Ethology

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An Experimental Analysis of Spatial Position Effects on Foraging and Vigilance in Brown-Headed Cowbird flocks

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Abstract

Several observational studies have found that the costs and benefits of social foraging vary as a function of spatial position in the group. However, it is difficult to make mechanistic inferences because several confounding factors, such as food deprivation levels, food availability, neighbor distance, and group size can mask or amplify spatial position effects. We attempted to address experimentally the effect of spatial position on foraging and vigilance in a group, controlling for many confounding factors. We used enclosures that restricted physical but not visual interactions between brown-headed cowbirds and manipulated spatial position, flock size, and neighbor distance. Pecking rate (number of pecks per trial duration) was not related with position, but instantaneous pecking rate (number of pecks per foraging bout duration) was higher at the edge. The proportion of time spent head-up (scanning and food-handling) was also higher at the edge. For pecking rate and proportion of time spent scanning, changes in neighbor distance influenced the behavior of edge birds to a lesser extent than central birds. These results suggest that cowbirds at the edge perceived greater predation risk and that during the limited foraging time available, edge birds tried to compensate by foraging at a faster rate.

Introduction

The costs and benefits of social foraging vary as a function of spatial position in the group in many species (Krause 1994; Romey 1997; Hirsch 2007). In particular, foraging opportunities and predation risk often differ for individuals at the edge relative to those at the center of the group. For instance, foraging success may be greater at the edge than at the more crowded center because resource depletion may occur faster at the center (Rowcliffe et al. 2004) or because individuals at the edge may disturb prey inducing a reduction in prey availability for subsequent foragers (Petit & Bildstein 1987; Janson 1990; Rayor & Uetz 1990; Black et al. 1992; Krause et al. 1992; di Bitetti & Janson 2001; Stahl et al. 2001; Minderman et al. 2006). In other cases, resource depletion can take place from the front to the back of the group generating a decrease in food availability for center birds (Stahl et al. 2001). On the other hand, foragers at the edge may be forced into suboptimal habitats and experience a decrease in foraging success (Goss-Custard 1977; Safina 1990). With respect to predation risk, individuals at the edge of the group may be more exposed to predators attacking from the outside, thus providing a safety buffer to more centrally-located companions (Hamilton 1971; Beauchamp 2005; Hoogland et al. 2006; Quinn & Cresswell 2006). Vigilance against predators is thus often reported to be higher for foragers at the edge of the group (Lazarus 1978; Petit & Bildstein 1987; Burger et al. 2000; Di Blanco & Hirsch 2006; Inger et al. 2006; Lung & Childress 2007; Radford & Ridley 2007).

Observational data on changes in vigilance and foraging as a function of spatial position in the group are difficult to interpret because several ecological factors covary with spatial position. For instance, the observation that anti-predator vigilance is higher at the edge of groups can reflect lower food availability as well as increased predation risk. In addition, foragers that occur at different positions in the group may also vary in traits that are themselves related with foraging and vigilance (e.g. dominance and sex), making it difficult to disentangle the effect of spatial position *per se* from the effect of phenotype. Subordinate foragers, for example, may be forced to search for food at the edge of the group (Barta et al. 1997; Stahl et al. 2001; Ost et al. 2007). In such a case, vigilance and foraging may vary with position depending on the need to monitor the behavior of other foragers in the group to reduce the chances of kleptoparasitic events. Similarly, if hungrier foragers occur at the edge of the group, then vigilance may be found to be lower peripherically irrespective of food availability or predation risk (Krause et al. 1992; Romey 1995).

To distinguish between alternative hypotheses about spatial position effects, observational studies need to measure the confounding factors and control for them statistically (Di Blanco & Hirsch 2006) or careful experimental work is needed. Here, we provide an experimental analysis to assess spatial position effects on foraging and vigilance in a species, the brown-headed cowbird (*Molothrus ater*), that forages in flocks (Lowther 1993). In our experiment, each individual foraged in an enclosure that separated birds physically but not visually. Birds were allocated randomly to an edge or central position in the group and food density was manipulated within each enclosure to provide all birds with similar foraging opportunities. We manipulated group size by adding individuals to the flock around a centrally-located focal bird and manipulated the distance to neighbors by changing the distance between enclosures.

