Ethology

The Effects of Predation Risk, Food Abundance, and Population Size on Group Size of Brown-Headed Cowbirds (*Molothrus ater*)

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Abstract

Social and ecological conditions can influence flock formation (e.g. number of flocks, flock size, etc.) depending on the degree of social attraction of a species. We studied group formation in brown-headed cowbirds (*Molothrus ater*) over short time periods (30 min) in two semi-natural experiments conducted under controlled conditions. First, we determined the shape of the relationship between intake rate and flock size by manipulating group size in a single enclosure. Second, we assessed the role of population size, food abundance, and predation risk, and their interactions, in flock size formation in a system of four enclosures (two with and two without food) connected to a central refuge patch. In the first experiment, we found that pecking rates peaked at intermediate flock sizes (three to six individuals), which was influenced by greater availability of foraging time and more aggressive interactions in large groups. In the second experiment, flock sizes in the patches with food increased with population size likely due to the benefits of patch exploitation in groups. Flock size decreased after predator attack probably because refuge availability reduced perceived predation risk more than flocking in larger groups. Food abundance had minor effects, varying flock sizes between the two patches with food, under high food availability conditions when population size was high, probably due to social cohesion effects. Our results suggest that: (1) this species has an inverted-U food intake–group size relationship with a range of intake-maximizing flock sizes rather than a single peak, (2) the presence of a near refuge modifies the expected benefits of group patch exploitation under high predation risk, and (3) an increase in population size would more likely be translated into rapid increases in the size of the flocks rather than in more new flocks.

Introduction

Social foraging is a common phenomenon among birds (Beauchamp 1998, 2002). Theoretical and empirical research has extensively addressed the costs and benefits of joining groups (e.g. Giraldeau & Caraco 2000; Krause & Ruxton 2002; Caro 2005), and many of the mechanisms involved in foraging with others (Beauchamp 2003). For instance, dilution and collective detection effects may translate into increase survival in larger groups (e.g. Powell 1974; Kenward 1978; Kus 1986). Furthermore, time competition between foraging and anti-predator/conspecific vigilance or between foraging and interference (e.g. aggressive interactions) may increase or decrease, respectively, the proportion of time devoted to foraging in larger groups (e.g. Caraco 1979; Beauchamp & Livoreil 1997; Norris &

Johnstone 1998). The degree of relevance of these mechanisms for a given species can be influenced by several social and ecological factors, such as sex, spatial distribution of prey, prey availability, etc. (Beauchamp 1998, 2002, 2004). Interactions between these factors and behavioral mechanisms are expected to balance out grouping costs and benefits and give rise to group sizes in which individuals can maximize their fitness returns (Krause & Ruxton 2002). Therefore, group size can be considered a good indicator of changes in ecological conditions (Beauchamp 2002; but see Pöysä 1994; Fernández-Juricic et al. 2004a).

We assessed the role of social and ecological factors affecting group sizes in brown-headed cowbirds (*Molothrus ater*), a species that forms foraging aggregations during the non-breeding season (Lowther 1993), in two experiments conducted under semi-natural conditions. First, we established the intake-maximizing group sizes to better understand the costs and benefits of grouping in this species by manipulating the number of individuals foraging in a single enclosure, controlling for several confounding factors (food availability, patch size, and food deprivation). We used pecking rate as a proxy of food intake in this species (Fernández-Juricic et al. 2007). We also studied one type of anti-predator behavior, vigilance, as a proxy of the costs of predator detection in flocks (Siegfried & Underhill 1975; Kenward 1978; Williams et al. 2003).

Second, we determined the role of population size, food abundance, and predation risk, and their interactions, in modifying group size in a system of four enclosures of the same size as that used in the first experiment. Enclosures were connected to a central refuge, defined as a safe area in which animals restricted their activity under high levels of predation risk (Caro 2005). The system consisted of two patches with food, and two patches without food. Cowbirds were expected to have three choices that would provide foraging (patches with food) and anti-predator (refuge) benefits. This experiment intended to ascertain changes in group sizes over short time spans (30 min), as opposed to previous studies that assessed similar changes over longer periods of time (e.g. seasonal, Williams et al. 2003).

An increase in population size is expected to increase the number of individuals available to join flocks (Spinage 1969; Wirtz & Lörscher 1983; Crockett & Eisenberg 1987; Ostro et al. 2001). The distribution of individuals across patches with similar food availability may also vary with population size depending on the shape of the intake-maximizing–group size relationship. If intake rate decreases with group size steadily (e.g. interference effects, Sutherland 1996), then individuals are expected to be distributed evenly across patches with food, resembling an ideal-free distribution. However, if intake rate peaks at intermediate group sizes (e.g. due to foraging or anti-predator benefits), then group size under non-saturating population sizes would vary to maintain the cohesion of the intake-maximizing group size (Vásquez & Kacelnik 2000; Gauvin & Giraldeau 2004). Either of these two outcomes is expected if group members do not control access to groups.

