Original Article

Where does a flock end from an information perspective? A comparative experiment with live and robotic birds

Esteban Fernández-Juricic[a] and Victor Kowalski[b]
[a]Department of Biological Sciences, Purdue University, 915 W. State Street, West Lafayette, IN 47907, USA and [b]Department of Biological Sciences, California State University Long Beach, 1250 Bellflower Blvd, Long Beach, CA 90840, USA

Predator detection is improved when individuals join groups. Theory assumes that the transfer of social information about predators among individuals is immediate and accurate. However, animals in groups space themselves at different distances. Little is known about the shape of the social information transfer function over distance, which can affect group cohesion and ultimately the costs and benefits of group living. Our goal was to study the flow of social information in 3 bird species with different visual acuity (European starling, brown-headed cowbird, and house finch). We used robotic birds to manipulate the availability of social information. In a previous study, we demonstrated that birds react to robotic birds in the same way as they do to live birds. We measured the probability of 3 linearly placed live birds reacting to the flushing behavior of 2 robotic birds of the same species. Our study species were tested independently. We found a nonlinear decrease in social information flow with increasing distance between the robots and live birds; however, this decrease was more pronounced in species with lower visual acuity. Additionally, social information apparently degraded when flowing between closely spaced individuals, which could lead to false alarms. Our findings suggest that the benefits of social information flow are restricted to small neighbor distances and that larger species, with higher visual acuity, may have a greater spatial domain of collective detection. This mechanism may explain the spatial limits of flocks based on the transfer of social information. *Key words:* antipredator behavior, collective detection, predator detection, social information, vigilance, visual acuity. *[Behav Ecol 22:1304–1311 (2011)]*

INTRODUCTION

One of the benefits of joining a group is that predator detection can be improved through the combined vigilance of group members or collective detection (e.g., Quinn and Cresswell 2005; Fairbanks and Dobson 2007; Ward and Mehner 2010). Theory assumes that when an individual detects a predator, information (e.g., alarm calls, flushing responses, chemical signals) will pass to the other members of the group immediately and accurately to ensure a timely escape (Pulliam 1973; Lazarus 1979; Pulliam et al. 1982; Hart and Lendrem 1984; Lima 1987). Recent theoretical work has relaxed the assumption of immediate information transfer to represent a decrease in information flow over distance (Proctor et al. 2003). This is because, all else being equal, distance may degrade 1) visual information through a reduction in visual contrast and the ability to resolve changes in the behavior of group mates (Fernández-Juricic et al. 2004), 2) acoustic information through an increase in attenuation and reverberation (Balsby et al. 2003), and 3) chemical information through a reduction in the concentration of chemicals cues from the source (Ferrari et al. 2010). Therefore, longer neighbor distances are expected to reduce the availability of social information and increase the perception of risk because

the protection provided by the presence and number of group mates decreases (Proctor et al. 2003).

Empirical evidence suggests that greater spacing between group mates increases the perception of risk and delays the speed of response to a threat (Pöysä 1994; Lima and Zollner 1996; Hilton et al. 1999; Rolando et al. 2001; Fernández-Juricic and Kacelnik 2004; Quinn and Cresswell 2005). However, little is known about the shape of the function by which information flow decreases with neighbor distance and the extent to which the shape of this function varies between species. This is relevant from both theoretical and empirical perspectives. Theoretically, models assume either linear or nonlinear functions whose shapes can affect the speed of information transfer and as a result the area a flock occupies and the individual investment in vigilance and foraging (Proctor et al. 2003; Jackson and Ruxton 2006). Additionally, models assume that information flows without being degraded among close group mates irrespective of the number of individuals in the group (Bahr and Bekoff 1999; Jackson and Ruxton 2006; Proctor et al. 2006). However, if information quality is reduced as it transfers between close group mates, it could lead to false alarms (e.g., individuals misinterpreting a sudden flight caused by a nonthreatening stimulus as if it were a predator attack; Proctor et al. 2001). An increase in false alarms can reduce the benefits of collective detection and actually become a cost for individuals joining groups by increasing energetic expenditure in unnecessary flights and reducing the amount of time foraging (Beauchamp and Ruxton 2007). Empirically, individuals are expected to distance themselves

Address correspondence to E. Fernández-Juricic. E-mail: efernan@purdue.edu.

from group mates to avoid interference competition but up to a certain distance (Krause and Ruxton 2002), above which the chances of detecting the behavior of group mates accurately may be too low, thereby reducing the benefits of collective detection. This distance threshold above which the costs of gathering social information are higher than the benefits may represent the spatial limits of a flock.

