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Foraging strategy in a social bird, the alpine chough: effect of variation in quantity and distribution of food

ANNE DELESTRADE
Centre de Recherches sur les Ecosystèmes d'Altitude, Chamonix

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I conducted feeding experiments to determine the effect of variations in food availability on individual flocking behaviour and foraging efficiency in a social corvid, the alpine chough, *Pyrrhocorax graculus,* which lives in large flocks all year round. In 37 trials I varied both food quantity and the number of food patches. A decrease in the amount of available food reduced the mean flock size, the proportion of birds that had access to food, and their mean pecking rate. A decrease in the number of patches, on the other hand, reduced only the proportion of birds that had access to food. The number of choughs foraging was not influenced by food competition but depended only on the number visiting the site. Females competed less well than males: when food was made scarce, they frequented the site in the same proportion as did males, but had less access to food. I suggest that in this social corvid, long-term advantages to flocking related to social bonds, such as the maintenance of pair bonds, may compensate for short-term costs such as a reduction in foraging efficiency.

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Individual foraging decisions depend mostly on the efficiency with which food may be exploited, which in turn depends mostly on environmental circumstances (Pulliam & Caraco 1984; Barnard & Thompson 1985). A critical decision is whether to forage in a flock. Many bird species forage in flocks (review in Barnard & Thompson 1985), especially when food is scarce, such as in winter (Pulliam & Caraco 1984; Goss-Custard 1985). Flock foraging is known to improve food location, reduce predation risk (Crook 1965; Krebs 1974; Bertram 1978) and increase food intake (Powell 1974; Caraco 1979a; Barnard 1980); however, it can also lead to increased intraspecific competition, particularly when food is limited (Baker et al. 1981; Milinski & Parker 1991). Negative relationships between bird density and intake rate as a result of an increase in agonistic interactions have been found in some studies (Goss-Custard 1985; Elgar 1987; Goss-Custard & Durell 1988). Optimal foraging theory predicts that individuals should optimize their intake rate (Charnov 1976). Because individuals often have different competitive abilities and foraging efficiencies, flock members are likely to react differently to variations in food supply. In the most competitive situations (e.g. clumped or ephemeral food sources) the cost of flocking should be high for subordinates, which are less efficient foragers than dominants (Hogstad 1988; Milinski & Parker 1991). This may result in either spatial segregation of the unequal competitors within the flock (Harper 1982), or the dispersal of subordinates (Caraco 1979b).

Competition for food is related mainly to its abundance and/or distribution (e.g. Wrangham 1980; Schluter 1982; Pulliam & Caraco 1984). The ideal free distribution theory predicts that a decrease in food quantity typically results in a decrease in flock size (Pulliam & Caraco 1984). Similarly, clumped food allows fewer individuals to exploit a food source than dispersed food (Goss-Custard et al. 1992). However, although these relationships are widely accepted, experimental evidence for them is scarce. Moreover, the few tests that have been carried out have involved only small and/or captive flocks (Feare & Inglis 1979; Barnard 1980; Theimer 1987), and have rarely included the combined effects of food quantity and distribution (Schluter 1982; Pulliam & Caraco 1984). Lastly, none of these experiments has considered social bird species, and most of the models have ignored social relationships between foragers within a flock. In contrast to gregarious species, flocks of social species are stable and structured groups, rather than simple aggregations of individuals. Social groups are more constrained than social aggregations, and individual foraging decisions could be affected by social bonds between group members. For example, in social species, pair bonds are often

Correspondence: A. Delestrade, Centre de Recherches sur les Ecosystèmes d'Altitude, 400 route du Tour, Montroc, 74400 Chamonix, France (email: crea@lycosmail.com

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maintained throughout the year (Owen et al. 1988) and in some cases, juveniles accompany their parents (Lamprecht 1986; Cloutier & Bédard 1992). In such cases, it is likely that increasing competition may not necessarily result in the departure of the subordinates, such as females or juveniles, and the distribution of birds may not necessarily reflect food distribution. Long-term benefits of flocking for subordinates, related, for example, to the maintenance of pair bonds or prolonged family associations could compensate for the reduction in short-term advantages caused by the high level of food competition with dominant flock members (Matthysen 1993).

My aim in this study was to test the assumption that flocking behaviour in social species is affected by social associations between flock members, and individual decisions will not depend only on the short-term balance of costs and benefits. I experimentally varied the quantity and distribution of food in the natural environment of a social corvid species with dominance-structured flocks to test the following predictions: (1) individual foraging efficiency will decrease when competition increases, and competition will reduce the efficiency of subordinates more than that of dominants; but (2) foraging flock size will not necessarily decrease when food quantity and number of patches decrease; and (3) subordinates will not leave the flock when competition with dominants increases, even if they do less well.