Conditions in which patches have higher food abundance are expected to increase flock size by increasing the payoffs of food exploitation (Alonso et al. 1987; Delestrade 1999; Amano et al. 2006), and attracting more individuals from the refuge to the patches with food (Martín et al. 2003).

Flocks tend to be larger in areas that have been subject to predation risk for a long period of time (Thiollay & Jullien 1998; Beauchamp 2004). However, we studied only short-term responses after a predator attack in a closed system with a refuge available. Flocks are expected to split temporarily to use a refuge patch, but after returning to the foraging patches, two outcomes are possible: flock size in the foraging patches may (1) increase due to the enhanced benefits of flocking after a temporary increase in predation risk (Caraco et al. 1980; Szekely et al. 1989) or (2) decrease due to the higher benefits of refuge use than those of patch exploitation (Hugie 2003).

Methods

Study Area and Subjects

We conducted both experiments (first, to determine intake-maximizing flock sizes; second, to ascertain the effects of population size, food abundance, and predation risk on flock size formation) at the California State University Long Beach campus from May 2005 to Aug. 2005, on a grassy area shaded by an old Italian stone pine (*Pinus pinea*). The experimental area was 20 m away from the closest pathway, which received low pedestrian traffic, and encircled by a 1.80 m high fence covered with black plastic.

We caught and color-ringed brown-headed cowbirds from the Prado Dam population, Riverside County, California. Animals were housed in indoor cages (0.85 m × 0.60 m × 0.55 m), under a 12L:12D light cycle (lights on at 07:00). Birds were in visual and auditory contact, with four to five individuals per cage. Water and food (Mazuri® Small Bird Maintenance pellets; Mazuri, USA) were available *ad libitum* except during experimental trials. Experimental protocols were approved by the University Institutional Animal Care and Use Committee (Protocol #219).

First Experiment: Intake-Maximizing Flock Sizes

We used 56 adult cowbirds (28 males, 28 females). Eight animals were randomly chosen as focal subjects with an equal number of individuals of each sex. The remaining birds acted as companions in flocks of different sizes ranging from 1 to 8. We used a bottomless mesh wire cylindrical enclosure (diameter = 0.53 m, height = 0.38 m) in which we manipulated flock size. The enclosure was placed on a circular wooden tray covered with 3 cm of sawdust. We scattered 15 g of finch mix (Royal Feeds; Leach Grain and Milling, Co., Downey, CA, USA) on top of the sawdust, and shook the trays to mix the food items with the substrate and maintain a random food distribution. Some seeds were left visible on the substrate to encourage foraging activity, which started almost immediately.

Animals were transported from the animal-care facility in soft cloth bags and released into the enclosures. We recorded observations with a Sony DCR-TRV38 digital video camera that was placed at a fixed distance of 3 m. Trials lasted 15 min from the first peck of the focal bird. Trials were not performed under rainy or windy conditions. The eight focal birds were exposed to the eight flock-size conditions in a random order, without being used more than once per day, yielding a total of 64 trials. We ran between three and six trials per day in the morning (08:00–13:00). We kept a 1:1 sex ratio for flocks with an even number of individuals, while flocks with an odd number of individuals had an additional male.

Foraging and scanning behaviors were scored on the focal birds using an event recording program, JWATCHER 1.0 (Blumstein et al. 2006). We only recorded behavior while brown-headed cowbirds were on the ground and excluded sequences when birds hung from the enclosure wall. While on the ground, a cowbird could be head-down or head-up, depending on whether its head was below or above its shoulder. While birds were with their heads up on the ground, we recorded the number and duration of scanning events (excluding food-handling) and aggressive interactions (e.g. fights, displacements, etc.). We also measured the number and duration of food-handling events while cowbirds were with their heads up and down. We calculated the rate (events per minute) and proportion of time scanning (head-up) and food-handling, and aggressive interaction rate on a trial basis. While the birds were head-down, we recorded the number of pecks and the duration of food searching events. We then calculated pecking rate (events per minute), and the proportion of time allocated to food searching. Because of the significant correlation between pecking and food handling rates (r = 0.38, p = 0.002), we only presented the former and assumed that pecking rates were a good indicator of food intake rate. One student recorded these behaviors after extensive training in analyzing pilot video tapes, with an error rate less than 5% before coding the trials.

For each trial, we recorded the food deprivation time of the focal bird (range 60–265 min), its body mass (range 26.94–43.71 g), and wing length (range 61–98 mm). As body condition can influence group sizes (Ranta 1993), we calculated it as body mass/wing length ratio and included it in the analyses.

Second Experiment: Effects of Population Size, Food Abundance, and Predation on Mean Flock Sizes

We used a central group of 67 (34 males, 33 females) brown-headed cowbirds. For each combination of factors, we chose randomly from this group of individuals (without using the same bird more than once per day) and complemented the flocks with other birds that were captured every 3 wk to reduce habituation/sensitization effects.

