

Flock density, social foraging, and scanning: an experiment with starlings

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Social foraging differs from individual foraging because it alters both resource availability and the forager's behavior. We examined responses of starlings to the presence of conspecifics by manipulating foraging-group density experimentally, while ensuring that each subject's foraging opportunities were unchanged. To do this, we used individuals foraging simultaneously in four bottomless enclosures placed at various separations in natural foraging grounds. We measured foraging and scanning intensity and qualitative aspects of scanning of focal individuals. Additionally, we examined the temporal distribution of scanning between individuals. The focal individual analysis showed that (1) food-searching activity increased, while time spent scanning, time off the ground and scanning bout length decreased with flock density; (2) food finding per unit of searching effort increased with density; (3) head orientation during scanning was sensitive to companions' proximity: heads pointed away from the companions at close distance, toward them at intermediate distance, and was random farther away. The analysis of the (temporal overlapping in scanning) temporal distribution of scanning for the group showed that scanning was significantly synchronized when companions were adjacent to each other but was not significantly different from random at further separations. We conclude that behavioral responses of individuals to the presence of others generate important changes in foraging performance even in the absence of physical interference and, more generally, that assessing the mechanisms that control the behavior of group members at different flock densities offers a way to understand the functional and ecological significance of foraging aggregations. *Key words:* conspecific scanning, flock density, neighbor distance, social foraging, starlings, *Sturnus vulgaris*, vigilance. [*Behav Ecol* 15:371–379 (2004)]

The proximity of conspecifics may alter foraging performance through information sharing (Smith et al., 1999; Templeton and Giraldeau, 1996; Valone, 1989), scrounging (Coolen et al., 2001; Giraldeau and Lefebvre, 1986), the opportunity for kleptoparasitism (Goss-Custard et al., 1999; Stillman et al., 2000), or the release of time otherwise required for predator detection (e.g., the collective detection hypothesis; Bednekoff and Lima, 1998a; Caraco, 1979; McNamara and Houston, 1992). At the same time, aggregation may cause interference and local resource depression so that being joined by others basically hinders food intake, leading to various derivatives of the "ideal free distribution" models (Sutherland, 1996; Tregenza, 1995). Clearly, social foraging differs profoundly from isolated foraging, both because other foragers modify resource availability and because they affect how each forager behaves (Giraldeau and Caraco, 2000).

The distinction between the effects mediated by resource availability and by responses to the location and behavior of conspecifics is sometimes ignored, but this distinction is particularly important for the interpretation of correlations between group density and intake rate (Beauchamp, 1998). Although classic ideal free distribution models predict equalization of intake across individuals (Fretwell and Lucas, 1970; Kacelnik et al., 1992), numerous violations of the original assumptions allows for the accommodation of positive, negative, and no correlation between foraging performance and group density (Beauchamp, 1998), depending on how individuals actually respond to their social companions, with the consequence that observed correlations do not provide evidence for specific ecological models. The

study of behavioral mechanisms does not replace theorizing about the origin and function of these mechanisms or about the relation between resources and the distribution of individuals, but understanding these mechanisms is essential to inform and complement theoretical approaches. This is because the balance between attraction and repulsion between conspecifics reflects the costs and benefits of group living (Krause and Ruxton, 2002).

We present an experimental study of group foraging in starlings (*Sturnus vulgaris*). Our aim was to uncover behavioral mechanisms of the response of individuals to the presence of conspecifics that are foraging at different neighbor distances but excluding physical effects of conspecifics. Previous studies on the effects of neighbor distance have mainly dealt with the group size effect (Elgar et al., 1984; Lima and Zollner, 1996) and used correlational data without controlling experimentally for the number and location of conspecifics (Pöysä, 1994; Rolando et al., 2001). We looked at how manipulation of interindividual distance (while controlling for group size and resource availability) in a seminatural situation affected the rate at which individuals foraged, their rate of success, the amount of time individuals spent with their head up (scanning), and two qualitative aspects of scanning: the direction of gaze (which we assumed to be an indication of the target of visual attention) and the temporal distribution of scans between individuals.

Different types of information can be gathered through visual scanning (Bekoff, 1995, 1996; Catterall et al., 1992; Valone and Wheelbarger, 1998). We reasoned that the direction of gaze as a function of companions' presence and proximity may help us understand the function of scanning and whether it is mostly affected by the need to monitor for clues internal to the flock (information from conspecifics about the current patch) or external to it (information about the surroundings of the current patch). It is also possible that these competing functions can be better understood by observing departures from randomness in the temporal occurrence of scans between individuals at different separa-

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Received 14 October 2002; revised 16 May 2003; accepted 30 May 2003.