In our experiment, spatial position can exert an effect on foraging and vigilance through differential predation risk as individual birds cannot interact directly (e.g. physical interference effects are controlled for) and food availability is similar across the group. We predicted that edge birds would feed at a lower rate and be more vigilant than more centrally-located companions because of greater perceived predation risk (Proctor et al. 2006; Beauchamp 2007).

Furthermore, additional predictions can be made in relation to potential interactions among spatial position, group size, and nearest-neighbor distance. An increase in group size is expected to decrease vigilance and to increase foraging rate through factors, such as collective detection of predation threats and dilution of predation risk (Elgar 1989; Beauchamp 2003). An increase in nearest-neighbor distance is expected to increase vigilance and decrease foraging rate because of less effective collective detection and because the domain of danger of each forager increases with neighbor distance (Lima & Zollner 1996; Blumstein et al. 2001; Treves et al. 2001; Fernández-Juricic & Kacelnik 2004). Individuals at the center of the flock are generally surrounded by neighbors, which would make variations in flock size and neighbor distance more noticeable than for individuals at the periphery whose field of view would not encompass as many flock-mates. Therefore, we predicted that the effect of flock size and neighbor distance would be less pronounced for foragers at the edge than those at the center of the group because the former are more constrained by the amount of time allocated to vigilance, thereby reducing the scope for adjustments in other behaviors.

Methods

Study area and subjects

This study was conducted at the California State University Long Beach (CSULB) campus on a grassy area surrounded by a black plastic fence to screen out visual stimuli. We ran experiments from Dec. 21, 2004 to Feb. 4, 2005.

Our model species is best-known as a brood parasite. Brown-headed cowbirds are small, sexually-dimorphic birds common in open habitats (Lowther 1993). Cowbirds forage on the ground in small flocks and have a mixed diet including invertebrates and seeds (Morris & Thompson 1998). In a previous paper, we detailed the effect of flock size and neighbor distance on foraging rate and vigilance for centrally-located cowbirds foraging in the same enclosures (Fernández-Juricic et al. 2007). In line with much empirical work (Elgar 1989; Beauchamp 1998), we documented a general decrease in vigilance with flock size and an increase in vigilance with neighbor distance suggesting that cowbirds forage in this sort of enclosure with no obvious departures from natural conditions.

Brown-headed cowbirds were caught from the Prado Dam population, Riverside County, California with live traps. We housed animals in indoor cages (0.85 × 0.60 × 0.55 m) with three to four individuals per cage under a 12L:12D light cycle (lights on at

07:00 AM). Animals were housed in groups because of constraints in the availability of indoor space and to minimize stress in solitary conditions. We provided water and food (Mazuri® Small Bird Maintenance pellets) *ad libitum* except during experimental trials. Experimental protocols were approved by the Institutional and Animal Care Committee at CSULB (protocol no. 205).

We captured 48 adult birds (23 males and 25 females). From these individuals, we haphazardly chose 14 focal center birds and 14 focal edge birds (with equal number of individuals of each sex per position). The remaining birds were used as companions. A given focal edge bird was paired with the same focal center bird across all experimental treatments.

The experimental set-up was composed of one central enclosure surrounded by six edge enclosures in a circular arrangement (see details of experimental set-up in Fernández-Juricic et al. 2007). We chose a circular arrangement to avoid problems associated with variations in the behavior of animals because of flock shape variations (Bekoff 1995; Stankowich 2003). Each mesh-wire enclosure (diameter 0.60 m; height 0.45 m; opening 0.008 m, percentage open area = 85%) housed a single bird and was placed on wooden trays with 3 cm of sawdust and 5 g of Mazuri® Small Bird Maintenance pellets + 15 g of finch mix (Royal Feeds; Leach Grain and Milling, Co, Downey, CA, USA), which were scattered and mixed with the sawdust before the beginning of each trial.

We formed flocks of different sizes (3, 5, and 7 individuals) with the focal center and the focal edge birds always present across treatments. The same edge cage position was used across trials to minimize potential biases because of spatial variations in the location of the focal edge individual in relation with the focal center individual. All edge enclosures were present during all treatments. Companion birds in flock sizes 3 and 5 were placed in the same enclosures across treatments. We manipulated minimum neighbor distance by modifying the distance between the edge and the central enclosures: close (0 m separation), intermediate (2.5 m separation), and far (5 m separation). Although cowbirds can form larger flocks than those manipulated in this study, the flock sizes used in this study were similar to those found in natural conditions (Friedmann 1929; Morris & Thompson 1998).