Our experimental set-up consisted of four cylindrical mesh wire enclosures (diameter 0.53 m; height 0.38 m) that were attached symmetrically to a central enclosure (diameter 1.00 m, height 0.58 m) via rectangular mesh wire corridors (opening 0.15 m, length 0.28 m), allowing birds to move freely among patches (Fig. 1). The central enclosure was placed upon a circular plywood tray lined with paper, and had four perches intersecting at the center. The perches had the same position throughout the experiment. Artificial foliage was attached to the inside wall of the enclosure leaving all four peripheral-enclosure entrances and the top of the cage unobstructed. Circular plywood trays were placed underneath each of the four peripheral patches and filled with 3 cm of sawdust which was replaced with fresh sawdust after each trial. The peripheral enclosures did not have foliage or perches. The four peripheral enclosures acted as foraging patches, and the central enclosure, as a refuge patch (Fig. 1). In each trial, irrespective of the treatment, two of the

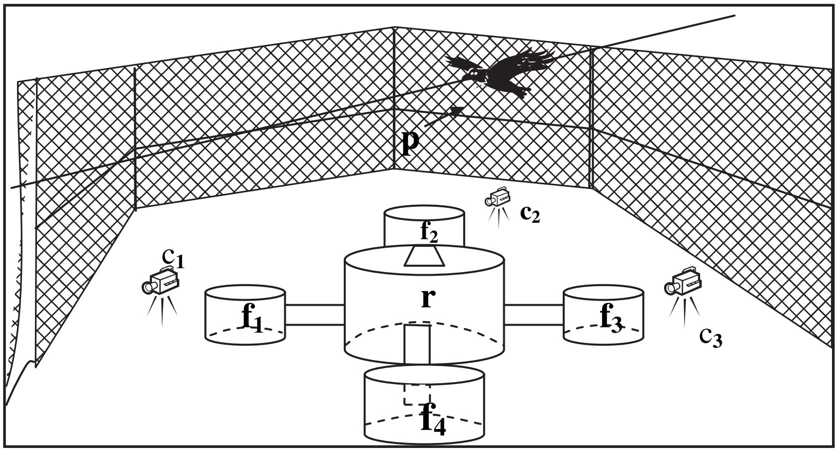

Fig. 1: Schematic representation of the set-up of the second experiment, with four foraging patches (f_1–f_4), four video cameras (c_1–c_3, camera 4 is not shown), central refuge patch (r, four perches and artificial vegetation not shown), and a predator model (p) sliding above the system.

foraging patches had food (food present) whereas the other two did not (food absent). Our intention was to assess the time it would take cowbirds to establish food availability in the system and to distribute themselves accordingly; however, they did so from the start of trials (see Results). We randomized the foraging patches with and without food between trials.

We manipulated three factors simultaneously: population size, food abundance, and predation risk. We set two different population sizes by varying the number of individuals present in the experimental arena (7 and 14). We set two levels of food abundance per patch: low (2 g per patch) and high (10 g per patch). Each of the two patches with food on a given trial had the same food abundance. We used the same type of finch mix as the one used in the first experiment. Food was randomly distributed by shaking the trays to mix food items with the substrate. We set two levels of predation risk: low (before exposure to a predator model) and high (after exposure to a predator model). The predator model consisted of a taxidermic red-shouldered hawk (*Buteo lineatus*) in flight position that was released directly over the center of the experimental arena (height 2.5 m) via a pulley system moving from south to north (Fig. 1). The trial began when at least one individual entered a foraging patch and pecked for food. Trials lasted 30 min: 15 min before and 15 min after the exposure to the predator.

Animals were transported from the animal-care facility to the study site in soft cloth bags and released into the refuge patch through a gated opening at the top. We recorded observations in the four foraging patches with four Pelikan Cam color bullet cameras (TC855) connected to a Digital Quad Splitter (Clover Electronics, CA, USA), which allowed for simultaneous recording using a time lapse recorder (Wooju Communications Co. Ltd, Incheon, South Korea). Trials were not conducted during rainy or windy days. Our design was balanced, with 14 replicates per level of a fixed factor [population size: 14 (low) + 14 (high) = 28 trials; food abundance: 14 (low) + 14 (high) = 28 trials; including two levels of a repeated-measures factor, predation risk, in each of these trials], resulting in 56 trials.

For each trial, we recorded the number of birds in each of the four foraging patches every 15 s, totaling 90 recordings, to assess the temporal changes in flock size per patch. We excluded birds not using the foraging patches, such as those hanging on the enclosure wall or perching in the foraging patch entrance. We then computed mean flock sizes and only included those recordings with at least one individual in a patch to avoid biases due to the inclusion of 0's that indicate the absence of birds. Results using median and typical flock size were similar to those for mean flock size, and are not reported. Additionally, we do not present refuge patch results because these would mirror those found in the foraging patches.