Alpine choughs, *Pyrrhocorax graculus* (Corvidae) provide an ideal social species to compare individual foraging strategy when food competition varies: (1) they are easy to attract to artificial food sources, and experimental trials can easily be conducted in their natural environment; (2) mates are highly faithful (Büchel 1983) and associate throughout the year (unpublished data); (3) group members have unequal competitive abilities, females being dominated by males and immatures by adults (Büchel 1983; Delestrade 1993a); (4) this species always forages in flocks of more than 50 individuals (Delestrade 1994), and frequents either alpine grasslands for naturally distributed food sources (invertebrates and berries, Rolando & Laiolo 1997), or clumped food sources such as human refuse (Delestrade 1995).

METHODS

Study Population and Locality

I studied a free-living alpine chough population, which spends most of its winter time at the ski station of Le Tour (1500 m) in the Northern French Alps (Chamonix Valley, Haute-Savoie; Delestrade 1993b). In this tourist region, alpine choughs often forage at ski stations, refuse dumps, towns, or picnic areas on human food supplies (Delestrade 1994). I studied this flock from January to April 1992 and from November 1992 to April 1993. Since 1988, this flock has been extensively colour banded permitting individual identification of up to 30% of individuals (median flock size 160, range 50–310, N=41; see Delestrade & Stoyanov 1995). The sex of ringed birds was distinguished (1) by behaviour when the male feeds its mate, (2) by laparoscopy by H. Richner (see Richner 1989) and (3) using discriminant function analysis on external measurements (unpublished data). I assessed pairing status by the male's courtship feeding which took place in spring. Because the proportion of first-year birds in this flock in winter was low (<6%, see Delestrade 1994), I excluded them from the analyses. Population structure consisted of an assemblage of stable groups that were recorded in different massifs during summer and that gathered in flocks at various foraging sites in winter (Delestrade 1994). Using identified birds, I could divide the Le Tour flock into three such distinct groups, each comprising around 100 individuals. These groups were defined on the basis of their distinct foraging locations in summer (unpublished data). However, two of these groups regularly frequented the study site (and are thus referred to as 'residents'), whereas the third did so only occasionally, and is referred to as the 'visitor' group.

Table 1. Number of experiments according to food quantity and distribution (N=37)

Number of patches	Food quantity (kg)			
	*1**	2	4	20
1	*2 (2)*	5 (3)	4 (2)	7 (3)
6	—	2 (2)	4 (2)	3 (2)
12	—	3 (3)	2 (2)	3 (3)
300	*2 (2)*	—	—	—

Number of trials using a video camera (N=26) is indicated in parentheses. Italics indicate extreme situations analysed only in some cases.

*When food quantity=1 kg and patch number=1, the food was a piece of fat; when patch number=300, the food was dry raisins; otherwise, the food was apples.

Trials

Observations were made on a snow-covered field (surface area of ca. 50 m^2), at Le Tour Village which the choughs visited daily in winter. I provided variable quantities (2, 4, 20 kg) of apples, a food naturally consumed by the alpine chough, at various densities, that is, at a number of evenly distributed patches (1, 6, 12; Table 1). The quantity was equally distributed in each patch. Food quantity and patch number were selected at random for each trial and only one trial was carried out per day. Trials were usually conducted in runs of 6 successive days, at least 3 weeks apart, during two winter seasons. No trials were performed during extreme weather conditions (e.g. heavy snow fall, strong winds). Food was distributed just before sunrise, and each trial lasted until the birds either left the area, or until the food was finished. Foraging choughs were present for between 15 min and 3 h. I conducted 33 trials with apples as well as four trials with two extreme cases of food distribution, using a small quantity (1 kg) of highly attractive food (Table 1): maximum food dispersion and minimum food quantity (1 kg of dry raisins randomly distributed over the area, i.e. more than 300 raisins), and minimum food dispersion and minimum food quantity (a 1 kg piece of fat). These four trials were analysed separately.

Parameters Studied

I recorded 10 parameters during each trial, either using scan (i.e. flock), or focal animal (i.e. individual) sampling (Altmann 1974). A distinction was made between visiting birds (i.e. those that visited the site, N=37 trials) and foraging birds (i.e. visiting birds that settled down at the food source, N=36 trials).