Behavioral observations

We recorded cowbirds with two Sony DCR-TRV38 digital video cameras that were placed at a fixed distance (5 m) from the focal birds across trials. A trial started when the center focal bird showed foraging activity (e.g. pecking) and lasted 15 min. Trials were not conducted under high winds or rain. We conducted 14 trials in each of the nine combinations of flock size and neighbor distance (total = 126 trials) keeping the sex ratio of companions constant across trials. Center and edge focals were exposed to all treatment conditions in a random order, and trials were conducted in the mornings (08:00 AM–13:00 PM).

We used JWatcher 1.0 (Blumstein et al., 2006) to score foraging and scanning behaviors of cowbirds while on the ground, but excluding sequences when off the ground (e.g. wall hanging). We recorded the number and duration of scanning and food-handling events. We calculated the proportion of time, rate (events per min), and average bout duration (min) of scanning (head-up), food-handling (head-up and down), and total head-up scanning (scanning with and without food handling) events on a trial basis. Although total head-up scanning might overlap with each of its components, we decided to present all these variables because scanning and food handling may show opposite or synergistic patterns that would only be evident when adding them up as both are involved in vigilance (see Discussion). While the birds were head-down, we recorded the number of pecks directed at food, and calculated pecking rate (events per min considering the full trial time), and instantaneous pecking rate (events per min considering only bouts in which the animals were head-down). Behaviors not directly related with head-up on the ground vigilance (e.g. wall-hanging, walking, and flying) are not reported.

For each trial, we recorded ambient temperature in the experimental location (range 9–27.6°C), and the food deprivation time of the focal bird (range 3–7 h). We also measured focal body mass (range 23.40–48.80 g) 5 min before the beginning of a trial and wing length (range 90–111 mm) to estimate body condition (body mass/wing length). Two students performed all video analyses after extensive training in analyzing pilot video tapes yielding an error rate of 5% or less for each of the main variables and between observers.

Statistical analysis

We used balanced repeated-measures linear models including flock size, neighbor distance, and position in the flock as crossover factors and their interactions.

In addition, we considered the potentially confounding effects of food deprivation time and body condition. A previous study reported the effects of flock size and neighbor distance on central birds (Fernández-Juricic et al. 2007), so we omitted discussing the independent effects of these two factors.

In each model, we considered the main effects of flock size, neighbor distance, and position, along with their interactions. All effects were included in the models. When an interaction term proved significant, we used pair-wise planned comparisons to examine differences between flock sizes or between neighbor distances at each of the two positions (edge and center). Rate and duration data were $\log_{10}$-transformed and proportions were arcsine square-root transformed to normalize distributions. Statistical analyses were conducted with SAS version 9.1 (Cary, NC, USA). We present back-transformed means ± SE throughout.

Results

Pecking rate

Pecking rate increased with flock size ($F_{2,26} = 5.8$, $p = 0.008$), decreased with neighbor distance ($F_{2,26} = 15.5$, $p < 0.001$), but was not related with position ($F_{1,13} = 0.06$, $p = 0.816$, Fig. 1a). Pecking rate did not interact with flock size ($F_{2,158} = 2.1$, $p = 0.127$), but it did interact with neighbor distance ($F_{2,158} = 4.6$, $p = 0.012$). For central birds, pecking rate decreased with neighbor distance and was different at each level ($p < 0.014$). For edge birds, pecking rate was only higher at the near rather than far distance ($p = 0.026$). The interaction between flock size and neighbor distance did not have a significant effect on pecking rate ($F_{4,158} = 1.2$, $p = 0.319$).

Instantaneous pecking rate

Instantaneous pecking rate did not vary with flock size ($F_{2,26} = 1.9$, $p = 0.173$), but increased with neighbor distance ($F_{2,26} = 4.7$, $p = 0.018$; Fig. 1b). Overall, birds at the edge pecked at a higher instantaneous rate than those at the center ($F_{1,13} = 14.6$, $p = 0.003$; Fig. 1b). Instantaneous pecking rate was not significantly influenced by the interaction between position and flock size ($F_{2,158} = 1.2$, $p = 0.307$), between position and neighbor distance ($F_{2,158} = 0.3$, $p = 0.739$), and between flock size and neighbor distance ($F_{4,158} = 1.6$, $p = 0.185$).

