



## Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds

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Empirical studies on the group-size effect (a reduction in time allocated to vigilance with an increase in group size that releases more time for foraging) have generally assumed that the influence of companions is the same irrespective of nearest-neighbour distance. However, social information transmission has been found to be affected by neighbour distance. Our goal was to assess the role of both group size and neighbour distance in explaining foraging and scanning behaviour in flocks of brown-headed cowbirds, *Molothrus ater*. We conducted a seminatural experiment in which we simultaneously manipulated group size (3, 5, 7 individuals) and minimum neighbour distance (0, 2.5, 5 m) of birds in visual but not physical contact. Foraging and vigilance were affected by both flock size and neighbour distance in different ways. Flock size generally influenced foraging and scanning behaviour, with an initial increase/decrease and then a leveling off at higher flock sizes. Neighbour distance also affected individual behaviour in a nonlinear fashion, but we also found patterns for pecking rate and proportion of time scanning that suggest linear changes. We found that the strength of the group-size effect varied with neighbour distance and was weakest when the birds were furthest away from each other. Future studies should consider as members of a group only those individuals within a radius that allows detection and dilution effects to operate.

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Several factors influence feeding rate and vigilance in animal groups. Dilution of risk, caused by the presence of several companions in a group, and collective detection of predation threats, for instance, may allow foragers to devote less time to vigilance against predators and more time to foraging (Krause & Ruxton 2002). While numerous empirical studies in the field have shown adjustments in feeding rate and vigilance as a function of changes in group size, few have been able to control potentially confounding variables, such as food density, which can influence feeding rate and vigilance as much as can group size (Elgar 1989; Beauchamp 1998; but see van Gils & Piersma 2004). Measurement of these confounding variables or

manipulation of group size in an experimental setting is necessary to assess the arrow of causation in social-foraging studies.

Two further problems complicate the interpretation of empirical results of the group-size effect. First, outcome variables, such as feeding rate and time spent vigilant, may not always be strongly associated with group size. For instance, the expected decrease in vigilance with group size may be masked by a concomitant increase in vigilance directed at companions either to detect food patches discovered by others or to avoid more dominant group members (Treves 2000; Beauchamp 2001; Barbosa 2002). Similarly, the expected increase in feeding rate with group size may be masked by a decrease in local food availability caused by the activity of companions or by an increase in competition for limited resources (Charnov et al. 1976; Goss-Custard 1980). To gain a better understanding of the mechanisms underlying group-size effects, the effects of companions on local foraging contingencies must be taken into account.

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Second, it is not always clear how to define group size, the key independent variable. The question is just how far the influence of companions can reach, hence where a group ends (Elgar et al. 1984). This simple question has not been satisfactorily answered (Beauchamp 2003). In many studies, a group is defined as a collection of individuals within a given radius regardless of whether companions can really influence the behaviour of each other at those distances. While some studies have failed to uncover evidence for behavioural monitoring of vigilance (Lima 1995; Beauchamp 2002), others suggest that nearby companions, through their presence and escape behaviour, exert a stronger influence on feeding rate and vigilance than do those further away (Lima & Zollner 1996; Stillman et al. 2000; Blumstein et al. 2001; Treves et al. 2001; Fernández-Juricic & Kacelnik 2004). Therefore, we need more information about the effect of distance between companions on feeding rate and vigilance. This information will be useful to provide a more biologically grounded definition of group size and to determine how information flows between group members.

Both flock size and neighbour distance should independently influence feeding and vigilance. In each case, we predict a rapid change with an increase in flock size or neighbour distance levelling off in larger flocks or when companions are further away. Such effects are expected because detection and dilution effects, which directly influence the amount of time spent vigilant and indirectly influence the amount of time spent foraging, are inherently nonlinear (Treisman 1975; Dehn 1990; Bednekoff & Lima 1998; Blumstein et al. 2001; Viscido & Wethey 2002; Proctor et al. 2003). Dilution effects should decrease asymptotically with group size, reflecting an increase in the domain of danger. Detection effects should decrease asymptotically with the area over which a group is scattered, reflecting the lower probability of detecting fright reactions. Therefore, as a consequence of these nonlinear effects, we predicted that the effect of flock size on feeding and vigilance would be reduced as neighbour distance increased, since the benefits from detection and dilution are less likely to apply when companions are foraging further apart.