The goal of this study was to estimate the probability of social information about predation risk flowing within flocks of 3 different avian ground foragers (house finch *Carpodacus mexicanus*, brown-headed cowbird *Molothrus ater*, and European starling *Sturnus vulgaris*). These 3 species have been shown to differ in visual acuity (cycles per degree; house finch, 4.69 ± 0.06; brown-headed cowbird, 5.10 ± 0.25; and European starling, 6.27 ± 0.11; Dolan and Fernández-Juricic 2010). Previous studies have tried manipulating the flushing behavior of specific individuals in the group by exposing them to a threatening stimulus and then measuring the response of unexposed group mates (Lima 1995a, 1995b; Lima and Zollner 1996; Roth et al. 2008). However, this approach cannot control for the variations in the behavioral responses of the individuals exposed to the threat and hence the ambiguity in the quality of social information flowing through the group (Lima 1995b). To minimize this problem, we used robotic birds to manipulate the availability of social information. Robotic birds have been used successfully in the past to manipulate different behaviors and assess the reaction of live individuals (reviewed in Patricelli 2010). In a previous study under conditions similar to the present one and using one of our study species, we demonstrated that 1) birds do react to robotic birds and 2) the responses to robotic birds are similar to those given to live birds (Fernández-Juricic et al. 2006).

We studied social information flow in a flock composed of robotic birds (information producers) and live birds (information receivers) of the same species. We manipulated the distance between information producers and receivers but kept the receivers at very close distances among themselves. We asked the following questions. First, how is social information about potential threats transferred from producers to receivers at different distances? Second, how does the shape of the social information transfer function vary in species with different visual acuity? Third, how is social information transferred among closely spaced receivers?

From a visual information perspective, the ability to resolve stimuli against the background is the main mechanism behind the flow of social information in groups (Hilton et al. 1999; Fernández-Juricic et al. 2004). We predicted that as the distance between information producers and receivers increases, the probability of receivers detecting the producers would decrease (Proctor et al. 2003). We also predicted that the decrease in information flow with distance would be more pronounced in species with lower visual acuity (Kiltie 2000). Finally, following theoretical assumptions, we predicted that all receivers would respond with the same probability to the producers (i.e., information would not degrade among closely spaced group mates; e.g., Bahr and Bekoff 1999; Jackson and Ruxton 2006).

METHODS

We conducted the experiment outdoors to enhance the perception of risk under semicontrolled conditions. Our experimental arena consisted of 2 robotic birds (1 male and 1 female) closely spaced but facing opposite directions. Perpendicular to the robots, we laid out an enclosure with transparent partitions such that there was 1 live bird in each of the 3 compartments (close, middle, and far in relation to the robots; Figure 1). The robots and live birds belonged to the same species. Details of the experimental arena are presented in Supplementary Appendix A.
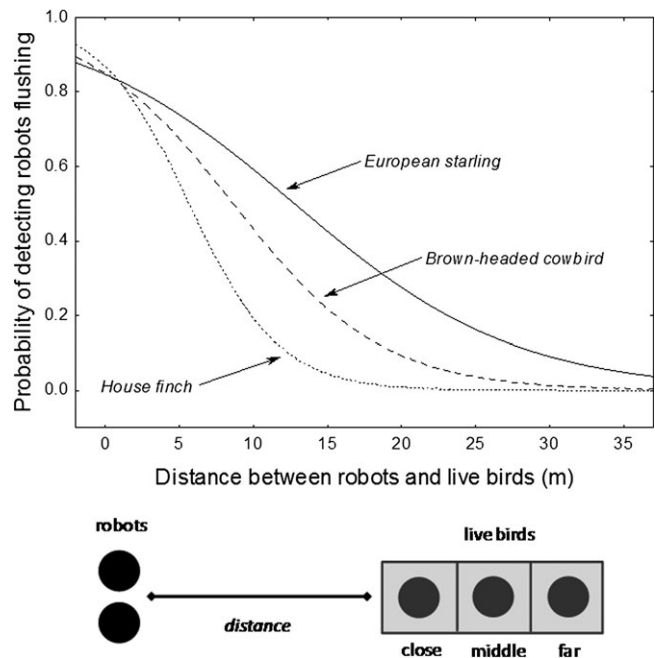

Figure 1
Probabilities of detecting robots flushing at different distances between the live birds and robots of 3 different species (European starling, brown-headed cowbird, and house finch). Probability functions estimated with generalized linear models.

We controlled for several factors that can affect the flow of social information. First, we only manipulated the distance between producers and receivers but kept the receivers at the same distance among themselves. Second, we kept flock size constant and relatively small by having 2 information producers (robots) and 3 information receivers (live birds). Collective detection is expected to be more prevalent in small rather than in large flocks (e.g., Dehn 1990). Third, a relatively large proportion of our artificial flock flushed (2 robots), which would increase the chances of receivers responding to this flushing behavior based on theoretical (Lima 1994a; Ruxton 1996) and empirical grounds (Lima 1995b; Roberts 1997; Cresswell et al. 2000). Fourth, we focused on the transmission of visual information by eliciting a visual alarm (e.g., robot flushing) and considering responses in which live birds never alarm called. Fifth, we controlled for individual identity, food density, and habituation (i.e., each live individual was exposed to the robots only once).

The experiment was conducted on a grassy area surrounded by a 1.8 m tall tarp to reduce visual distractions. We captured 105 birds of each of the 3 species from local populations in collaboration with APHIS (USDA). Birds were housed in animal facilities under a 12–12 h daylight cycle and kept at 21 °C. All birds were fed ad libitum: brown-headed cowbirds with Mazuri small bird mix, European starlings with cat food (protein content 30% or higher), and house finches with a finch mix. A nutritional supplement of mealworms was given to European starling 3 times a week. Birds were food deprived for 2–6 h on a given experimental day to encourage foraging while in the experimental arena. Experimental procedures were approved by the Institutional Animal Care and Use Committees of Purdue University (#09-018) and California State University Long Beach (#257).