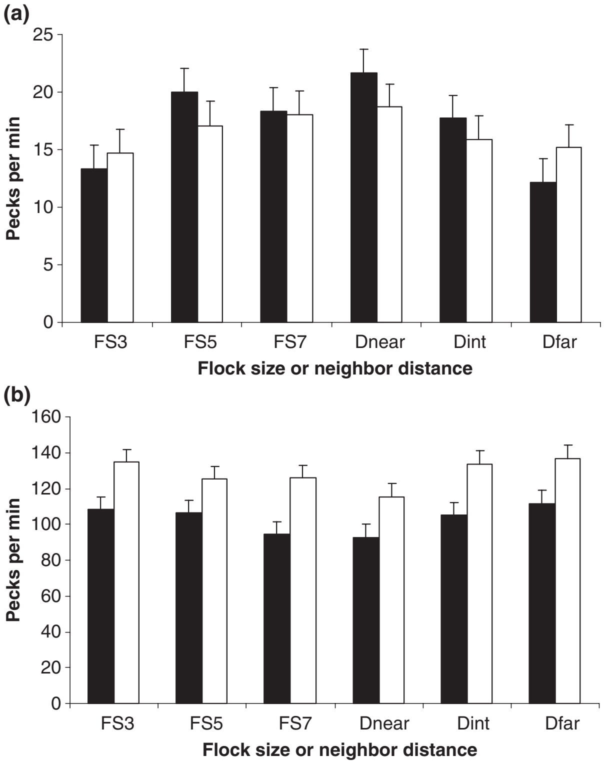

Fig. 1: Mean pecking rate (a) and mean instantaneous pecking rate (b) for central (black bars) and edge (white bars) birds foraging in semi-captive flocks of brown-headed cowbirds as a function of flock size (3, 5, and 7) and as a function of neighbor distance (near: 0 m; intermediate: 2.5 m; and far: 5 m). Pecking and instantaneous pecking rates are calculated over overall trial duration and total foraging time, respectively. Bars show 1 SE and means are adjusted for covariables in the model.

Head-up scanning

Head-up scanning rate increased with flock size (flock size 3: 2.75 ± 0.29; flock size 5: 3.21 ± 0.29; flock size 7: 3.43 ± 0.29; $F_{2,26} = 4.8$, $p = 0.017$) and decreased with neighbor distance (near: 3.48 ± 0.26; intermediate: 3.05 ± 0.26; far: 2.87 ± 0.26; $F_{2,26} = 5.1$, $p = 0.014$), but was not related with position (edge: 3.26 ± 0.27; center: 3.00 ± 0.27; $F_{1,13} = 1.2$, $p = 0.292$). There was no interaction between position and flock size ($F_{2,158} = 0.5$, $p = 0.595$), between position and neighbor distance ($F_{2,158} = 0.13$, $p = 0.883$), and between flock size and neighbor distance ($F_{4,158} = 1.6$, $p = 0.190$).

Head-up scanning bout duration decreased with flock size (flock size 3: 0.28 ± 0.04; flock size 5: 0.17 ± 0.04; flock size 7: 0.17 ± 0.04; $F_{2,26} = 10.1$, $p < 0.001$), increased with neighbor distance (near: 0.14 ± 0.04; intermediate: 0.26 ± 0.04; far: 0.23 ± 0.04; $F_{2,26} = 19.8$, $p < 0.001$), but was not related with position (edge: 0.22 ± 0.03; center:

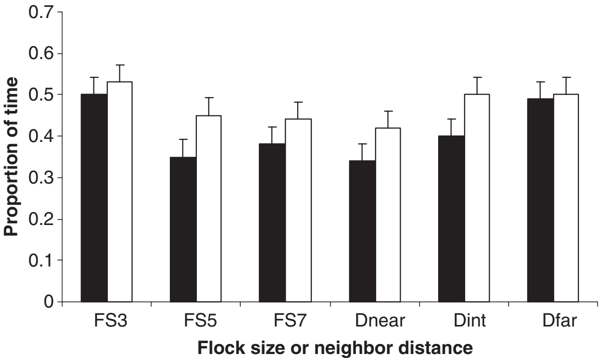

Fig. 2: Mean proportion of time spent head-up scanning for central (black bars) and edge (white bars) birds foraging in semi-captive flocks of brown-headed cowbirds as a function of flock size (3, 5, and 7) and as a function of neighbor distance (near: 0 m; intermediate: 2.5 m; and far: 5 m). Bars show 1 SE and means are adjusted for covariables in the model.