To address these issues, we examined adjustments in feeding rate and vigilance in groups of brown-headed cowbirds, *Molothrus ater*, foraging in a seminatural field setting. The brown-headed cowbird is best known as a brood parasite (Lowther 1993). The species is a small, sexually dimorphic icterid common in open habitats. Cowbirds forage on the ground in small flocks and have a mixed diet including invertebrates and seeds (Lowther 1993). In our experiment, each individual foraged in an enclosure that separated birds physically but not visually. Therefore, information about predation risk could flow between birds without interference from the actual presence of companions (Fernández-Juricic et al. 2004). Food density was manipulated within each enclosure to provide all birds with similar foraging contingencies. We manipulated group size by adding individuals to the flock around a centrally located focal bird. We manipulated the distance to neighbours by changing the distance between enclosures. Therefore, we examined the effect of group size,

the effect of neighbour distance, and the interaction between them in a seminatural environment while controlling for key confounding variables.

## METHODS

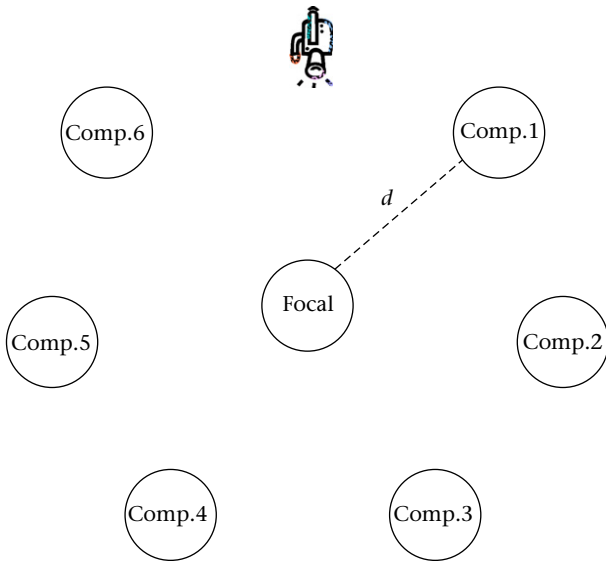
### Study Area and Subjects

We conducted the study at the California State University Long Beach (CSULB) campus from 21 December 2004 to 4 February 2005, on a grassy area shaded by an old Italian stone pine (*Pinus pinea*). The experimental location was 20 m away from the closest pathway, which received low pedestrian traffic, thus minimizing noise levels. The study area was surrounded by a 1.80-m-high fence covered with black plastic to screen out external visual stimuli.

We caught and colour-ringed 48 adult cowbirds (23 males, 25 females) belonging to the Prado Dam population, Riverside County, southern California. Fourteen animals were haphazardly chosen as focal subjects, with an equal number of individuals of each sex. We used the remaining birds as companions in flocks of different sizes. Animals were housed in indoor cages (0.85 × 0.60 × 0.55 m), under a 12:12 h light:dark cycle (lights on at 0700 hours) at Animal Facilities. Birds were in visual and auditory contact, with three to four individuals per cage. Water and food (Mazuri Small Bird Maintenance pellets, Brentwood, Missouri, U.S.A.) were available ad libitum except during experimental trials. Experimental protocols were approved by the Institutional Animal Care and Use Committee at CSULB (Protocol no. 205).

During experimental sessions, each bird was housed in a circular bottomless enclosure (diameter 0.60 m; height 0.45 m) completely made of mesh wire (opening 0.008 m, percentage open area = 85%). The experimental set-up consisted of one central enclosure surrounded by six peripheral enclosures in a circular arrangement (Fig. 1). The central enclosure was occupied by the focal bird and the peripheral enclosures were occupied by companions. Enclosures were placed on wooden trays with 3 cm of sawdust. We scattered a mix of 5 g of Mazuri Small Bird Maintenance pellets and 15 g of finch mix (Royal Feeds, Leach Grain and Milling, Co., Downey, California) on top of the sawdust, and shook the trays to mix the food items with the substrate. Some seeds were left visible on the substrate to prompt foraging activity, which started almost immediately despite variations in food deprivation levels.

