of top ranking birds after the alpha, beta, and gamma were removed from the main aviary. Each dominant was the alpha bird just prior to his removal and each dropped in status after reintroduction. All 3 dominants were housed together in a peripheral aviary during removal. RB was the first removed and last reintroduced and was out of the main aviary for 76 days. GB was out for 55 days. GY was out for 28 days

Prior to experiments (30 Dec–16 March)				During reintroduction (26 May–16 July)		
Code	N	Percentage of interactions won	Rank	Rank	Percentage of interactions won	N
RB	118	98.3	1	4	67.3	110
GB	75	88.0	2	7	38.5	78
GY	96	74.0	3	6	55.8	95
BR	75	57.3	4	1	100.0	41
YW	120	74.2	5	5	75.9	108
BrW	85	70.6	6	8	50.0	58
B	114	50.0	7	2	95.8	48
RY	61	68.9	8	3	72.7	77

Fig. 9. Yelling rates by 3 alpha males while in the group (*filled bars*) and when reintroduced. Yelling was only measured as hungry birds (4 days without food) approached food. Note elevated zero line: none yelled after reintroduction. Yell rates before removal are averages (+ 1 SD) from $N=16$ (RB), $N=13$ (GB), and $N=8$ (GY) 1 min samples during focal observations of each male

Fig. 10. The influence of hunger on yelling (observer not visible) by 10 hand-reared fledglings (approximately 2 months old at start of tests). *Boxes* indicate rates of yelling per 10 birds averaged over 4 tests spanning 11 days. Each test lasted 1 day and included responses before and after 2 feedings. All 10 nestlings were observed yelling during the course of a test. Error bars are $+/-1$ SD

Especially surprising was the change in RB's status. As the former alpha he was extremely dominant but upon reintroduction he was consistently displaced by 3 birds for nearly 2 months.

Associated with drop in the former alpha birds' status was a change in their foraging behavior and yelling. Reintroduced former dominants rarely were the first to approach food and were even less frequently defensive of food they approached (Fig. 8). Neither of the 3 former alpha birds yelled during the experiment following reintroduction (Fig. 9). Only after 2 months did RB occasionally yell when he approached food. Reintroduced alphas did not regain the status and did not continue to behave tyrannically at food nor suppress others from yelling.
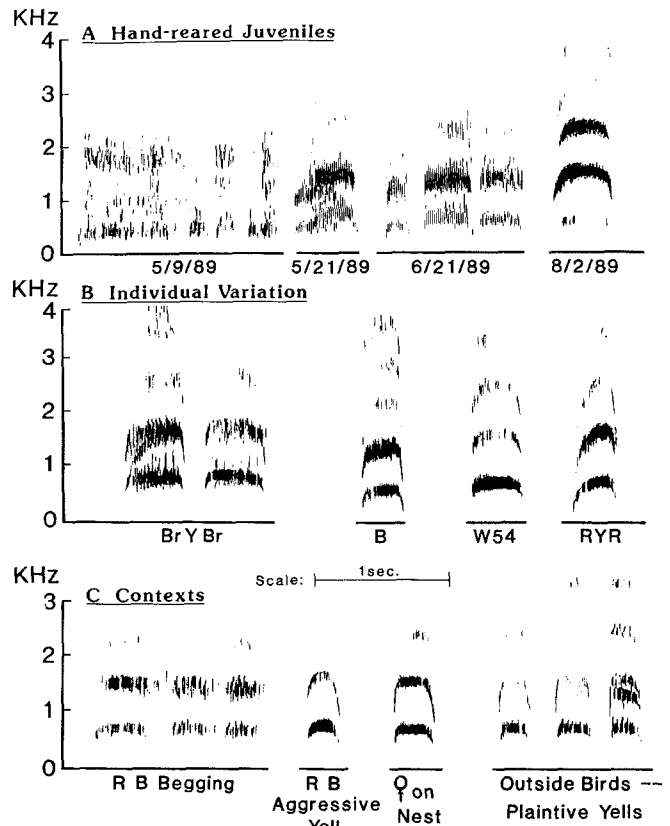
Ontogeny of yelling

Yelling in response to hunger develops early in life. We hand-reared 10 nestlings in the spring of 1989. On four occasions we allowed them to go through a series of hunger-feeding cycles (Fig. 10). Nestlings began to make yell-like calls (Fig. 11 A) after 2–3 h without food, however, within a few minutes of eating yelling was silenced. The rate of yelling declined significantly as a function of time since feeding (Kruskal-Wallis $W=10.2\ P=0.006$) The transition from hoarse begging calls to clear yells occurs over a 3 month period (Fig. 11 A).