Our robots were built with skins obtained from a project to study the visual system of our study species (Dolan and Fernández-Juricic 2010). Each robot had a 3-servo system that allowed us to control its body movement (head-up and head-

down) simulating pecking, move its head sideways simulating vigilance while head-up, and propel the robot vertically simulating flushing behavior (see Supplementary Appendix B for details on the robots). A trial consisted of the robots pecking 4 times per min and moving their heads sideways randomly 50 times per min. This simulated a situation in which the robots were investing a large amount of time in vigilance behavior on a given head orientation. Our intention was to convey vigilance cues associated with a potential threat before flushing the robots. We kept the same pecking and head movement rates across species to reduce the number of confounding factors that could influence interspecific responses. The head movement rate of the robots was within the ranges of each of the study species (head movements per min; house finch, 21–153; brown-headed cowbird, 48–122; and European starling, 34–112). After the robots performed the combination of vigilance and foraging behaviors for 3 or 5 min (depending on the species, see below), we made them flush and recorded the response of the live birds (Supplementary Appendix C). Both robots flushed at approximately the same time (i.e., within 0.5 s of each other).

The enclosure containing the live birds was aligned perpendicularly to the axis of the robot cages (Figure 1, Supplementary Appendix A). For each species, we conducted a similar number of trials with the closest bird to the robots being a male or female. We alternated the sexes of the live birds to avoid the occurrence of 2 birds of the same sex next to each other. The live birds were placed from 1 to 35 m (at 1 m intervals) away from the robots (Figure 1). We conducted 105 trials total (35 per species).

We used video cameras to record the behavior of the birds before and after the robots flushed. Because of interspecific differences in the latency to start foraging, house finches and brown-headed cowbirds were recorded for 3 min and European starlings for 5 min before the robots flushed (following Tisdale and Fernández-Juricic 2009). Recordings were made using PelikanCam CRM-36DW BandW weatherproof infrared cameras and a GANZ DigiMaster Digital Video Recorder (Model # DR4N) with a Radical DVR Multiplexer (Model HDC-0912) attached to a Pelikan-Cam PLm750 Monitor. This equipment allowed us to record 8 cameras simultaneously on one video screen: one lateral and top-view camera on each live bird and one camera behind each robot (Supplementary Appendix A). Cameras were secured to a PVC-tubing frame to ensure that data were collected in the same manner across trials. We also used a Sony Handycam camcorder to record the live birds and ensure that they were not alarm-calling when the robots flushed.

To code the reaction to the robots, we compared the behavior of each live individual during 30-s intervals (1) before and (2) during/after the robots flushed. We classified the live bird responses as "no-reaction" or "reaction" and used a generalized linear modeling approach to calculate the probability of social information flow (see "Statistical analysis"). We considered that an individual showed no reaction when it continued the behavior it was engaged in uninterrupted during and after the robots flushed (e.g., maintained the same rates of scanning and pecking behaviors; Fernández-Juricic and Schroeder 2003). We considered that an individual did respond to the robots when it showed any of the following behaviors during or 30 s after the robots flushed: change in head orientation while head-up, change in head orientation while head-down, stretched neck, body upright, decreased head movement rate, freezing, crouching, and walking/hopping (following criteria in Tisdale and Fernández-Juricic 2009; definitions in Supplementary Appendix C). Head movement rates were used to record the occurrence of some of the responses to the robots as this parameter has been shown to be sensitive to changes in predation risk (Jones et al. 2007). All these re-

sponses were given when animals were on the ground, but in some cases, individuals were hanging on the enclosure walls when the robots flushed. We did not code the reaction of these individuals (10 of 315) nor did we include them in the analyses because we could not determine any clear behavioral response from that position in the cage.

We coded the videos by first watching each trial in real time and then watching it again frame by frame to determine the presence of subtle body and head movements using Virtual-Dub (Avery Lee, Version 1.9.4). We could not discriminate whether a given bird reacted to the robots themselves or to the behavior of their group mates. However, because no predator was used as a stimulus, all the responses of the live birds to the robots (which were built to mimic conspecifics) can be considered as part of social information about predation.

We also recorded three factors that could affect information flow; the proportion of time spent in head-up vigilance before the robots flushed and body posture and head orientation of the live birds upon the robots flushing. A greater investment in vigilance can enhance the chances of spotting a predator early (Lima 1994b). Birds could use their peripheral vision even when the head is down searching for food to gather social information (Bednekoff and Lima 2005). Additionally, when a bird is head-up, certain head orientations can increase the chances of detection (Devereux et al. 2006; Tisdale and Fernández-Juricic 2009) based on the position of the fovea (i.e., high visual resolution spot in the retina). We recorded the time each live bird spent in the head-up position scanning during 3 min before the robots flushed using JWatcher 1.0 (Blumstein and Daniel 2007). We then calculated the proportion of time vigilant for each live individual in the flock. We measured body posture and head orientation of each live bird with ImageJ (http://rsbweb.nih.gov/ij/) using the frame immediately preceding its first response behavior (see above). Body posture was defined as the angle created by a vector connecting the center of the bird's eye with the tip of its bill (v1) and the vector beginning at the center of the bird's eye and extending to the ground perpendicularly (v2). For instance, a body posture of 20° would represent an individual in the head-down position, 85° would represent an individual in the head-up position, and 110° would represent an individual with its bill pointing up (see also Tisdale and Fernández-Juricic 2009). Head orientation was defined as the angle created by a vector connecting the center of the bird's crown with the tip of its bill (v3) and a vector perpendicular to the side of the enclosure facing the robots (v4). For example, a head orientation of 10° would represent the bill oriented toward the robots, 90° would represent the bill oriented parallel to the robots (i.e., sideways looking), and 175° would represent the bill away from the robots (see also Tisdale and Fernández-Juricic 2009).