We formed different flock sizes by varying the number of companions in the peripheral enclosures (2, 4, 6), which resulted in three flock size treatments: 3, 5 and 7 individuals. We did not have a solitary treatment (i.e. focal subjects foraging alone) because, in preliminary trials, cowbirds showed behaviours that suggested high stress levels (e.g. no foraging attempts, high proportion of time scanning while hanging from the enclosure walls, high rates of flying within the enclosure, etc.; Fernández-Juricic et al. 2005). All peripheral enclosures were present during all treatments. In flock sizes 3 and 5, we placed companions in the same enclosures in relation to focal subjects



**Figure 1.** Experimental set-up showing the location of the central enclosure occupied by the focal bird, the peripheral enclosures occupied by the companions (comp.), and the digital video camera. Peripheral enclosures were always present irrespective of the group-size treatment (3, 5, 7). When group size was 3, companions were in locations 3 and 6. When group size was 5, companions were in locations 1, 3, 5 and 6. Enclosures were placed at three neighbour distances ( $d = 0, 2.5, 5$  m).

across treatments to avoid a confounding effect of companion location (Fig. 1).

We manipulated minimum neighbour distance by varying the distance between the peripheral and the focal enclosures (following Fernández-Juricic et al. 2004; Fig. 1): close (0-m separation), intermediate (2.5-m separation) and far (5-m separation). The flock sizes used were compatible with those observed in the field. Cowbirds flock with other blackbirds in the autumn and winter at densities of 5–10 birds/m<sup>2</sup> (Friedmann 1929; Williamson & Gray 1975; King & West 1988), which approximates the level that we simulated at the closest distance. The combination of flock sizes and neighbour distances yielded a total of nine treatments (3 flock sizes  $\times$  3 distances).

## Behavioural Observations

Animals were transported from Animal Facilities to the experimental set-up in soft cloth bags and released in the enclosures. The observer moved away and closed the fences to reduce external visual stimuli. We recorded observations with a Sony DCR-TRV38 digital video camera that was placed at a fixed distance (5 m from the focal subject) across trials. Thus, the camera was never closer to the focal subject than to the companions. A trial started when the focal bird searched for food on the ground and ended 15 min later. Trial duration was short enough to keep the birds foraging actively throughout. Trials were not performed in high winds or rain. At the end of each trial, animals were transported back to Animal Facilities, where food was provided ad libitum. We conducted 14 trials in each of the nine treatments, totalling 126 trials. We kept

the sex ratio of companions as 1:1 across trials. Focal subjects were exposed to all treatment conditions in a random order. We ran between three and five trials per day in the morning (0800–1300 hours).

From the videotapes, we scored foraging and scanning behaviour using the event-recording program JWatcher version 1.0 (Blumstein et al. 2006). We established different behavioural categories to analyse foraging and scanning behaviour. We recorded behaviour only while cowbirds were on the ground in a head-down or head-up posture, depending on whether the bird's head was below or above its shoulder. While birds were in the head-up posture on the ground, we recorded the number and duration of scanning behaviours excluding food-handling sequences. We also measured the number and duration of food-handling events while cowbirds had their heads up and down. We calculated the proportion of time spent scanning and food handling, and the rate (events per min) and average bout duration (min) of scanning (head-up) and food-handling (head-up and down) events on a trial basis. We decided to treat head-up food handling as a separate category from head-up scanning to assess how much time was allocated to food handling versus vigilance, although we discuss the influence of the former on vigilance in the Discussion. While the birds were head-down, we recorded the number of pecks directed at food and calculated pecking rate (events per min). Behaviours that were less frequent or not obviously related to feeding and vigilance (e.g. wall-hanging, flying) were omitted from analyses, so the sum of the proportions presented in the Results is less than 1.

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) and wing length (range 93–111 mm) 5 min before the beginning of a trial to estimate body condition (body mass/wing length). One student performed all video analyses after extensive self-training in analysing pilot videotapes, yielding an error rate of 5% or less for each of the main variables.