(1) Maximum flock size of visiting birds, derived from the highest recorded visiting flock size over the trial (flock size counted half-hourly).

(2) Proportion of females among visiting birds as deduced from ringed birds that were checked every 15 min.

(3) Proportion of females among foraging birds as deduced from the average of scan-samples. Ringed individuals among foraging birds were scan-sampled every 4 min when the food quantity was 20 kg, or every 2 min for quantities of 1, 2 or 4 kg.

(4) Number of times per trial each ringed bird was observed among foraging birds was also deduced from scan-sampling and averaged per sex.

I used a video camera to record a second set of parameters. The camera was set on an elevated viewpoint, to monitor feeding birds more accurately (N=26 trials, Table 1). Films were taken whenever birds were present. Cassettes were analysed at either 2- or 4-min sampling rates, depending on food quantity (see above). The following variables were obtained for each trial.

(5) Average number of foraging birds on the trial surface. To avoid the effects of food depletion the mean number of foraging birds for each trial was derived from the first half of the time that birds spent at the site.

(6) Median interindividual distances: 10 nearest-neighbour distances (number of bird lengths) were measured directly on the screen using 10 randomly chosen individuals, and the median was calculated. The camera was placed above the experimental site to avoid any perspectival bias.

(7) The proportion of birds that did not interact with one another. An interaction was defined as one bird displacing the other from the patch.

(8) The proportion of birds that did not take any food.

(7) and (8) were both averaged from the total of focal sampling recorded during each trial. I followed birds for 1 min as soon as they landed within the area.

(9) Pecking rate per min.

(10) Interaction rate per min.

(9) and (10) were recorded simultaneously (N=1956 observations) using the focal animal sampling method (Altmann 1974), and averaged per trial to minimize variance. Four birds were recorded every 4 min, or eight birds every 2 min according to food quantity (see above). Data for ringed birds were also analysed separately. The mean pecking rate and mean interaction rate per min per trial were calculated for each ringed bird (N=451 observations on 113 ringed birds), and averaged for each sex to compare individual foraging efficiency between the sexes. When not enough data were available per sex for each class, I pooled the data from the trials with 2 and 4 kg of food (=small food quantity) in contrast to the trials with 20 kg of food (=large food quantity).

Statistical Analysis

I used the SAS/PC software (SAS Institute 1989). Analyses of variance (ANOVA) using the GLM procedure were used to test for the effect of variations in food quantity and food distribution on the variables studied. When analysing mean pecking rate or mean interaction rate, I excluded zero values (i.e. those birds that never had access to food, or never interacted). Analyses of covariance (ANCOVA) were used to test the effect of variations in food quantity and distribution controlled for the effect of variations in foraging flock size. Assumptions of normality and homogeneity of variance were checked. There was no significant effect of seasons between experiments or of days within experiments, so I pooled data from different periods. The proportion of birds that did not interact and the proportion that did not take any food were arcsine square-root transformed to allow the use of parametric tests. Because not all ringed individuals were observed at all trials, repeated measures ANOVA could not be performed. Thus, the mean data of each ringed individual were averaged per sex and per trial before analysis. For analyses of the behaviour of flock members, the Bonferroni correction was applied to correct for the number of tests performed in parallel. All tests are two-tailed.

RESULTS

Flock Response to Increasing Competition

Variations in flock size

The maximum number of birds visiting the experimental site varied from 70 to 300 ($\bar{X} \pm SD=192 \pm 85$, N=33). This number increased with food quantity (two-way ANOVA: $F_{2,32}=8.8$, $P<0.01$), but was not affected by variations in food distribution ($F_{2,32}=0.5$, NS). An average ± SD of 49 ± 19 birds (N=32) were foraging at the same time. This number of foraging birds was correlated with the maximum flock size (ANCOVA: $F_{1,31}=15.8$, $P<0.001$), but was not affected by food quantity ($F_{2,31}=1.5$, NS) or its dispersion ($F_{2,31}=0.6$, NS), when variation in the maximum flock size was controlled for. Thus, the number of birds at the experimental site did not change with variations in food quantity or food dispersion but depended only on the maximum flock size visiting the site. Of the birds visiting the site, 28 ± 0.1% ($\bar{X} \pm$ SD, N=32) were foraging at any one time.