Statistical analysis

Our main response variable was whether each live bird reacted (1) or not (0). Therefore, we used a generalized linear model (binomial distribution, logit-link function) to estimate the probability of live birds detecting the robots flushing. The first model included species (European starling, brown-headed cowbird, and house finch) as the independent factor, along with distance (1–35 m) and position in the live bird enclosure from the robots (close, middle, and far) as continuous and categorical factors, respectively. We also included the 2-way interactions between these factors. We then ran one generalized linear model per species, including distance, position in the live bird enclosure, and sex to determine the relative importance of these factors within species. We did not have enough degrees of freedom (df) to run all interaction effects, which could have led to redundancy problems in the design

matrix that are characteristic of overparameterized generalized linear models (Statsoft Inc 2010). Thus, to determine if the results would vary with higher order interactions, we conducted extra-generalized linear models assessing 2-way interactions when considering all species and 3-way interactions when considering single species.

We conducted general linear models considering the variation in the proportion of time spent vigilant in relation to position in the live bird enclosure, distance to the robots, species, and the 2-way interactions among these factors. In one species (house finch), we also conducted a segmented regression with SegReg (www.waterlog.info/segreg.htm) because the relationship between vigilance and distance resembled 2 lines with different slopes. Finally, we analyzed with general linear models whether there were variations in head orientation and body position in relation to position in the live bird enclosure and distance to the robots for each species. Analyses were conducted with Statistica 10. We present means (±standard errors) throughout.

RESULTS

All species

Individuals of all species responded to the robots flushing. European starlings showed the highest frequency of responses, house finches showed the lowest, and brown-headed cowbirds showed intermediate frequencies (Supplementary Appendix C). The most frequent behavioral responses to the robots flushing were changes in head orientation while head-up and body upright reactions (Supplementary Appendix C).

In the model considering all the 3 species, position in the live bird enclosure, distance to the robots, and the interaction between species and distance to the robots influenced significantly the probabilities of detecting the robots flushing (Table 1). Across all species and distances (Table 1), individuals that were in the close (0.34 ± 0.05) and middle (0.33 ± 0.05) positions in the live bird enclosure had higher probabilities of detecting the robots flushing than those positioned far from

the robots (0.13 ± 0.03). In general, the probability of detecting the robots flushing decreased with distance between the live birds and the robots (Table 1). However, the strength of this decrease varied between species (Table 1, Figure 1). The decrease in the probability function was more pronounced in the house finch, intermediate in the brown-headed cowbird, and less pronounced in the European starling (Figure 1). The model with the 3-way interaction among distance, position in the live bird enclosure, and species was not significant ($\chi^2 = 1.67$, df = 4, $P = 0.796$).

Species differed significantly in the proportion of time vigilant (Table 2). European starlings spent significantly less time vigilant (0.74 ± 0.01) than brown-headed cowbirds (0.81 ± 0.01, Tukey test, $P < 0.001$) and house finches (0.80 ± 0.01, Tukey test, $P < 0.001$), without significant differences between the latter 2 species (Tukey test, $P = 0.786$). The direction of the relationship between time spent vigilant and distance to the robots varied between species giving rise to a significant interaction effect (Table 2, see relationships below). All other factors included in the model did not significantly affect the proportion of time vigilant (Table 2).

Individual species

The probability of house finches detecting the robots flushing decreased significantly with increasing distance between the live birds and the robots (Table 1; Figure 2a). Position within the live bird enclosure also decreased significantly the probability of house finches detecting the robots flushing (Figure 2a): close (0.26 ± 0.07), middle (0.17 ± 0.06), and far (0.06 ± 0.04) positions from the robots. Sex did not affect significantly the probability of detecting the robots flushing (Table 1). The model with the 2-way interaction between distance and position in the live bird enclosure was not significant ($\chi^2 = 0.40$, df = 2, $P = 0.813$).

Table 1

Effects of position in the live bird enclosure from the robots (close, middle, and far), and distance to the robots on the probabilities of detecting the robots flushing considering all species, house finches, brown-headed cowbirds, and European starlings

	df	χ^2	P
All species			
Position in the enclosure	2	10.95	**0.004**
Distance to the robots	1	117.36	**<0.001**
Species	2	0.16	0.924
Position in the enclosure × species	4	6.62	0.157
Position in the enclosure × distance	2	0.66	0.719
Species × distance	2	8.42	**0.015**
House finch			
Position in the enclosure	2	10.82	**0.004**
Distance to the robots	1	48.56	**<0.001**
Sex	1	0.22	0.641
Brown-headed cowbird			
Position in the enclosure	2	13.11	**0.001**
Distance to the robots	1	47.53	**<0.001**
Sex	1	0.15	0.698
European starling			
Position in the enclosure	2	11.18	**0.004**
Distance to the robots	1	32.25	**<0.001**
Sex	1	0.79	0.374

Results from generalized linear models with a binomial distribution and a log-link function. Significant factors are marked in bold.