## Statistical Analysis

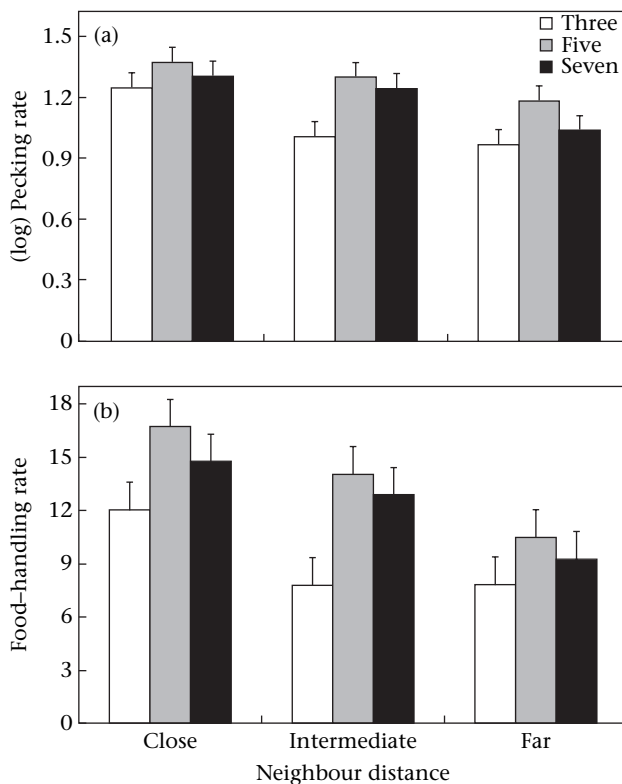
We used general linear models (GLM) with flock size and neighbour distance as repeated measures factors, and their interaction. In addition, we considered the potential confounding effects of temperature, food deprivation time and sex. Body condition was closely related to sex, reflecting sexual dimorphism in body size in this species (GLM,  $P < 0.001$ ); thus, we decided not to include body condition in the analysis. Of the three confounding factors, only temperature influenced some of the response factors (see Results). We also ran two extra sets of models: (1) without including sex and body condition, and (2) without including sex, body condition and temperature. In both cases, we obtained similar results (available from the authors upon request).

We used pairwise planned comparisons to test our a priori hypotheses about the effect of flock size and

neighbour distance at each level of the other factor. Specifically, we tested the following comparisons: level A versus level B, level B versus level C and level C versus level A. These were all two-tailed comparisons. We describe the results in terms of linear (e.g.  $A < B < C$ ) or non-linear effects ( $A < B = C$ ) following the rationale presented in the Introduction. We only report significant comparisons. We checked for normality and homoscedasticity, and transformed some variables to meet the assumptions of GLMs with  $\log_{10}$  transformations (pecking rate, food-handling bout duration, scan bout duration). We present means  $\pm$  SE throughout.

## RESULTS

Pecking rate of cowbirds across treatments averaged  $17.35 \pm 0.89$  pecks/min. Pecking rate increased with flock size and decreased with neighbour distance (Fig. 2a, Table 1). When assessing the variation in pecking rates with flock size across neighbour distances, we found significant differences between flock size levels at intermediate (planned comparisons within GLM: size 3 versus 5:  $t_{50} = 3.39$ ,  $P = 0.001$ ; 3 versus 7:  $t_{50} = 2.73$ ,  $P = 0.009$ ; Fig. 2a) and far distances (size 3 versus 5:  $t_{50} = 2.41$ ,  $P = 0.020$ ; Fig. 2a). When assessing the variation in neighbour distance across flock sizes, we found significant differences between neighbour distances at the three flock sizes studied: 3 (close versus intermediate:  $t_{50} = 2.60$ ,  $P = 0.012$ ; close versus far:  $t_{50} = 3.02$ ,  $P = 0.004$ ), 5 (close



**Figure 2.** (a) Pecking rates and (b) food-handling rates of brown-headed cowbirds in relation to flock size (3, 5, 7 individuals) and neighbour distance (0 m, close; 2.5 m, intermediate; 5 m, far).

**Table 1.** Effects of flock size, neighbour distance and three confounding factors (sex, ambient temperature, food deprivation time) on pecking rate, food-handling rate, food-handling bout duration and proportion of time food handling for brown-headed cowbirds