Group attendance

The three groups constituting the visiting flock did not frequent the experimental site equally, in terms of number of birds or time spent. The ‘visitor’ group was

Table 2. Number of ringed birds belonging to each group in trials with different quantities of food available

	2 kg (*N*=10)	4 kg (*N*=10)	20 kg (*N*=13)	*P*
Group A	16.1±5.2	14.9±7.5	24.2±5.7	<0.005
Group B	2.6±3.8	3.1±5.0	12.1±6.4	<0.001
Group C	10.5±5.0	9.6±4.9	14.6±5.9	NS

Means are given±SD.

totally absent (i.e. no member was observed) in nine trials, while 'resident' groups were always present. In eight of these nine trials, a small food quantity (i.e. 2 or 4 kg) was involved. The number of ringed birds belonging to each group per trial was significantly influenced by food quantity, but only for two groups (two-way ANOVA for each group: Group A: $F_{2,32}=7.5$, $P<0.005$; Group B: $F_{2,32}=13.3$, $P<0.001$; Group C: $F_{2,32}=3.1$, NS; Table 2). The number of ringed birds belonging to each group per trial was greater at 20 kg of food than at small food quantities (2 and 4 kg; Table 2). Variation in patch number did not affect the number of individuals from any group ($F_{2,32}=0.5$, $F_{2,32}=0.2$, $F_{2,32}=0.1$, NS, for each group, respectively), and interactions were not significant ($F_{4,32}=0.8$, $F_{4,32}=1.1$, $F_{4,32}=0.7$, NS, for each group, respectively). Thus, an increase in food quantity attracted more groups but also more individuals from each group. Thus, variations in visiting flock size depended partly on group attendance.

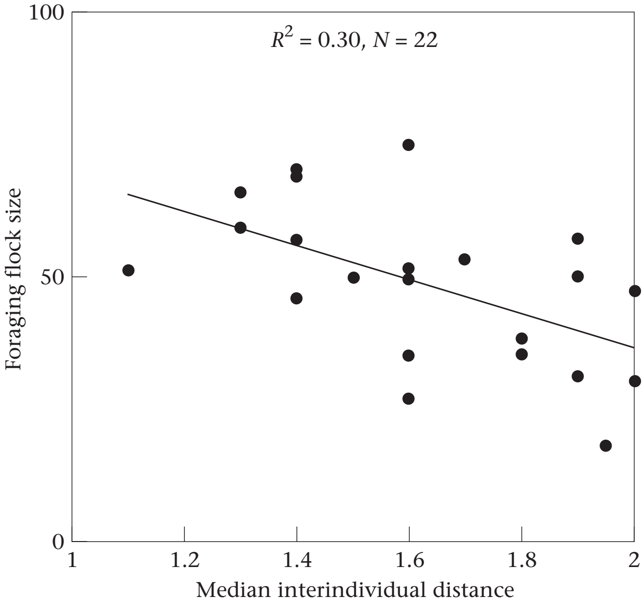

Figure 1. The relationship between foraging flock size and median interindividual distance (measured as number of bird lengths).

Behaviour of flock members

The median interindividual distance between birds was negatively affected by variation in the mean foraging flock size (ANCOVA: $F_{1,21}=12.0$, $P<0.005$; Fig. 1). Variations in food quantity or food distribution did not affect interindividual distance when variations in foraging flock size were controlled for (for food quantity: $F_{2,21}=1.4$, NS; for food distribution: $F_{2,21}=1.7$ NS, for quantity*distribution: $F_{4,21}=0.5$, NS).

The proportion of birds that did not interact with others was not affected by variation in food quantity ($F_{2,21}=0.2$, NS), patch number ($F_{2,21}=2.1$, NS), or foraging flock size ($F_{1,21}=6.2$, NS; for quantity*distribution: $F_{4,21}=0.7$, NS). However, when extreme trials (1 kg in 1 or 300 patches) were included in the analysis, it was significantly affected by the distribution of food: there was no agonistic interaction between birds when food dispersion was maximal ($N=128$ observations), while 90% ($N=775$ observations) of foraging birds interacted at least once when food was provided in only one patch. The mean rate of interactions among foraging birds that interacted at least once was not affected by food quantity ($F_{2,23}=0.3$, NS), food distribution ($F_{2,23}=2.3$, NS) or the number of foraging birds ($F_{1,23}=2.3$, NS, for quantity*distribution: $F_{4,23}=0.9$, NS).