Statistical Analysis

To establish intake-maximizing flock sizes in the first experiment, we assessed the effects of flock size on foraging behavior (pecking rate, proportion of time food searching). We also analyzed the effects of flock size on vigilance (scanning rate, proportion of time scanning) and aggressive (aggressive interaction rate) behaviors to understand the costs of grouping in terms of time lost from foraging activities. We used a repeated-measures design because each of the eight focal birds was exposed to each of the eight flock sizes. We employed general linear models. Temperature was not included in the models as a confounding factor because it did not affect pecking ($F_{1,55} = 2.74$, $p = 0.103$) or scanning ($F_{1,55} = 1.26$, $p = 0.267$) rates. Given our limited sample size (eight replicates per level of flock size), we followed two strategies to avoid reducing the power of the tests when incorporating other confounding factors. First, we only included the effects of body condition, because there was a marginally non-significant correlation between body condition and food deprivation time ($r = -0.703$, $p = 0.052$). Second, we first ran models including body condition. However, if a non-significant body condition effect was found, we ran our models again without this variable. If the effect of body condition was significant, our models included the following factors: flock size (repeated measures), body condition, and the interaction between the two. When using repeated-measures factors with more than two levels, the sphericity assumption may be violated. We tested this assumption using the Mauchley sphericity test (a significant p-value indicates violation of the assumption). When the data did not meet this assumption, we ran the model using a multivariate approach and calculated the Wilks statistic. To better characterize intake-maximizing flock sizes in relation to solitary foraging, we compared pecking rates between different flock sizes with planned comparisons. Some variables were log (pecking rate, scanning rate) and arcsin (proportion of time allocated to searching food) transformed to meet the normality assumption of general linear models.

Given the differences in flock size between patch types in the second experiment (see Results), we only present results for patches with food. We assessed the effects of population size, food abundance, and predation risk on mean flock sizes with a general linear model. We considered predation risk as a repeated-measures factor because the same flock composition was subject to before- and after-predator exposure conditions. Temperature and food deprivation time of the whole population per trial were added to the models as continuous factors due to their potentially confounding effects. All individuals at the start of a given trial had similar food deprivation levels. We did not use body condition due to the many individuals used per trial.

If individuals adopt an Ideal Free Distribution, we would expect that they would be distributed evenly between the two patches with food. To assess this, we ran another general linear model with patch identity (patch 1 and patch 2) as the repeated-measures factor under two scenarios: before and after exposure to the predator. The same factors as described above were included in this model, but we only present those that yielded significant effects. We analyzed differences between levels of different factors with planned comparisons.

The ratio of males to females in the second experimental system varied between 0.75 and 1.33. We ran models with sex ratio, but did not find any significant effect, so we excluded this factor from the reported models to increase the power of our tests. Variables met the normality and homogeneity of variances criteria for general linear models. Throughout, we present mean values (±SE).

Results

First Experiment: Intake-Maximizing Flock Sizes

Pecking rate varied with flock size (Fig. 2a). The effect of body condition was not significant ($F_{7,42} = 1.99$, $p = 0.091$), so we reanalyzed the data without this variable. We found a significant effect of flock size (Table 1), and the sphericity assumption was met ($\chi^2 = 27.62$, d.f. = 27, $p = 0.430$). However, a visual inspection of the relationship between flock size and pecking rates suggested two peaks at flock sizes 3 and 6 (Fig. 2a). Further analyses with planned comparisons indicated that: (1) pecking rates at flock size 3 were significantly higher than those at flock sizes 1 ($F_{1,7} = 9.97$, $p = 0.016$), 2 ($F_{1,7} = 5.82$, $p = 0.047$), and 7 ($F_{1,7} = 6.93$, $p = 0.034$); (2) pecking rates at flock size 6 were significantly higher than those at flock size 7 ($F_{1,7} = 6.68$, $p = 0.036$), and marginally higher than those at flock sizes 1 ($F_{1,7} = 4.47$, $p = 0.072$) and 2 ($F_{1,7} = 4.98$, $p = 0.061$); (3) pecking rates did not differ between flock sizes 3 and 6 ($F_{1,7} = 0.07$, $p = 0.797$); and (4) there were no significant differences between solitary individuals and flock sizes 2, 4, 5, 7, and 8 ($F_{1,7} < 2.15$, $p > 0.186$). All other contrasts were non-significant ($p > 0.05$). These results suggest a range of intake-maximizing flock sizes from three to six individuals per 0.22 m^2, taking into account, pecking rate.