0.19 ± 0.03; $F_{1,13} = 0.6$, $p = 0.441$). There was no interaction between position and flock size ($F_{2,158} = 0.3$, $p = 0.725$), between position and neighbor distance ($F_{2,158} = 1.2$, $p = 0.293$), and between flock size and neighbor distance ($F_{4,158} = 1.4$, $p = 0.247$).

The proportion of time spent head-up scanning decreased with flock size ($F_{2,26} = 6.5$, $p = 0.005$) and increased with neighbor distance ($F_{2,26} = 9.5$, $p < 0.001$; Fig. 2). Overall, the proportion of time spent head-up scanning was marginally higher for edge (0.47 ± 0.42) than for central birds (0.41 ± 0.42; $F_{1,13} = 4.6$, $p = 0.062$, Fig. 2). There was no interaction between position and flock size ($F_{2,158} = 1.0$, $p = 0.354$), between position and neighbor distance ($F_{2,158} = 2.2$, $p = 0.120$), and between flock size and neighbor distance ($F_{4,158} = 0.4$, $p = 0.819$).

Head-up food handling

Head-up food handling rate did not vary with flock size ($F_{2,26} = 2.5$, $p = 0.103$), neighbor distance ($F_{2,26} = 2.6$, $p = 0.091$), or position in the flock ($F_{1,13} = 0.4$, $p = 0.525$, Fig. 3a). There was a marginally non-significant interaction between position and flock size ($F_{2,158} = 2.8$, $p = 0.062$; Fig. 3a), but none between position and neighbor distance ($F_{2,158} = 0.7$, $p = 0.489$), and between flock size and neighbor distance ($F_{4,158} = 1.1$, $p = 0.381$). For central birds, head-up handling rate was lower in flocks of three than in flocks of five ($p = 0.010$). For edge birds, head-up handling rate did not vary with flock size ($p > 0.064$).

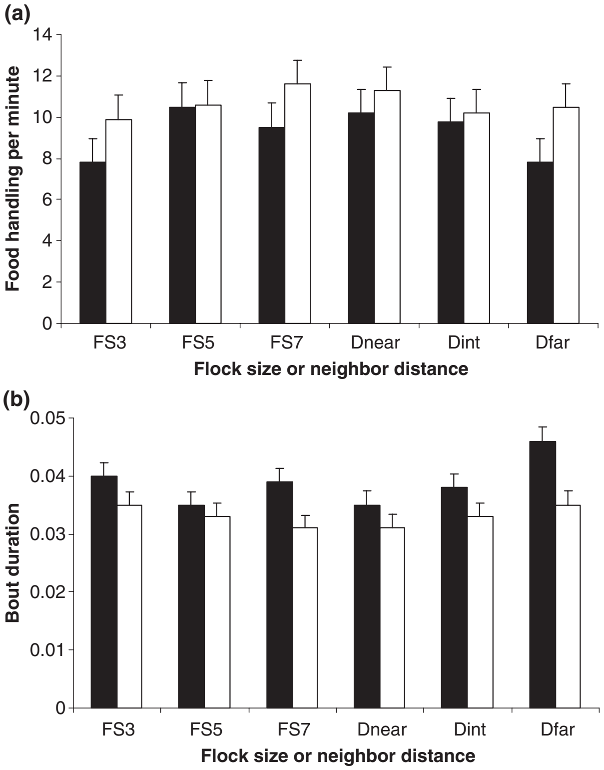

Fig. 3: Mean head-up food-handling rate (a) and head-up food-handling bout duration (b) for central (black bars) and edge (white bars) birds foraging in semi-captive flocks of brown-headed cowbirds as a function of flock size (3, 5, and 7) and as a function of neighbor distance (near: 0 m; intermediate: 2.5 m; and far: 5 m). Bars show 1 SE and means are adjusted for covariables in the model.