|   | <i>F</i> | <i>df</i> | <i>P</i>         |
|---|----------|-----------|------------------|
| <b>(log) Pecking rate</b>                     |          |           |                  |
| Flock size (FS) ( $R^2=0.08$ )                | 6.52     | 2, 26     | <b>0.005</b>     |
| Neighbour distance (ND) ( $R^2=0.12$ )        | 7.06     | 2, 26     | <b>0.004</b>     |
| FS $\times$ ND                                | 1.03     | 4, 50     | 0.404            |
| Sex   | 1.54     | 1, 50     | 0.221            |
| Temperature                                   | 2.30     | 1, 50     | 0.136            |
| Food deprivation                              | 1.02     | 1, 50     | 0.316            |
| <b>Food-handling rate</b>                     |          |           |                  |
| Flock size (FS) ( $R^2=0.08$ )                | 6.61     | 2, 26     | <b>0.005</b>     |
| Neighbour distance (ND) ( $R^2=0.12$ )        | 10.01    | 2, 26     | <b>&lt;0.001</b> |
| FS $\times$ ND                                | 0.72     | 4, 50     | 0.584            |
| Sex   | 1.16     | 1, 50     | 0.286            |
| Temperature                                   | 7.39     | 1, 50     | 0.009            |
| Food deprivation                              | 0.34     | 1, 50     | 0.560            |
| <b>(log) Food-handling bout duration</b>      |          |           |                  |
| Flock size (FS) ( $R^2=0.05$ )                | 4.48     | 2, 26     | <b>0.021</b>     |
| Neighbour distance (ND)                       | 2.62     | 2, 26     | 0.092            |
| FS $\times$ ND                                | 0.64     | 4, 50     | 0.639            |
| Sex   | 0.12     | 1, 50     | 0.729            |
| Temperature                                   | 4.33     | 1, 50     | <b>0.043</b>     |
| Food deprivation                              | 0.04     | 1, 50     | 0.842            |
| <b>Proportion of time spent food handling</b> |          |           |                  |
| Flock size (FS)                               | 1.75     | 2, 26     | 0.194            |
| Neighbour distance (ND)                       | 0.85     | 2, 26     | 0.439            |
| FS $\times$ ND                                | 0.45     | 4, 50     | 0.769            |
| Sex   | 3.35     | 1, 50     | 0.073            |
| Temperature                                   | 0.63     | 1, 50     | 0.403            |
| Food deprivation                              | 0.20     | 1, 50     | 0.653            |

$R^2$  values are presented for significant effects of flock size or neighbour distance. Significant results are marked in bold.

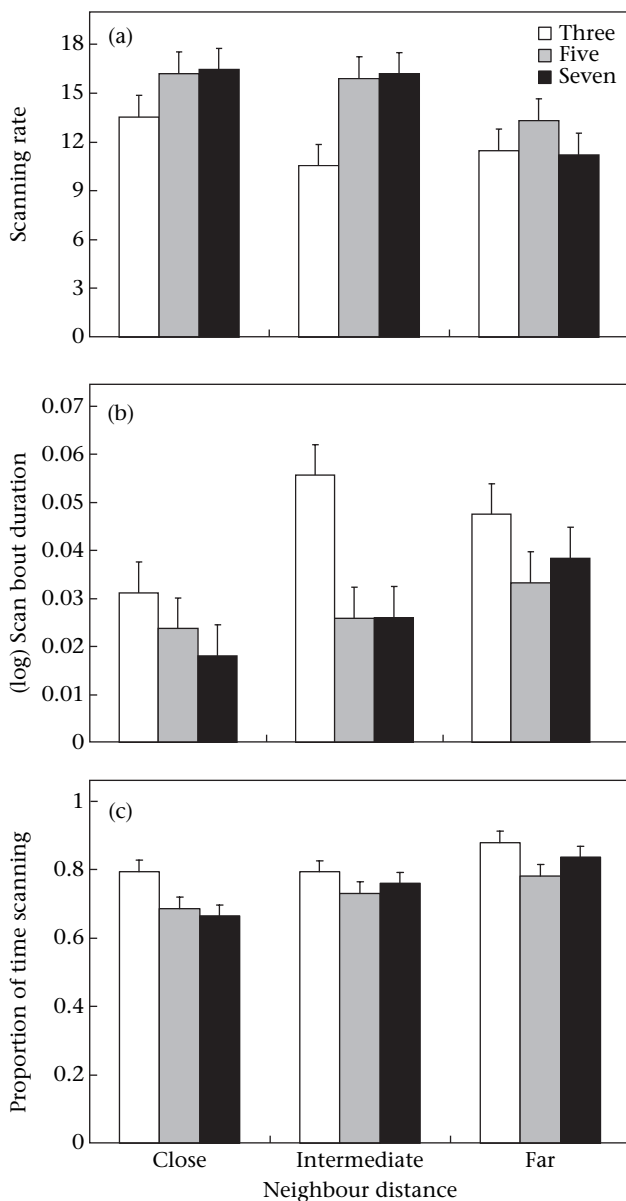
versus far:  $t_{50} = 2.07$ ,  $P = 0.043$ ) and 7 (close versus far:  $t_{50} = 2.89$ ,  $P = 0.006$ ; intermediate versus far:  $t_{50} = 2.23$ ,  $P = 0.030$ ).