Table 2

Effects of position in the live bird enclosure from the robots (close, middle, and far), and distance to the robots on the proportion of time vigilant (head-up body postures) considering all species, house finches, brown-headed cowbirds, and European starlings

	df	χ^2	P
All species			
Position in the enclosure	2, 291	0.35	0.708
Distance to the robots	1, 291	0.98	0.322
Species	2, 291	9.78	**<0.001**
Position in the enclosure × species	4, 291	0.44	0.782
Position in the enclosure × distance	2, 291	0.08	0.922
Species × distance	2, 291	14.97	**<0.001**
House finch			
Position in the enclosure	2, 97	0.17	0.842
Distance to the robots	1, 97	18.39	**<0.001**
Sex	1, 97	2.45	0.121
Position in the enclosure × distance	2, 97	0.03	0.966
Brown-headed cowbird			
Position in the enclosure	2, 98	0.38	0.683
Distance to the robots	1, 98	6.92	**0.010**
Sex	1, 98	0.67	0.415
Position in the enclosure × distance	2, 98	0.31	0.733
European starling			
Position in the enclosure	2, 89	0.78	0.464
Distance to the robots	1, 89	6.64	**0.012**
Sex	1, 89	0.93	0.338
Position in the enclosure × distance	2, 89	0.22	0.802

Results from general linear models. Significant factors are marked in bold.
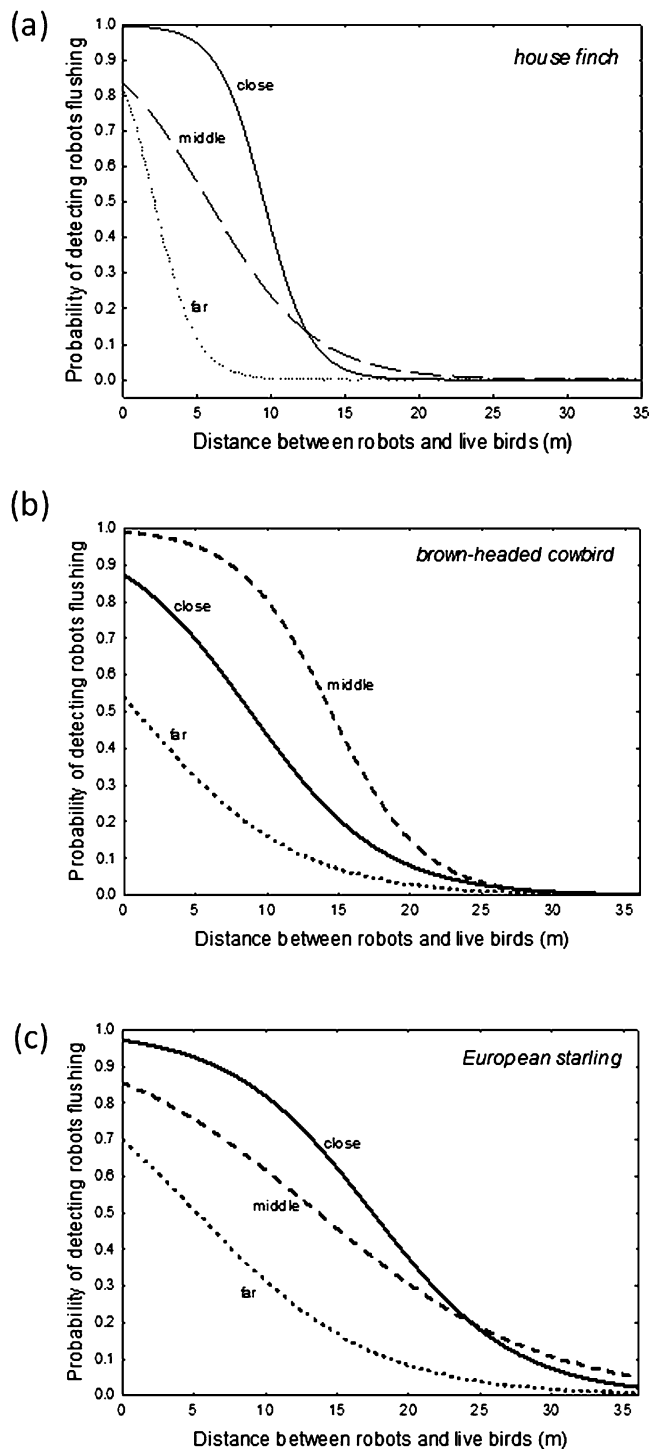
Figure 2
Probabilities that (a) house finches, (b) brown-headed cowbirds, and (c) European starlings detected robots flushing at different distances between the live birds and robots and in different positions (close, middle, and far) within the live bird enclosure in relation to the robots (Figure 1). Probability functions estimated with generalized linear models.