The proportion of time allocated to head-down searching for food was significantly affected by flock size (Table 1, Fig. 2b). The model met the sphericity assumption ($\chi^2 = 7.64$, d.f. = 27, $p = 0.999$). Cowbirds increased the time searching for food up to flock size 8 (Fig. 2b). Furthermore, we found a significant interaction between flock size and body condition (Table 1), in which no relationship was found between body condition and the proportion of

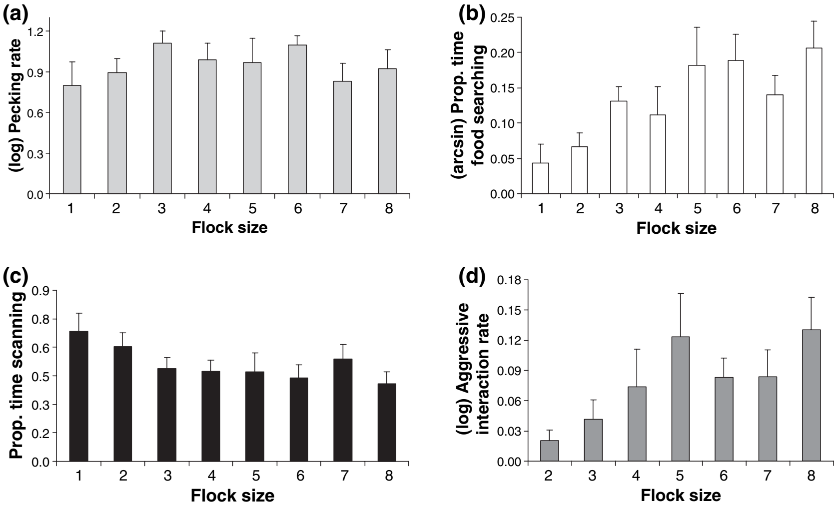

Fig. 2: Relationship between brown-headed cowbird flock size and (a) pecking rate, (b) proportion of time allocated to head-down food searching, (c) proportion of time scanning, and (d) aggressive interaction rate.

Table 1: General linear models assessing the relationship between flock size and brown-headed cowbird behavior (pecking rate, proportion of time head-down food searching, head-up scan rate, proportion of time head-up scanning, aggressive interaction rate) in experiment 1. Significant results are marked in bold

	d.f.	F	p
(log) Pecking rate			
FS	7, 49	2.34	**0.039**
(arcsin) Proportion of time head-down food searching			
FS	7, 42	2.88	**0.015**
BC	1, 6	2.61	0.157
FS × BC	7, 42	3.30	**0.007**
(log) Head-up scan rate			
FS	7, 49	2.32	**0.040**
Proportion of time head-up scanning			
FS	7, 49	2.38	**0.036**
(log) Aggressive interaction rate			
FS	7, 42	2.61	**0.033**
BC	1, 6	0.98	0.358
FS × BC	7, 42	2.90	**0.021**

FS, flock size; BC, body condition.

time allocated to head-down searching in flocks of 1, 2, 3, and 4 individuals, a negative relationship characterized flocks of five individuals, and a positive relationship was found in flocks of six, seven, and eight individuals.

The effect of body condition on head-up scan rate was not significant ($F_{1,6} = 0.02$, $p = 0.879$), so we ran another model without this factor. In this second model, flock size significantly affected head-up scan rate (flock sizes, 1 = 1.82 ± 0.52, 2 = 2.66 ± 0.33, 3 = 3.45 ± 0.46, 4 = 2.86 ± 0.37, 5 = 2.79 ± 0.34, 6 = 3.14 ± 0.19, 7 = 3.98 ± 0.48, 8 = 3.16 ± 0.49, Table 1). However, the model did not meet the sphericity assumption ($\chi^2 = 64.29$, d.f. = 27, $p < 0.001$). After running the correction, the effects of flock size on head-up scan rate became non-significant (Wilks = 0.001, $F_{7,1} = 116.61$, $p = 0.071$).

Body condition did not affect the proportion of time allocated to scanning ($F_{1,6} = 0.18$, $p = 0.685$), so we eliminated this factor from the model. The proportion of time allocated to scanning was significantly affected by flock size (Table 1, Fig. 2c), with a model that met the sphericity assumption ($\chi^2 = 36.92$, d.f. = 27, $p = 0.097$). The proportion of time scanning decreased from flock size 1 to 3, and remained relatively similar up to flock size 8 (Fig. 2c).

Finally, the aggressive interaction rate was significantly influenced by flock size (Table 1, Fig. 2d). The model met the sphericity assumption ($\chi^2 = 16.80$, d.f. = 20, $p = 0.666$). Figure 2d shows two peaks of aggressive interactions at flock sizes 5 and 8; however, these aggressive interaction rates were not significantly different from those at flock sizes 4, 6, and 7 ($F_{1,6} = 1.82$, $p = 0.226$). We also found a significant interaction between flock size and body condition (Table 1), in which no relationship was found between body condition and aggressive interaction rate in flocks of two, three, four, five, and seven individuals, and a positive relationship was found in flocks of six and eight individuals.