Cowbirds handled food  $11.73 \pm 0.58$  times/min on average. Food-handling rate increased with flock size and decreased with neighbour distance (Fig. 2b, Table 1). Furthermore, food-handling rate increased with temperature ( $\beta = 0.14$ ; Table 1). We found differences between flock size levels at two neighbour distances: close (size 3 versus 5:  $t_{50} = 2.40$ ,  $P = 0.020$ ; Fig. 2b) and intermediate (size 3 versus 5:  $t_{50} = 3.23$ ,  $P = 0.002$ ; size 3 versus 7:  $t_{50} = 2.62$ ,  $P = 0.012$ ; Fig. 2b). We found differences between neighbour distance levels at three flock sizes: 3 (close versus intermediate:  $t_{50} = 2.22$ ,  $P = 0.031$ ; close versus far:  $t_{50} = 2.20$ ,  $P = 0.032$ ), 5 (close versus far:  $t_{50} = 3.27$ ,  $P = 0.002$ ) and 7 (close versus far:  $t_{50} = 2.88$ ,  $P = 0.006$ ).

Focal subjects spent on average  $1.43 \pm 0.04$  s handling food per bout. Food-handling bout duration changed significantly with flock size but not with neighbour distance, with the highest values at flock sizes of 3 ( $3.16 \pm 0.02$  s) and 7 ( $3.15 \pm 0.02$  s), and the lowest values at a flock size of 5 ( $3.10 \pm 0.02$  s; Table 1). We found significant differences only between flock sizes of 3 and 5 ( $t_{50} = 2.85$ ,  $P = 0.009$ ) and between flock sizes of 5 and 7 ( $t_{50} = 2.24$ ,  $P = 0.034$ ). Finally, temperature decreased handling bout

duration ( $\beta = -0.0006$ ; Table 1). The average proportion of time that cowbirds allocated to food handling was  $0.36 \pm 0.01$ . None of the studied factors significantly affected the variation in the proportion of time spent handling food (Table 1).

The average scanning rate was  $13.88 \pm 0.79$  events/min. Scanning rate increased with flock size and decreased with neighbour distance (Fig. 3a, Table 2). We found significant differences between flock size levels only at intermediate distances (size 3 versus 5:  $t_{50} = 3.57$ ,  $P = 0.001$ ; size 3 versus 7:  $t_{50} = 3.76$ ,  $P < 0.001$ ; Fig. 3a). Furthermore, we found differences between neighbour distance levels only at flock size 7 (close versus intermediate:  $t_{50} = 3.12$ ,  $P = 0.003$ ; close versus far:  $t_{50} = 3.26$ ,  $P = 0.002$ ).



**Figure 3.** (a) Scanning rates, (b) scan bout duration and (c) proportion of time spent scanning for brown-headed cowbirds in relation to flock size (3, 5, 7 individuals) and neighbour distance (0 m, close; 2.5 m, intermediate; 5 m, far).

**Table 2.** Effects of flock size, neighbour distance and three confounding factors (sex, ambient temperature, food deprivation time) on head-up scanning rate, scan bout duration and proportion of time scanning for brown-headed cowbirds

|  | F     | df    | P                |
|--|-------|-------|------------------|
| <b>Scanning rate</b>                   |       |       |                  |
| Flock size (FS) ( $R^2=0.08$ )         | 8.32  | 2, 26 | <b>0.002</b>     |
| Neighbour distance (ND) ( $R^2=0.08$ ) | 5.95  | 2, 26 | <b>0.008</b>     |
| FS×ND                                  | 2.04  | 4, 50 | 0.104            |
| Sex                                    | 0.17  | 1, 50 | 0.684            |
| Temperature                            | 0.02  | 1, 50 | 0.884            |
| Food deprivation                       | 0.00  | 1, 50 | 1.000            |
| <b>(log) Scan bout duration</b>        |       |       |                  |
| Flock size (FS) ( $R^2=0.10$ )         | 8.11  | 2, 26 | <b>0.002</b>     |
| Neighbour distance (ND) ( $R^2=0.06$ ) | 5.91  | 2, 26 | <b>0.008</b>     |
| FS×ND                                  | 1.68  | 4, 50 | 0.170            |
| Sex                                    | 1.45  | 1, 50 | 0.235            |
| Temperature                            | 0.21  | 1, 50 | 0.646            |
| Food deprivation                       | 0.00  | 1, 50 | 0.948            |
| <b>Proportion of time scanning</b>     |       |       |                  |
| Flock size (FS) ( $R^2=0.08$ )         | 5.36  | 2, 26 | <b>0.011</b>     |
| Neighbour distance (ND) ( $R^2=0.13$ ) | 13.26 | 2, 26 | <b>&lt;0.001</b> |
| FS×ND                                  | 1.46  | 4, 50 | 0.230            |
| Sex                                    | 0.09  | 1, 50 | 0.761            |
| Temperature                            | 0.83  | 1, 50 | 0.366            |
| Food deprivation                       | 0.02  | 1, 50 | 0.896            |