Variation in yelling

2 sources of variation in yells were apparent. First, individuals produced yells differing in tone (Fig. 11 B). Second, yells given by dominants as they approached food differed from yells given in less aggressive situations (Fig. 11 C). Aggressive yells were of short duration and sharp, sounding like an emphatic "who!". Yells given by hungry, but non-aggressive birds were more drawn


Fig. 11. Sonograms of yells. (A Ontogeny of the yell. *Left* = raspy calls on 9 May, 1 week before fledging. *Center* = 21 June, 7 weeks after fledging. *Right* = 2 August, 9 weeks of age. B Variations in the yell of 4 different individuals. C *Left* = submissive begging near dominant adults. *Center* = the aggressive "who!" yell and (for right) female yelling on nest. *Right* = plaintive begging near screened-in meat

out and plaintive sounding. Adults rarely yelled, however, as in many corvids, adult females use calls similar to juvenile begging calls when receiving food from their mates (Fig. 11 C; Goodwin 1986). Yells given by adult females on the nest also were drawn out.
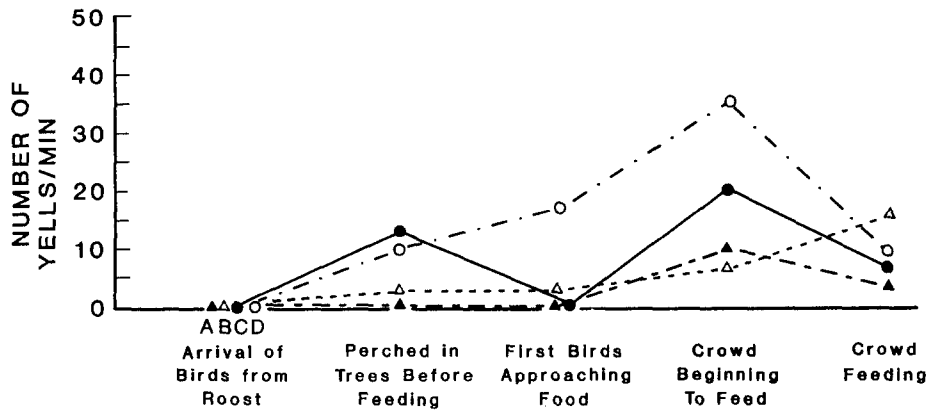
Fig. 12. Temporal changes in yelling by free-ranging birds at 4 carcasses in 1989. *A* Approximately 30 birds feeding on a cow on 8 April. *B* Approximately 20 birds feeding on a moose on 11 April. *C* Approximately 30 birds feeding on a deer and a bear on 8 Nov. *D* Approximately 50 birds feeding on a cow on 23 Nov. These 4 observations were made 1 to 3 days after a large crowd gathered at each bait. Time span of observations varies depending on disturbance during arrival (Times from arrival at feeding site to crowd eating: $A = 37$ min, $B = 2$ h 20 min, $C = 1$ h 7 min, $D = 53$ min)

Comparisons to free-living birds

Behavior in the aviary closely matched that observed in nature. In the field, dominant ravens also were responsible for the marjority of yelling. 8 tagged birds were observed yelling at carcasses. All yelled as they approached food, displaced another bird, and took over a choice feeding spot. Yelling by wild ravens typically peaks as they begin to feed approximately 0.5–1 h after birds arrive from their nocturnal roost (Fig. 12). During peak yelling, most yells are short, sharp "who!" yells given by birds claiming prime feeding spots. Prior to feeding, most yells are long, loud and given by unidentified perched birds.

The status and behavior of our captive immatures persisted after they were reintroduced into the wild 1 year after their original capture. We observed 3 dominants, 4 subdominants, 2 intermediates, and 3 subordinates for a 2 week period after their release. These birds foraged at carcasses along with 10–30 wild vagrants and a pair of resident adults. The dominants and subdominants deferred to few birds and held choice feeding positions. The intermediates and subordinates deferred to most birds they encountered, fed infrequently, and rarely controlled foods.