Head-up food handling bout duration decreased with flock size ($F_{2,26} = 4.1$, $p = 0.029$) and increased with neighbor distance ($F_{2,26} = 7.1$, $p = 0.004$; Fig. 3b). Overall, head-up food-handling bout duration was lower in edge than in central birds ($F_{1,13} = 8.2$, $p = 0.013$, Fig. 3b). There was no interaction between position and flock size ($F_{2,158} = 2.4$, $p = 0.097$), between position and neighbor distance ($F_{2,158} = 1.3$, $p = 0.287$), and between flock size and neighbor distance ($F_{4,158} = 1.1$, $p = 0.371$).

The proportion of time spent head-up food handling rate did not vary with flock size (flock size 3: 0.30 ± 0.03; flock size 5: 0.34 ± 0.03; flock size 7: 0.34 ± 0.03; $F_{2,26} = 1.6$, $p = 0.229$), neighbor distance (near: 0.33 ± 0.02; intermediate: 0.32 ± 0.02; far: 0.32 ± 0.02; $F_{2,26} = 0.3$, $p = 0.768$), or position in the flock (edge: 0.31 ± 0.03; center: 0.34 ± 0.03; $F_{1,13} = 0.3$, $p = 0.612$). There was no interaction between position and flock size ($F_{2,158} = 0.6$, $p = 0.528$), between position and neighbor distance ($F_{2,158} = 0.2$, $p = 0.863$), and between flock size and neighbor distance ($F_{4,158} = 0.9$, $p = 0.489$).

Total head-up (scanning plus food handling)

Total head-up rate increased with flock size (flock size 3: 11.6 ± 0.87; flock size 5: 13.8 ± 0.87; flock size 7: 14 ± 0.87; $F_{2,26} = 5.5$, $p = 0.010$), decreased with neighbor distance (near: 14.2 ± 0.84; intermediate: 13.0 ± 0.84; far: 12.1 ± 0.84; $F_{2,26} = 4.0$, $p = 0.031$), but was not related with position in the flock (edge: 13.9 ± 0.90; center: 12.3 ± 0.90; $F_{1,13} = 0.6$, $p = 0.446$). There was no interaction between position and flock size ($F_{2,158} = 2.2$, $p = 0.111$), between position and neighbor distance ($F_{2,158} = 0.6$, $p = 0.560$), and between flock size and neighbor distance ($F_{4,158} = 1.4$, $p = 0.245$).

Total head-up bout duration decreased with flock size (flock size 3: 0.16 ± 0.02; flock size 5: 0.10 ± 0.02; flock size 7: 0.10 ± 0.02; $F_{2,26} = 10.5$, $p < 0.001$), increased with neighbor distance (near: 0.08 ± 0.02; intermediate: 0.15 ± 0.02; far: 0.13 ± 0.02; $F_{2,26} = 19.6$, $p < 0.001$), but was not related with position (edge: 0.13 ± 0.02; center: 0.12 ± 0.02; $F_{1,13} = 0.1$, $p = 0.761$). There was no interaction between position and flock size ($F_{2,158} = 0.4$, $p = 0.686$), between position and neighbor distance ($F_{2,158} = 1.4$, $p = 0.254$), and between flock size and neighbor distance ($F_{4,158} = 1.8$, $p = 0.138$).

Overall, edge birds spent a higher proportion of total time head-up than central birds ($F_{1,13} = 5.3$, $p = 0.039$; Fig. 4; similar significant results were found for proportion of time spent head-down but are not presented because there are redundant). Proportion of time spent head-up decreased with flock size ($F_{2,26} = 12.3$, $p < 0.001$) and increased with neighbor distance ($F_{2,26} = 20.8$, $p < 0.001$). There was no interaction between position and flock size ($F_{2,158} = 1.3$, $p = 0.291$), and between flock size and neighbor distance ($F_{4,158} = 2.0$, $p = 0.093$). However, position did interact with neighbor distance ($F_{2,158} = 3.7$, $p = 0.027$). Total proportion of time spent head-up increased with nearest-neighbor distance and differed at each level ($p < 0.037$) for central birds. Total proportion of time spent head-up by edge birds was lower at the near than at the intermediate ($p = 0.007$) and far ($p = 0.003$) neighbor distances. Edge birds spent more time head-up than central birds at the near ($p = 0.020$) and intermediate distances ($p = 0.005$), but not at the far distance ($p = 0.947$).