Figure 3
Relationship between the proportion of time spent vigilant (head-up body posture) in relation to distance between the robots and the live birds in (a) house finches, (b) brown-headed cowbirds, and (c) European starlings.

The proportion of time house finches spent vigilant increased significantly with the distance between the live birds and the robots (Table 2, Figure 3a). However, a closer exami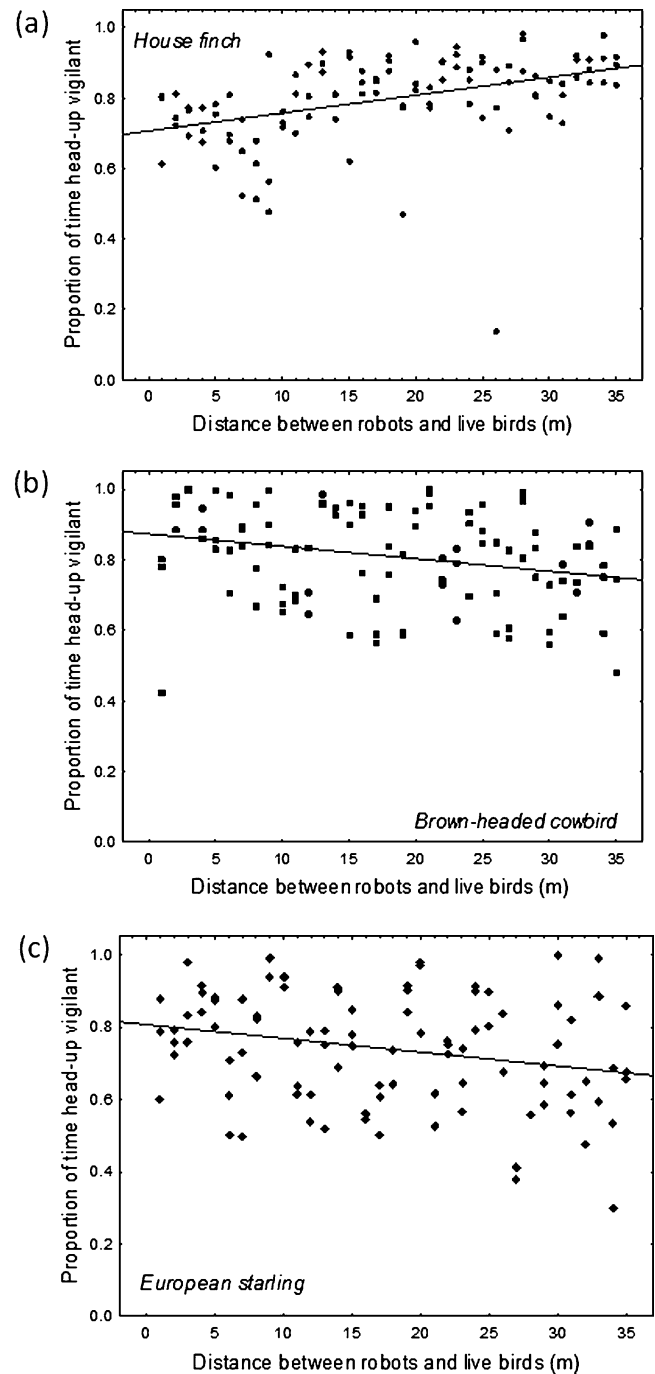nation of this relationship showed 2 different trends depending on distance. We then conducted a segmented regression, which identified the breaking point at a distance of 9.16 m. The segmented regression fitted a function type 6, which consisted on 2 disconnected lines in which both regression coefficients were significant. The segmented regression significantly accounted for the data over the linear regression ($F_{1,101} = 13.045$, $P < 0.001$). Consequently, the proportion of time vigilant actually decreased significantly with distances <9.16 m (head-up vigilance $= 0.78–0.02 \times$ distance; $F_{1,25} =$

5.47, $P = 0.028$) but did not vary significantly when considering distances >9.16 m (head-up vigilance = 0.78 + 0.002 × distance; $F_{1,75} = 2.00$, $P = 0.161$).

The proportion of time house finches spent vigilant was not affected by position in the live bird enclosure, sex, and the interaction between distance and position (Table 2). House finch body posture and head orientation did not vary significantly with position in the live bird enclosure (body posture, $F_{2,100} = 0.35$, $P = 0.705$ and head orientation, $F_{2,100} = 1.45$, $P = 0.240$) or distance to the robots (body posture, $F_{1,100} = 0.85$, $P = 0.359$ and head orientation, $F_{1,100} = 0.47$, $P = 0.495$).

The probability of brown-headed cowbirds detecting the robots flushing decreased significantly with increasing distance between the live birds and the robots (Table 1; Figure 2b). The chances of detecting the robots flushing were higher in the middle position within the live bird enclosure (0.40 ± 0.08), followed by the close position (0.26 ± 0.07), and the far position (0.11 ± 0.05). This suggests that individuals at the center of the enclosure were more sensitive to changes in the behavior of the robots or flock mates. Sex did not affect significantly the probability of detecting the robots flushing (Table 1). The model with the 2-way interaction between distance and position in the live bird enclosure was not significant ($\chi^2 = 1.53$, df = 2, $P = 0.466$).