Discussion

In the forests of northeastern North America, ravens generally forage for carcasses and other food (Bruggers 1988) in the winter by flying singly or in pairs. However, large numbers of vagrant, nonbreeding birds are commonly found at food bonanzas. One of the vocalizations commonly heard from vagrants at the aggregations in the "yell," and playbacks of this call are highly effective in attracting those ravens which are already aggregated in the surrounding forest (or passing through) near a food bonanza (Heinrich 1985, 1988). Grouping is adaptive because it allows vagrants, who are subordinate to territorial adults, to access and profitably forage on defended foods (Heinrich 1988 b, 1989; Marzluff and Heinrich in prep.).

In nature commonly only one or a few birds of any feeding crowd yell before feeding begins (Heinrich 1989). Which birds yell? Our field and aviary observations suggest that the first yellers of the morning are hungry birds that experienced poor feeding on preceding days. These

birds give loud, drawn out yells while perched in trees around a carcass. When feeding begins yelling reaches a peak as many birds descend to the ground and walk up to claim their feeding positions. Dominant juveniles give the majority of yells and they walk with erect feathers, spread their shoulders and take the prime feeding spots. Our experiments indicate that these dominant immatures suppress the yelling of the closest subdominant immatures.

Proximate reasons for yelling

As we argued in the *Introduction* it is necessary to understand the proximate basis of recruitment signals, such as the yell. Our results suggest that hunger and status advertisement are the primary proximate factors causing yelling. Overpowering territorial adults is not a proximate reason for yelling as yells were rarely given by immatures in the presence of adults. In addition, if attraction of others was a proximate reason for yelling then dominant vagrants would not be expected to inhibit subordinates from calling. Instead, dominants should punish subordinates for *not* calling, as occurs in spider monkeys (Chapman and Lefebvre 1990). We conclude that the accumulation of ravens at the site of yelling represents recruitment because attraction of ravens by yelling enhances the fitness of the signaler, but assembling a crowd is not a proximate reason for yelling.

The ontogeny of yelling can be traced to the nestling stage. Sonograms of individual birds beginning while they are still in the nest indicate a progression from rasping disharmonic calls to the loud harmonic yells typically heard at food (Fig. 11). Thus, initially the birds yell proximately in response to the presence of food (or the expectation of food), provided they are hungry. The following winter (and winters) they continue to do the same, except now the yell is restrained by social superiors.

Adaptive significance of yelling

Most species of birds produce begging calls as nestlings when they are fed. However, these are lost shortly after independence from parental care. We know of no other cases where begging calls develop into louder, more easily located calls indicative of food. Presumably this is rare because in most cases it is disadvantageous to

broadcast the presence of food. On the contrary, it is advantageous for vagrant ravens to advertise the location of food because most foods are defended and therefore unavailable until a crowd assembles and overpowers the defending territory owners.

Yelling may be of further adaptive significance as a status signal. As has previously been determined (Gwinner 1964), captive ravens kept within a flock form and maintain a linear dominance hierarchy, and social dominance in these birds is an important correlate of pair formation. At least in part, the food bonanzas on which ravens specialize serve as a site where dominance is established, reinforced and/or maintained by fighting and by appropriate signalling of both dominance and submission. It therefore seems likely that the yelling we observed in our captive birds is related to status signalling that might ultimately translate to mate and food acquisition.

If yelling by immatures ultimately functions in their gaining access to defended foods, it may at first appear curious that they did not yell in the presence of the adults. Indeed the adults inhibited, rather than facilitated, yelling. However, the presence of defensive adults may not trigger yelling because adults attack yelling vagrants, thus discouraging their display of status and reducing recruitment to the food the adults try to defend.

How can a signal that is proximally given as a show of hunger and status be ultimately functional also in recruitment? The show of status ultimately functions in sexual selection (Gwinner 1964; Komers and Dhindsa 1989). However, since the same display yields other advantages related to feeding and gaining access to food, it has likely become amplified rather than compromised through evolution. Presumably this is rare because in most cases it is disadvantageous to broadcast the presence of food. However, it is convenient for ravens to advertise status at food, and it is advantageous for vagrant ravens to advertise the location of food, because most foods are defended and therefore unavailable until a crowd assembles and overpowers the defending territory owners. As a result, even though yelling is stimulated by hunger and status it has likely been embellished by natural selection because of the benefits of group foraging. It seems unlikely that a display audible for several kilometers, such as the yell, would have evolved solely as a status signal. Quieter vocalizations or posturing, seem more likely because they would suffice for the first function. In typical jury-rigged fashion natural selection has embellished an existing behavior to serve a new function rather than create a new behavior. As a result, the proximate and ultimate reasons for yelling do not coincide.

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