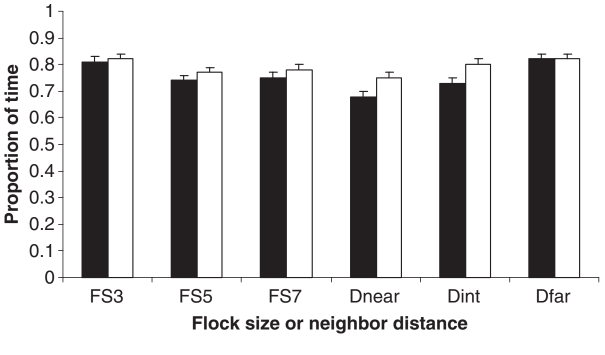

Fig. 4: Mean proportion of total time spent head-up (scanning plus food handling) for central (black bars) and edge (white bars) birds foraging in semi-captive flocks of brown-headed cowbirds as a function of flock size (3, 5, and 7) and as a function of neighbor distance (near: 0 m; intermediate: 2.5 m; and far: 5 m). Bars show 1 SE and means are adjusted for covariables in the model.

Effect of body condition and food deprivation

Level of food deprivation did not reach statistical significance in any of the above models ($p > 0.070$). Body condition was negatively related with pecking rate ($F_{1,158} = 23.5$, $p < 0.001$), head-up food handling rate ($F_{1,158} = 12.1$, $p < 0.001$), head-up food handling proportion ($F_{1,158} = 8.6$, $p = 0.004$), and total head-up rate ($F_{1,158} = 4.9$, $p = 0.028$). Body condition was positively related with head-up scanning rate ($F_{1,158} = 7.3$, $p = 0.008$), head-up scanning proportion ($F_{1,158} = 4.9$, $p = 0.027$), and food-handling bout duration ($F_{1,158} = 7.4$, $p = 0.007$).

Discussion

This study represents to our knowledge the first attempt to address experimentally the effect of spatial position in a group on foraging and vigilance without the confounding effect of several important ecological factors (food availability, food deprivation levels, etc.). Under these conditions, our results show that spatial position in the flock can affect the foraging and scanning behavior of social foragers in similar ways as reported previously (Stankowich 2003). In addition, we found that spatial position effects co-vary with flock size and neighbor distance for some foraging and vigilance variables.

Different studies have shown that edge birds are at a greater danger of predation than central birds (reviewed in Krause 1994; Stankowich 2003; Krause & Ruxton 2002): for instance, edge birds can be encountered first by a ground predator or singled out more quickly by an aerial predator. To examine the relevance of the higher perceived predation risk at the edges of the flock, we need to establish what constitutes vigilance in brown-headed cowbirds. In a granivorous species that handles food head-up, vigilance can be achieved through head-up scanning bouts as well as head-up food handling bouts. It is conceivable that vigilance can occur while handling food head-down because of the wide visual fields of brown-headed cowbirds (Fernández-Juricic et al. unpubl. data), but this sort of vigilance is more difficult to quantify (Fernández-Juricic et al. 2004). Overall, it is important to assess the different dimensions of vigilance (overall proportion, rates, and bout durations) to better understand scanning strategies. We found evidence that edge birds spent more time head-up (scanning and food handling) than central birds. Scan rates did not differ according to position at all flock sizes and at all neighbor distances. Scan bout duration was generally lower for edge birds while they were food-handling but not when they were scanning without food handling.

Other studies have documented higher vigilance at the edges of groups (Lazarus 1978; Petit & Bildstein 1987; Burger et al. 2000; Di Blanco & Hirsch 2006; Inger et al. 2006; Lung & Childress 2007; Radford & Ridley 2007); however, our results suggest that the effect of position may not be consistent at all combinations of neighbor distances. Neighbor distance effects on pecking rate and total time spent head-up occurred at all distances for central birds, but only at close distances for edge birds. This novel result suggest that the benefits of the flow of information (e.g. anti-predator) within a flock may be a function of the distance of flock mates *around* a given individual. As edge birds are farther from the flock, collective detection benefits may decrease and the domain of danger may increase to the extent that at some threshold distances the degree of attachment to the group may disappear (e.g. Fernández-Juricic & Kacelnik 2004).