Second Experiment: Effects of Population Size, Food Abundance, and Predation on Mean Flock Sizes

The mean percentage of individuals using the four patches (both with and without food) across treatments was 46.84 ± 2.34%. The patterns of change in mean flock size with time were relatively similar across treatments (Fig. 3). In general, in patches

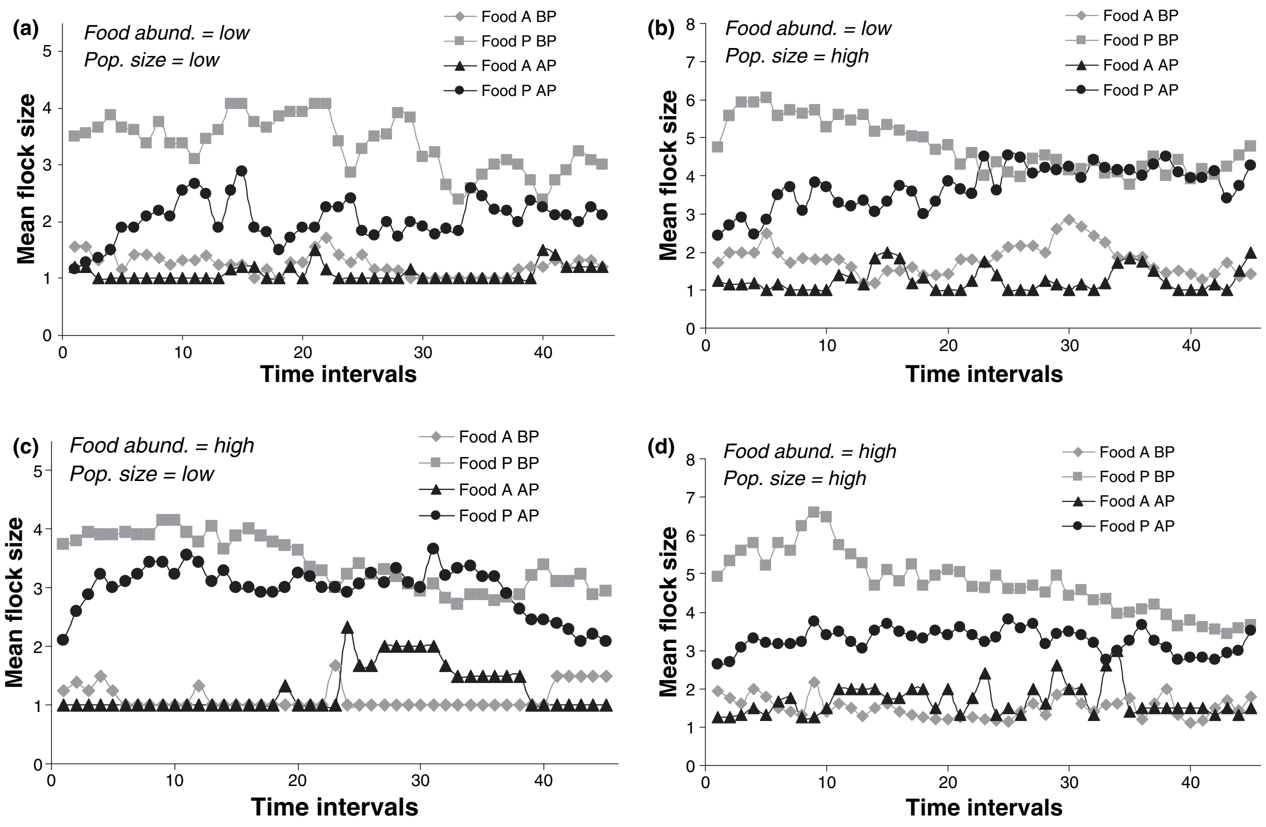

Fig. 3: Changes in brown-headed cowbird mean flock sizes with time in patches without (Food A) and with food (Food P) before (BP) and after (AP) the exposure of a predator under four conditions: (a) low food abundance (2 g) and low population size (7 individuals), (b) low food abundance (2 g) and high population size (14 individuals), (c) high food abundance (10 g) and low population size (7 individuals), and (d) high food abundance (10 g) and high population size (14 individuals). Each time interval lasted 15 s.

with food, mean flock sizes started at their highest values at the beginning of the trials, and between time intervals 10 (2.5 min) and 15 (3.75 min), they dropped slightly (with a concomitant increase in the number of individuals in the refuge patch). Immediately after the predator exposure, most of the individuals returned to the refuge patch probably to reduce the risk of predation. Afterwards, animals returned progressively to the patches with food, with different degrees of fluctuation in flock size depending on the treatments. Flock sizes after the predator tended to be lower than those before the predator until time interval 20 (5 min), and afterwards they varied around the flock sizes similar to the last part of the before-predator phases (Fig. 3). In the patches without food, mean flock sizes varied approximately around one (Fig. 3). Given the substantial differences in usage between patches with and without food, we only present results on the former.

Mean flock sizes in patches with food increased with population size (low, 2.66 ± 0.18; high, 4.14 ± 0.17) and decreased after the exposure to the predator (before predator, 4.16 ± 0.15; after predator, 2.64 ± 0.16; Table 2), with no interaction between these factors. Doubling the population size increased mean flock size by 49.09% before predation and by 70.14% after predation. Mean flock size was not significantly affected by food abundance (Table 2).