The proportion of foraging birds that did not have access to food was affected by food quantity ($F_{2,22}=7.7$, $P<0.005$; Table 3) and the foraging flock size ($F_{1,22}=10.6$, $P<0.005$), but not by patch number ($F_{2,22}=6.5$, NS; for quantity*distribution: $F_{4,21}=1.2$, NS). The proportion of birds that did not have access to food decreased when food quantity increased and when flock size increased. When extreme trials were analysed, all foraging birds had some food when its dispersion was maximal (i.e. 300

Table 3. Proportion of birds that did not have access to food and pecking rate of foraging birds (pecks/min) in trials with different quantities of food available

	2 kg (*N*=8)	4 kg (*N*=6)	20 kg (*N*=8)	*P*
Proportion of birds without access to food	0.2±0.20	0.1±0.08	0.07±0.04	<0.005
Pecking rate (pecks/min)	5.3±1.9	6.4±1.9	9.2±2.4	<0.005

Means are given±SD.

Table 4. Number of times males and females were observed foraging in trials with different quantities of food available

	2 kg (*N*=10)	4 kg (*N*=9)	20 kg (*N*=13)	*P*
Male	1.9±0.4	2.2±0.9	4.2±1.5	<0.001
Female	1.6±0.3	1.9±0.7	4.3±1.4	<0.001

Means are given±SD.

Table 5. Pecking rate (pecks/min) of males and females that had access to food in trials with different quantities of food available

	2 kg (*N*=4)	4 kg (*N*=6)	20 kg (*N*=6)	*P*
Male	6.7±2.0	7.3±2.8	10 ±1.0	<0.005
Female	4.6±2.6	6.9±2.7	8.9±1.6	<0.005

Means are given±SD.

patches, N=128 observations), as against only 82% when it was clumped in one patch (N=775 observations; χ^2_1=26.0, P<0.001). Thus, access to food for flock members depended on food quantity, food distribution and foraging flock size. The mean pecking rate of foraging birds increased with food quantity ($F_{2,23}$=6.8, P<0.005; Table 3) but was not affected by patch number ($F_{2,23}$=3.1, NS), or foraging flock size ($F_{1,23}$=0.3, NS; for quantity*distribution: $F_{4,23}$=1.7, NS).

Male Versus Female Behaviour with Increased Competition

Sex ratio

The proportion of females among visiting or foraging birds (average: 40.8 and 39.4%, respectively) was not influenced by food quantity ($F_{2,32}$=0.3, $F_{2,30}$=0.2, NS, for the percentage of females visiting or foraging, respectively) or food dispersion ($F_{2,32}$=0.9, $F_{2,30}$=0.5, NS; for quantity*distribution: $F_{4,32}$=0.9, $F_{4,30}$=0.4, NS for visiting or foraging females, respectively). Moreover, these proportions did not differ statistically from the proportion found in the total population of marked birds (i.e. 41.2%, χ^2_1=0.005 and χ^2_1=0.29, NS among visiting and foraging birds, respectively). This therefore suggests that males and females frequented the site and tried to gain access to the food source equally, irrespective of the intensity of competition, even though females are dominated by males.

Foraging behaviour according to sex

The number of times each ringed bird was observed foraging was averaged per sex and per trial. This mean number was not different between the sexes ($F_{1,63}$=0.3, NS) and increased significantly with food quantity ($F_{2,63}$=38.8, P<0.001; Table 4) but not with food dispersion ($F_{2,63}$=0.08, NS; for quantity*distribution: $F_{4,63}$=1.5, NS; for quantity*sex: $F_{2,63}$=0.3, NS; for distribution*sex: $F_{2,63}$=0.2, NS).

When large food quantities were available (i.e. 20 kg), the proportions of foraging birds that did not take any food were similar for the two sexes (4.8% for females (N=131) and 3.2% for males (N=231; χ^2_1=0.93, NS). In contrast, when small food quantities were available (i.e. 2 or 4 kg combined), a significantly higher proportion of foraging females did not take any food: 24.5% for females (N=98) against 9.1% for males (N=176; χ^2_1=10.8, P<0.001).

Among foraging birds that had access to food, the mean pecking rate per min averaged by sex per trial was not different between males and females (three-way ANOVA: $F_{1,31}$=2.3, NS); pecking rate increased with food quantity for both sexes ($F_{2,31}$=8.5, P<0.005; Table 5), but was not affected by variations in food dispersion ($F_{2,31}$=0.2, NS; for quantity*distribution: $F_{3,31}$=0.1, NS; for quantity*sex: $F_{2,31}$=0.001, NS; for distribution*sex: $F_{2,31}$=1.5, NS).