Significant results are marked in bold.

Scanning bouts lasted on average  $0.19 \pm 0.02$  min. Scan bout duration decreased with flock size and increased with neighbour distance (Fig. 3b, Table 2). We found significant differences only at intermediate neighbour distance (size 3 versus 5:  $t_{50} = 3.81$ ,  $P < 0.001$ ; size 3 versus 7:  $t_{50} = 3.82$ ,  $P < 0.001$ ; Fig. 3b). Neighbour distance levels differed significantly only at flock sizes 3 (close versus intermediate:  $t_{50} = 3.18$ ,  $P = 0.003$ ; close versus far:  $t_{50} = 2.13$ ,  $P = 0.038$ ) and 7 (close versus far:  $t_{50} = 2.64$ ,  $P = 0.011$ ).

The average proportion of time allocated to scanning was  $0.77 \pm 0.02$ . Proportion of time spent scanning decreased with flock size and increased with neighbour distance (Fig. 3c, Table 2). We found significant variations between flock size levels at close (3 versus 5:  $t_{50} = 2.72$ ,  $P = 0.009$ ; 3 versus 7:  $t_{50} = 3.29$ ,  $P = 0.002$ ; Fig. 3c) and far (3 versus 5:  $t_{50} = 2.43$ ,  $P = 0.019$ ; Fig. 3c) neighbour distances. Moreover, significant changes between neighbour distance levels were found at the three flock sizes studied: 3 (far versus close:  $t_{50} = 2.36$ ,  $P = 0.022$ ; far versus intermediate:  $t_{50} = 2.41$ ,  $P = 0.019$ ), 5 (far versus close:  $t_{50} = 2.64$ ,  $P = 0.011$ ) and 7 (close versus intermediate:  $t_{50} = 2.69$ ,  $P = 0.009$ ; intermediate versus far:  $t_{50} = 2.13$ ,  $P = 0.038$ ; close versus far:  $t_{50} = 4.76$ ,  $P < 0.001$ ).

## DISCUSSION

Results indicate that in a seminatural field setting, foraging and vigilance in brown-headed cowbirds are influenced by both flock size and neighbour distance. Food-handling rate and scanning rate increased with flock size, whereas time spent scanning and scanning bout duration decreased with flock size. The effect of flock size tended to level off beyond

five companions regardless of neighbour distance. We also found nonlinear trends for neighbour distance, but in some cases (pecking rate at flock size 7 and proportion of time scanning at flock sizes 3 and 7), there was no levelling off; instead, we found differences between intermediate and far distances, suggesting a linear trend. Nevertheless, these linear and nonlinear trends should be taken with care until future experiments are conducted with a wider range of flock sizes and neighbour distances.

Flock size effects on foraging and vigilance have been noted in many earlier studies (Beauchamp 1998). In a field study of brown-headed cowbirds, however, pecking rate and vigilance were poorly related to flock size (Morris & Thompson 1998). Brown-headed cowbirds tended to accumulate in areas of high food density, and males were more vigilant than females, presumably to fend off other males. In our experiment, we controlled food density and precluded direct contact between group members. Foraging interference among group members and scrounging have also been implicated in studies that report little effect of group size on foraging and vigilance (Treves 2000; Beauchamp 2001; Robinette & Ha 2001; Barbosa 2002; Hirsch 2002). By isolating foragers physically in our experiment, interference or scrounging could not counteract the expected effects.