Considering how flocks divided between the two patches with food (patch 1 and patch 2) *before the predator attack*, we did not find a patch identity effect ($F_{1,50} = 0.37$, $p = 0.544$). However, we found a significant interaction between patch identity and food abundance ($F_{1,50} = 5.40$, $p = 0.024$), in which mean flock sizes varied significantly between patch 1 (4.58 ± 0.27) and 2 (2.35 ± 0.26) at high food abundance (planned comparison, $F_{1,50} = 25.83$, $p < 0.001$), but without a significant effect (patch 1, 3.94 ± 0.25; patch 2, 3.17 ± 0.27) at low food abundance (planned comparison, $F_{1,50} = 3.33$, $p = 0.074$). *After the predator attack*, we did not find any

Table 2: General linear model assessing the effects of brown-headed cowbird population size, food abundance, and predation risk on mean flock size in patches with food during experiment 2. Significant results are marked in bold

	d.f.	F	p
Population size (PS)	1, 50	25.83	**<0.001**
Food abundance (FA)	1, 50	1.61	0.210
Temperature (T)	1, 50	0.46	0.501
Food deprivation time (FDT)	1, 50	3.12	0.083
PS × FA	1, 50	1.06	0.308
Predation (P)	1, 50	8.34	**0.006**
P × PS	1, 50	0.62	0.433
P × FA	1, 50	2.36	0.131
P × T	1, 50	0.88	0.352
P × FDT	1, 50	0.74	0.390
P × PS × FA	1, 50	1.31	0.257

significant patch identity effect or interaction with other factors ($F_{1,50} < 3.83$, $p > 0.05$).

Discussion

Overall, we found that the intake-maximizing flock sizes in brown-headed cowbirds peaked over a range (three to six individuals) rather than at a single flock size, and that mean flock sizes were mainly influenced by population size and predation risk, and to a lesser degree by food abundance. Interaction effects were not prevalent. Our discussion focuses on the potential mechanisms shaping the costs and benefits of flocking in brown-headed cowbirds.

A monotonic increase in food intake rate in relation to group size is the most common relationship found in birds (Beauchamp 1998); however, brown-headed cowbirds showed an inverted-U relationship. This non-linear pattern was likely influenced by time competition effects (e.g. Caraco 1979). Brown-headed cowbirds decreased the proportion of time head-up scanning with increasing group sizes, which released time for the increase in food searching time. However, the higher availability of foraging time did not translate directly into pecking rates, likely because searching for food became less effective due to interference effects. Probably aggressive encounters displaced or distracted foragers from efficiently locating food, which could have increased the costs of flocking. Higher aggressive interaction rates were exhibited by individuals of higher body condition, particularly in large flocks (>5 individuals), which also allocated more time to seeking food, perhaps because of their dominant status (e.g. Weatherhead & Teather 1987). We do not think food depletion played a major role in this experiment because: (1) there was plenty of food left at the end of the trials, and (2) a previous study on the same species under semi-natural conditions did not find depletion to influence foraging behavior (Fernández-Juricic et al. 2007).

Different social and ecological conditions are expected to modify intake-maximizing flock sizes due to changes in the costs and benefits of grouping, which can account for the variations in flock size over time (Fig. 3). Overall, mean flock sizes in patches with food in the second experiment were within the range of intake-maximizing flock sizes (three to six individuals) found in the first experiment, particularly before the predator attack (Fig. 3). Reaching intake-maximizing flock sizes quickly indicates that a few animals could have observed the seeds visible at the surface of the sawdust (although most were hidden), probably causing others to join and reducing the latency to obtain information about food abundance in the system (e.g. Krebs & Inman 1992; Valone 1989). The few individuals (one to two) in the patches without food could have been subdominant birds exploring these patches due to higher foraging costs in the patches with food (e.g. interference).

Doubling population size increased mean flock sizes under conditions of both high and low predation risk. This response follows theoretical predictions (Krause & Ruxton 2002) and has also been found in some empirical studies (Wirtz & Lörscher 1983; Crockett & Eisenberg 1987; Borkowski 2000; Hebblewhite et al. 2002, but see Moreira 2006). The increase in flock size with population size may suggest little control of group membership in this species. Although we observed aggressive interactions when newcomers, arriving at patches with food, tried to take over the foraging spots of residents, we did not record situations in which residents expelled newcomers from those patches.