DISCUSSION

Flock Versus Individual Response to Food Availability

When competition for food was low (large number of raisins scattered randomly), all alpine choughs had access to food without interactions between individuals, even when only 1 kg of food was available. This is precisely the situation that is naturally encountered by the alpine chough, when birds forage in alpine grassland in large flocks, exploiting insects and berries (Rolando & Laiolo 1997). In this natural situation, agonistic interactions are rare (unpublished data), which suggests that competition between individuals is low (Gauthreaux 1978). A similar result was found by Rohwer & Ewald (1981), who showed that there was no difference in pecking rates of dominant and subordinate Harris sparrows, *Zonotrichia querula*, when seeds were scattered over a large area. In both studies, the food consisted of distinct small items which could not be defended by one individual.

Conversely, when food items were large (e.g. apples in this study) and patchily distributed, agonistic interactions appeared between flock members and only some of the foraging birds had access to food. Thus, competition was experimentally increased through variations in either quantity or distribution of food. Access to food for foragers was dependent on the quantity and distribution of food and the foraging flock size. When the effect of the foraging flock size was controlled for, variations in food quantity affected the proportion of foraging birds that had access to food and their mean pecking rate. Variations in food distribution influenced the proportion of foraging birds that had access to food and that did not interact with other birds.

In the present study, different mechanisms regulated the foraging efficiency of flock members according to food availability. First, individual foraging efficiency, measured as the proportion of foragers that had access to food and as pecking rate, decreased with food quantity, which was the main factor accounting for foraging efficiency variations. Second, the number of visiting birds attending the site varied in response to variation in food quantity. This regulation operated at two levels: the number of groups visiting and the number of individuals belonging to each group. Variation in food distribution did not affect the number of birds attending the site, but affected their access to food. Conversely, food availability appeared not to affect the number of foraging birds, while a greater attraction of foragers to the food source decreased interindividual distance and decreased the proportion of individuals that had access to food. The number of foraging birds did not depend on food accessibility, but depended exclusively on the size of the flock visiting the site. Thus, the level of competition between foragers did not affect their decision to land near the food source in order to forage while it did affect their foraging efficiency.

These results do not support the ideal free distribution theory which predicts that the distribution of organisms between resource sites should match the distribution of resources (Fretwell & Lucas 1970). They do, however, support the assumption that the optimal foraging efficiency of individuals may be constrained by the long-term social associations between flock members.

Male Versus Female Response to Competition

Social factors are known to affect individual foraging success (Barnard & Thompson 1985; Elgar 1987; Theimer 1987). Competitors react differently according to their competitive abilities and food competition (Gauthreaux 1978; Milinski & Parker 1991) and dominants are usually more efficient foragers than are subordinates (Caraco 1979a; Hogstad 1988; Milinski & Parker 1991). In the alpine chough, males dominate females (Büchel 1983; Delestrade 1993b). As predicted, when competition was low, males and females had the same foraging efficiency but when competition was high females were less efficient than males, and had less access to food.

Previous field studies have shown that a difference in competitive abilities between the sexes usually results in a spatial segregation when feeding (e.g. Greig et al. 1985). The ideal free distribution theory with unequal competitors predicts that better competitors are overrepresented in the better sites, while poorer competitors are overrepresented in the poorer sites. In my study, however, the sex ratios of visiting or foraging birds were not affected by the level of competition. I suggest that this is a result of the strength of pair bonds, in this species, which forces individuals to react as pair members rather than as individuals. This may be detrimental to females when competition is severe but they may benefit by their continuous partnership over the whole year.

Short- Versus Long-term Benefits of Flocking

A foraging strategy is usually seen as an adaptive response to food availability or predation risk, that is, taking into account only the balance of short-term costs and benefits of flocking (Senar 1994). However, social associations may not necessarily be adaptive in the short term (Lefebvre et al. 1992; Matthysen 1993). My results support the assumption that foraging strategies adopted by flock members are affected by social associations: both the maintenance of group structure and pair bonds may have affected individual flocking decisions. Individual foraging strategies may thus depend not only on environmental conditions, such as the quantity and distribution of food, but also on behavioural traits of the species, such as the strength of bonds between flock members. The maintenance of pair bonds has long-term benefits (Black 1996): for example improving coordination and cooperation with a mate and reducing the cost involved in mate sampling. These advantages could offset the short-term costs that subordinates (e.g. females) suffer when they flock with dominants (e.g. males). In contrast, to simple aggregations, flocks of social species may therefore provide long-term advantages for individuals that could outweigh the costs.

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