The proportion of time brown-headed cowbirds spent vigilant decreased significantly with the distance between the live birds and the robots (Table 2, Figure 3b) but was not affected by position in the live bird enclosure, sex, and the interaction between distance and position in the enclosure (Table 2). Cowbird body posture and head orientation did not vary significantly with position in the live bird enclosure (body posture, $F_{2,101} = 0.17$, $P = 0.844$ and head orientation, $F_{2,101} = 0.66$, $P = 0.520$) or distance to the robots (body posture, $F_{1,101} = 1.99$, $P = 0.162$ and head orientation, $F_{1,101} = 0.43$, $P = 0.516$).

The probability of European starlings detecting the robots flushing decreased significantly with increasing distance between the live birds and the robots (Table 1; Figure 2c). European starling probability of detecting the robots flushing varies significantly depending on the position in the live bird enclosure (Figure 2c): close (0.53 ± 0.09), middle (0.45 ± 0.09), and far (0.21 ± 0.07). Sex did not affect significantly the probability of detecting the robots flushing (Table 1). The model with the 2-way interaction between distance and position in the live bird enclosure was not significant ($\chi^2 = 3.70$, df = 2, $P = 0.157$).

The proportion of time European starlings spent vigilant decreased significantly with the distance between the live birds and the robots (Table 2, Figure 3c) but was not affected by position in the live bird enclosure, sex, and the interaction between distance and position (Table 2). Starling body posture and head orientation did not vary significantly with position in the live bird enclosure (body posture, $F_{2,92} = 1.13$, $P = 0.330$ and head orientation, $F_{2,92} = 0.87$, $P = 0.421$). Distance to the robots did not influence significantly body posture ($F_{1,92} = 0.77$, $P = 0.384$). However, distance to the robots was associated with a reduction in the head orientation angle ($F_{1,92} = 4.54$, $P = 0.036$) such that starlings at longer distances tended to turn their heads more toward the robots.

DISCUSSION

We manipulated the availability of social information about predation risk using robotic animals and measured how information was transferred between information producers and receivers at different distances and between closely spaced receivers. Previously, we corroborated that birds react to robots in the same way as they do to live conspecifics (Fernández-Juricic et al. 2006). This experimental approach allowed us to characterize empirically the shape of the social information transfer func-

tion for the first time in 3 different bird species known to be affected by group size effects (Powell 1974; Fernández-Juricic and Beauchamp 2008; Fernández-Juricic et al. 2009). Understanding the shape of this function has important implications for the process of collective detection in animal groups.

We found that the probabilities of a receiver detecting a flushing robot decreased with distance from the producers for all species, but the shape of this function varied among species. At 1 m from the producers, receivers from all species detected the flushing behavior with around 90% probability, but at 15 m, the probability dropped to about 42% in European starlings, 21% in brown-headed cowbirds, and 4% in house finches. This difference is not likely to have been caused by interspecific difference in vigilance as European starlings actually spent the least proportion of time scanning. Our findings support Kiltie's (2000) hypothesis by which the distance to detect conspecifics scales hyperallometrically with body mass (within species, information producers, and receivers scale identically). Body mass is positively associated with eye size (Howland et al. 2004; Burton 2008), which in turn is correlated with visual acuity. In other words, the decrease in social information transfer over distance appears to be more pronounced in species with lower visual acuity. Although this conclusion should be taken with care because our study was limited to only 3 species due to logistical reasons, previous comparative studies controlling for phylogenetic effects have also found that species with low visual acuity react to stimuli at shorter distances than those with high acuity (Blumstein et al. 2005; Møller and Erritzøe 2010). Alternatively, the between-species differences we found may be the result of variations in species' height, visual attention, and/or motion detection abilities. Irrespective of the mechanism, the overall implication is that the spatial domain of collective detection will be a function of the ability of a species to resolve or respond to the behavior of group mates at a distance. Larger species would have a greater spatial domain of collective detection, which would allow individuals to be more spaced out without losing the benefits of social information transfer.

Within species, information transferred from producers to receivers decreased with distance following a nonlinear function, with a slow decay in the flow of social information at close neighbor distances but a sharper decline after a certain distance, which was species specific. An alternative interpretation is that receivers at farther distances from the producers flushing had lower motivation to respond because we were using robotic animals. However, in a similar study to the present one, we used live birds as information producers and found that house sparrows (*Passer domesticus*) decreased the probability of reacting to conspecifics flushing from 94% at 1 m to 24% at 35 m (Fernández-Juricic, Tisdale, unpublished manuscript). This supports our findings with the robotic animals. The implication is that group mates will benefit from high-quality information when they are at close distances. At farther distances, 2 nonmutually exclusive processes may be occurring. First, ambiguity in the quality of social information likely increases as it is more difficult to resolve changes in the behavior of group mates (e.g., determining whether the flushing behavior is in response to a threat or to the regular transition of individuals between food patches; Lima and Zollner 1996). Second, motivation to respond to social information may be reduced at far neighbor distance due to the lower chances of being targeted by a potential predator. Predators may take advantage of this nonlinear decline in the spatial domain of collective detection by targeting individuals located farther from the group, particularly those that reduce their time investment in vigilance (FitzGibbon 1989; Bednekoff and Lima 1998).