Based on the sensitivity of brown-headed cowbird flock size to population size in our system and the inverted-U relationship between pecking rate and flock size, we predict that an increase in population density in natural conditions would more likely be translated into rapid increases in the size of the flocks rather than in more new flocks. Assuming other fitness components also peak at similar flock sizes, this prediction would hold even in groups with densities higher than eight individuals per 0.22 m^2, because at that density, we did not find a decrease in intake rate below that corresponding to foraging alone, which is the theoretical limit to avoid joining an increasingly larger flock (Giraldeau 1988). Studies of other bird species have documented other types of relationships between population size and group size, which may be related to longer study periods and confounding factors prevalent in natural conditions (e.g. variations in food abundance, density of predators, etc.). For instance, a recent study that reduced through harvesting the population density of northern bobwhites (*Colinus virginianus*), a species which maintains a more stable group composition during the winter, did not find density-dependent effects on flocking behavior likely because individuals moved locally to maintain their optimal covey sizes (Williams et al. 2004). Another two studies on islands failed to find significant effects of variation in population density on mean flock sizes of mono- and mixed-species aggregations (Ewert & Askins 1991; Hart & Freed 2003).

Flocking reduces the chances of individuals being caught by predators (e.g. Jullien & Clobert 2000; Whitfield 2003); consequently, areas subject to higher predation risk tend to have higher group sizes (Beauchamp 2004). Temporary increases in predation risk can also increase group sizes, as found in birds and mammals (e.g. Caraco et al. 1980; Szekely et al. 1989; Hill & Lee 1998), or reduce the distance between group members (e.g. Forsman et al. 1998; Fernández-Juricic et al. 2004b). However, our system incorporated a refuge, which changed the grouping cost–benefit relationship under risky conditions. Brown-headed cowbird flocks split after the predator attack, with individuals rapidly seeking the refuge likely to reduce exposure (Caro 2005). Although some individuals did return to the foraging patches some time after the predator attack, mean flock sizes did not reach the levels found at the beginning of the trials. There are at least three potential explanations. First, trial duration may not have been long enough to increase the benefits of patch exploitation over those of risk avoidance (Ydenberg & Dill 1986). Second, food depletion could have reduced the relative value of patch exploitation (Kohlmann & Risenhoover 1998), which is suggested by the slight decrease in flock size over time in patches with food before the predator (Fig. 3). However, there are two results that argue against depletion: there was food left at the end of the 30 min trials, and depletion effects would have been stronger under high population sizes with low food abundance, but we did not find interaction effects between these factors (e.g. compare Fig. 3b with 3d). Third, anti-predator responses may have been confounded by satiation effects, as animals' energetic reserves may have been replenished in the first 15 min to a point at which the benefits of aggregating in the refuge were higher than in the foraging patch. If individuals had different satiation levels, it would explain why certain individuals returned to the foraging patch right away and others stayed in the refuge (Krause et al. 1998; Dowling & Godin 2002), as found in tits after predator attacks (e.g. Hegner 1985; Koivula et al. 1995). Despite the fact that satiation may have influenced predation effects in our system, we think that our results still have value because under natural conditions, predator attacks occur unexpectedly on flocks composed of individuals with different body reserves.

The combined effects of population size and predation risk may have implications for grouping in other species as well. At low population size, mean flock sizes were lower than the intake-maximizing flock sizes after the predator attack. If animals react in the same way in natural situations, then it could be predicted that in patches with high predation frequency, the persistence of intake-maximizing group sizes may be compromised in species with low local abundance. Under these conditions, individuals joining small flocks may not receive all the benefits of group foraging, which might in turn decrease foraging gains or increase mortality (e.g. Mooring et al. 2004).

A previous field study on brown-headed cowbird social behavior found larger flock sizes in areas with higher food density (Morris & Thompson 1998). However, in our semi-natural system, food abundance influenced flock sizes only through changes in the exploitation of the two patches with food. Under conditions of low food abundance, brown-headed cowbirds may have experienced interference effects, which could increase the turnover of individuals between patches to explore alternative foraging opportunities (Yamaguchi & Yahara 2002), leading to similar flock sizes between patches with food. The results of this study suggest that the aggressive component of interference is particularly higher in larger groups. However, at high food abundance, interference effects may have decreased (Sirot 2000), thereby increasing the value of larger groups due to enhanced foraging benefits and leading to variations in flock sizes between patches with food as a result of social cohesion (e.g. Vásquez & Kacelnik 2000), which is quite marked in this species (Miller et al. 2006; West et al. 2006; Fernández-Juricic et al. 2007). The unequal distribution of individuals between patches with food indicates that brown-headed cowbirds did not follow an ideal-free distribution despite similar food availability. These responses occurred under randomly distributed food, but may vary with other food distributions and types (Beauchamp 1998).

Our study contributes new knowledge to the social and ecological conditions leading to short-term changes (e.g. half an hour) in group sizes for a species that forms foraging aggregations during the non-breeding season. Theory predicts that certain factors (population abundance, presence of a refuge) will have specific effects on patch use and foraging behavior; however, these effects may be dependent on the shape of the relationship between intake rate and group size. Such relationship varies between species (Beauchamp 1998); therefore, more work is necessary to characterize its degree of variability in relation to environmental and phylogenetic factors. This could shed some light into the mechanisms that have shaped the evolution of different social foraging strategies in birds.

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