Furthermore, when flock size produced differential effects between positions in the flock, the behavior of central birds was more affected than that of edge birds. For instance, we documented a greater effect of flock size for central than edge birds for head-up food handling rate. Interestingly, (Jennings & Evans 1980) found that European starlings decreased their vigilance with group size, but this effect was much more pronounced for birds at the center than at the edge of flocks. However, another field study on European starlings showed the opposite effect (Keys & Dugatkin 1990). These differences could be related with different confounding factors (food availability, dominance, etc.) that were controlled for in our study. A recent theoretical study (Proctor et al. 2006) predicted a decrease in vigilance with group size for edge but not for central birds. This model varied the density of individuals, which allowed edge birds to be closer to conspecifics at larger flock sizes and as a result benefited from the detection of potential predator attacks through social cues; however, we kept density constant at a given flock size.

Edge birds concentrated their foraging activities into more active bouts than central birds as evidenced by their higher instantaneous feeding rates. Higher instantaneous feeding rates have been documented in response to direct competition (e.g. involving physical interactions) in other species (Lendrem 1984; Gotmark et al. 1986; Phelan 1987; Cézilly & Brun 1989; Carrascal et al. 1990); however, this can be ruled out in this study as all birds foraged in separate enclosures. Higher instantaneous feeding rate may also occur when animals perceive a higher risk of foraging competition in response to the mere visual presence of competitors at a distance (Barnard et al. 1983; Grand & Dill 1999); however, we showed a decrease in instantaneous feeding rate with an increase in flock size ruling out this mechanism. Higher instantaneous foraging rates were also reported in a captive study with oystercatchers *Haematopus ostralegus* in response to limitations in time available for foraging because of tidal variations (Swennen et al. 1989). We suggest that brown-headed cowbirds may compensate for foraging time constraints by foraging quicker at the edge of flocks. Actually, individuals at the edge of the flock also shortened the duration of food-handling bouts probably as a result of this compensatory effect to reduce food processing time. We speculate spatial vigilance-position variations within the flock would change foraging trade-offs because of time-constraints. For instance, the higher predation risk at the edge increases the investment in vigilance, reducing foraging time, and thus, changing foraging strategies, such as faster pecking, which may compensate for position effects without reducing food intake or may actually decrease food ingestion if food is not readily available (e.g. cryptic prey).

The index of body condition influenced brown-headed cowbird foraging behavior. Birds with poorer body conditions (lower index values) pecked at a higher rate and were less vigilant. We speculate that feeding rate and vigilance are adjusted to the value of the index so that birds in poorer condition are more motivated to feed. Motivation to feed was not captured well by short-term food deprivation level. In observational studies, hungrier foragers have been found to occur at the edges of groups more often

(Krause et al. 1992; Romey 1995). If spatial position is related with differential foraging opportunities, we might expect that factors such as hunger or body condition may confound the effect of spatial position when hungrier or generally more motivated foragers prefer certain positions in the group.

Our findings suggest some interesting lines of future research in light of the higher allocation of vigilance time, which is assumed to be anti-predator related (e.g. Proctor et al. 2006), by edge birds. First, the interaction effects between position and neighbor distance warrant some further investigation as to the mechanisms that are used (e.g. collective vigilance, dilution, detection of flocks by predators, etc.) at the combinations of flock size and neighbor distance that maximize position effects. Secondly, despite the fact that central and edge birds differed in their overall allocation of time to scanning, future studies should address whether this change is implemented through variations in the proportion of time scanning towards or away from the flock. The expectation is that edge birds would scan proportionally more away from the flock because of their higher risk of predation and central birds would allocate scanning time towards and away from the flock in similar ways. Thirdly, brown-headed cowbirds have wide peripheral vision, which would make it possible to gather information from both head-up and head-down body positions (Bednekoff & Lima 2005; Fernández-Juricic et al. 2005). Therefore, it would be important to establish in the future the role of this head-down scanning in the vigilance patterns of edge vs. central birds.

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