Vigilance has been found to increase with neighbor distance due to increasing risk perception (Rolando et al. 2001;

Fernández-Juricic and Beauchamp 2008). We found the opposite: Vigilance decreased with increasing neighbor distance. This may be due to our experimental design in which live birds were kept in a tight linear flock as they were farther spaced out from the robots, mimicking the fission of a flock into 2 smaller flocks. When the live birds were closer to the robots, they may have copied the high investment in vigilance of the robots (Fernández-Juricic and Kacelnik 2004; Fernández-Juricic et al. 2004), which can be a cue associated with the presence of a potential threat (Sirot 2006; Sirot and Touzalin 2009). The decrease in vigilance with distance may actually reflect a reduction of the influence of the robots on the behavior of live birds (Fernández-Juricic and Kacelnik 2004). Overall, our findings suggest that social cues associated with the vigilance behavior of group mates have lower spatial influence than those associated with their flushing behavior. This could partially explain the lack of empirical support for the monitoring of the vigilance of group-mates in systems in which individuals are still sensitive to group mates escaping (e.g., Lima 1995a). We propose that high vigilance investment and the escape behavior of conspecifics are social cues acting at different spatial scales within groups.

If group mates are close to each other, theory assumes that information will be passed without a reduction in quality (e.g., Bahr and Bekoff 1999; Jackson and Ruxton 2006) such that as information flows, group mates will react to one another with the same probability. Our findings suggest that social information may change as it moves along closely spaced neighbors. However, this conclusion is based on individuals being affected by the behavior of neighbors, which we could not conclusively determine with our behavioral assay. In house finches and European starlings, the probability of detection decreased from the individual closest to the one farthest from the robots within the live flock. This could actually be due to constraints in our technique: Robots may have not mimicked the subtle behaviors shown by live group mates flushing, increasing the ambiguity of the cue, hence reducing the intensity of the response. For instance Davis (1975) showed that pigeons can distinguish a true threat from a false alarm based on the type of flushing behavior of conspecifics. Another explanation is that the individual farthest from the robots was at the other edge of the linear flock, monitoring threats by itself and dealing with somewhat conflicting information (a potential threat detected through social information but no threat detected through personal information). Future studies should model the behavior of individuals based on information travelling through different number of neighbors to generate more specific behavioral predictions for empirical testing.

Brown-headed cowbirds showed a different pattern of information flow, with higher response probabilities at the center of the flock. An individual in a central position may have paid more attention to the vigilance behavior of the 2 individuals at the edges (as found in cowbirds previously, Fernández-Juricic and Beauchamp 2008), likely leading to a greater responsiveness to subtle changes in their behavior (see also Lima 1995b; Proctor et al. 2006). This amplifier effect merits more empirical attention as it suggests that individuals at the center of cowbird flocks may potentially alter the content of social information about threats, which could influence patch departure decisions depending on the shape of flocks (e.g., circular flocks with a greater proportion of central individuals might depart more often than linear flocks with a smaller proportion of central individuals).

Establishing the shape of the social information transfer function over distance can shed some light into the spatial limits of a flock. The key parameter is the threshold probability of detecting social information, beyond which it may not pay individuals to gather social cues due to the low quality of the information. This threshold probability can be associated with a neighbor distance at which individuals may be not perceive themselves as members of a flock. Although there are no empirical estimates of this threshold probability, a few approaches can be proposed. Proctor et al. (2003) used a 50% threshold probability of social information transfer in their theoretical model. Using this threshold in our empirical model, we predict that the maximum neighbor distance for group membership will be 13 m in European starlings, 8 m in brown-headed cowbirds, and 6 m in house finches. Hilton et al. (1999) found a consistent decrease in the proportion of birds flushing in response to group mates up to 21 body lengths; above this neighbor distance, the proportion flushing was less than 1% and seemed random. Using a 1% probability threshold, our empirical model predicts that the maximum neighbor distance for group membership will be 31 m for brown-headed cowbirds and 20 m for house finches (no prediction can be made for European starlings because the farthest neighbor distance sampled was associated with a 5% probability). A different approach is to estimate the threshold probability of social information flow based on field estimates of neighbor distance. For instance, during the peak of starling flocking activity in the nonbreeding season, the mean neighbor distance varies from 0.30 to 0.86 m (Williamson and Gray 1975; Whitehead 1994), which based on our empirical model corresponds to a 82% probability of social information flow. This high probability value will certainly favor collective detection as well as reduce the chances of false alarms because individuals may be able to better resolve visually the behavior of conspecifics.

Overall, our study established that the spatial extent of social information flow may be reduced in a species-specific manner and that social information is degraded in a nonlinear fashion over distance and even between close neighbors, contrary to theoretical assumptions. Our empirical model can make predictions about the spatial limits of flocks based on various assumptions. However, future research should focus on estimating these threshold probability values to better predict spacing behavior in different species under various ecological conditions (e.g., degree of habitat obstruction). Our results could also be used to model other behaviors associated with animal aggregations, such as the coordination of vigilance, the movement of flying flocks, and mate cohesion in large breeding groups.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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