Across all flock sizes, neighbour distance influenced foraging and vigilance to almost the same extent as did flock size in terms of explained variance. Pecking rate and food-handling rate decreased, while food-handling bout duration increased, with neighbour distance. The proportion of time spent scanning and the rate of scanning increased, while scanning bout duration decreased, with neighbour distance. In many cases, the influence of a large group at a large distance was similar to that of a small group nearby, negating the advantages of a larger group size. Thus, birds generally spent less time foraging and more time vigilant as companions occurred further away. A similar effect has been noted in other bird species (Lazarus 1978; Elgar et al. 1984; Pöysä 1994; Lima & Zollner 1996; Rolando et al. 2001; Fernández-Juricic et al. 2004; Randler 2005) and in rabbits (Roberts 1988) and monkeys (Treves 1998). Less clear, however, is the explanation for the negative influence of distance on foraging and vigilance.

Interestingly, besides the nonlinear effects of neighbour distance, we also documented a linear trend. This is unexpected because both dilution and detection effects predict nonlinear consequences as neighbour distance changes for any given flock size. It is perhaps the case that in our circular arrangement, with all companions located at the circumference, scanning was proportional to circumference rather than to area, thus leading to a linear rather than nonlinear effect. Even in this case, domain-of-danger arguments, such as dilution and selfish-herd effects, would still predict a nonlinear effect. A nonlinear effect of neighbour distance on vigilance has been noted in teals, *Anas crecca* (Pöysä 1994) and in starlings, *Sturnus vulgaris*, for both pecking rate and total time spent scanning (Fernández-Juricic et al. 2004). Clearly more work will be needed to predict in the first place how information about predation risk flows between group members as neighbour distance changes and how this factor interacts with risk

dilution to produce the overall effect of neighbour distance on foraging and vigilance.

Our most intriguing result was the discovery that the effect of flock size on foraging and vigilance depended on neighbour distance when both factors were manipulated simultaneously. With the exception of pecking rate and proportion of time spent scanning, we detected no significant effect of flock size when companions were furthest from the focal subjects. The most significant effects of flock size thus occurred at the close and intermediate distances. When companions are too far apart, the perception of flock size is probably altered, reducing the effects of detection and dilution. We found that in brown-headed cowbirds this can occur between a minimum of 2.5 and 5 m away from the focal bird with flocks ranging in size from three to seven. The relative contributions of detection and dilution remain to be documented. The probability of detecting alarm reactions of companions decreases with neighbour distance (Gerkema & Verhulst 1990; Lima & Zollner 1996; Hilton et al. 1999; Quinn & Cresswell 2005), although this does not rule out a role for dilution, which must weaken as neighbour distance increases.

The strength of the group-size effect on vigilance decreased with increased distance to neighbours in one study (Lima & Zollner 1996), but results were inconclusive in the other (Elgar et al. 1984). In these two studies, birds foraged at two distinct feeders (spaced 0–4 m apart), which creates two drawbacks. First, the spatial arrangement means that the number of companions in each bird's field of view at one feeder can be variable. This variability occurs because distant neighbours are detectable only in one direction, so each individual's perception of group size may vary as these neighbours move in front of each other. Second, the allocation of birds to the two feeders was not controlled. As a result of interactions between birds, the possibility arises that the phenotypic composition of birds at the two feeders, in terms of age, sex or hunger, for instance, differed in ways that altered vigilance and feeding. We avoided these issues by providing neighbours on several sides, controlling for hunger, sex and age, and preventing any interaction between birds.

The variable that showed the least response to changes in flock size and distance was proportion of time handling food. In a species such as the brown-headed cowbird that can handle seeds and look up at the same time, handling time is subject to the push and pull of two factors. On the one hand, an increase in flock size is expected to increase total handling time because of the increase in pecking rate and food-handling rate. However, at the same time, individuals are expected to be less vigilant in large flocks, which would tend to decrease food-handling time while birds are looking up. Contributions from each factor probably cancel each other out. A decrease in food-handling bout duration with flock size has been observed in other granivorous bird species handling seeds while looking up, suggesting that vigilance interferes with food handling (Popp 1985; Beauchamp & Livoreil 1997; Lima et al. 1999). The reason for this is not clear but may involve interference caused by the performance of two simultaneous tasks or suggest that acoustic vigilance is hampered by food handling (Lima et al. 1999).

The immediate implication of our findings is that the strength of group-size effects may vary with neighbour distance. Most studies only report group size, and those that report group density rarely provide a biological justification for the inclusion or exclusion of individuals from a group. We argue that group size should only include individuals within the radius that allows detection and dilution to operate, and therefore, that (1) the effect of group size on foraging and vigilance will vary with neighbour distance and (2) nearby companions will have a greater influence on foraging and vigilance of group mates than companions that are further away.

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