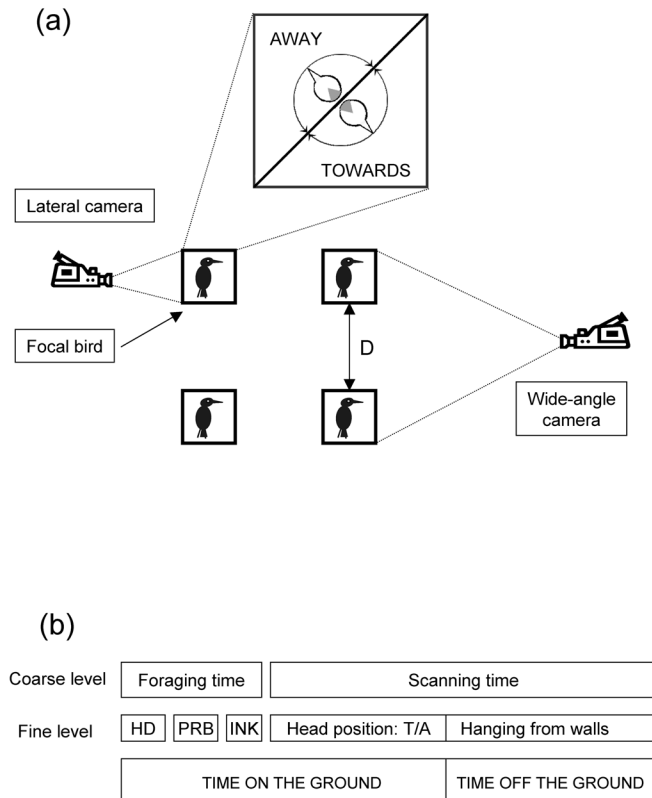


Figure 1
 (a) Experimental setup showing the position of the two cameras recording simultaneously the behavior of a focal bird and that of the four birds in bottomless enclosures located at different distances ($D=0, 1, 3\text{m}$). Also shown are the positions of the head (toward and away from conspecifics) and the relative size of the blind area of starlings at the rear of their heads (based on Martin, 1986). (b) Schematic representation of the two levels of measurements analyzed based on the allocation of time in different behaviors when foraging socially. Abbreviations: HD, head-down searching; PRB, probing in the ground; INK, intake; T, toward conspecifics; A, away from conspecifics.

tions, either toward synchronization (temporal overlapping in scanning) or toward coordination (taking turns to watch). These patterns are important because concepts such as shared predator detection depend on whether scanning is coordinated or synchronized.

We expected individuals to increase the time spent scanning as neighbor distance increased (Beauchamp and Livoreil, 1997; Pöysä, 1994), due to less information being available from conspecifics (distance effects; Elgar et al., 1984; Lima and Zollner, 1996) and increasing predation risk (less dilution of risk; Bednekoff and Lima, 1998b). Greater scanning time with increasing neighbor distance would decrease time available for foraging (Beauchamp, 1998; Elgar, 1989) and consequently decrease the rate at which individuals would find food.

The hypotheses of conspecific monitoring (Coolen et al., 2001; Metz et al., 1991) and predator monitoring (Bertram, 1980; Pöysä, 1987; Lima and Bednekoff, 1999) make opposite predictions as to the direction of gaze. If scanning is mostly for gathering information within the flock (this could be about conspecifics' cues for the location of food or predators), foragers will aim their gaze toward the center of the flock, but if scanning is driven by external information (such as direct detection of predators or distant cues for food), then gaze should be aimed away from the flock. As for the temporal occurrence of scans between individuals,

synchronization may be expected if head raising is driven mostly by external factors (Elcavage and Caraco, 1983; Quenette and Gerard, 1992), perhaps perceived through peripheral vision. Coordination would be the cooperative optimal solution for antipredator vigilance, as full-time coverage could be achieved with minimum vigilance time, but it seems unlikely to be evolutionarily stable or mechanistically realistic (Ward, 1985). Many variants of these extreme options and, indeed, no functional model at all, would lead to random, independent behavior.

METHODS

Study area and species

The experiment took place at the University Farm, Wytham, Oxfordshire, UK, in December 2000 and January 2001 in a permanent-pasture field frequented by wild foraging starlings (Whitehead et al., 1995). We caught and color-ringed 24 adult individuals from the local population. Starting 3 weeks before the experiment, birds were housed in indoor cages ($90 \times 70 \times 60\text{cm}$), under a 12:12 h light:dark light cycle (lights on at 0700 h). Birds were in visual and auditory contact, with two to three birds per enclosure. Water and food (turkey starter crumbs, Orlux pellets, and mealworms *Tenebrio molitor*) were available ad libitum except during experimental trials and the preceding periods of food deprivation (see below).

Experimental design

We used bottomless enclosures, placed in normal foraging grounds for starlings. Starlings respond well to this situation and quickly start foraging in the same general way as when free (Olsson et al., 2002; Tinbergen, 1981; Whitehead et al., 1995). We manipulated a proxy for group density by placing four enclosures, each with one bird, at various distances, and examining the foraging and scanning behavior of either a focal bird (for most dependent variables) or all four birds (for the analysis of temporal distribution of scans). During the experiment, wild starlings approached the experimental setup only on one day. Those trials were disregarded and were repeated the next day.

The four cubical enclosures (edge 0.5 m), completely made of chicken mesh, were placed at three levels of separation: close (enclosures were adjacent), medium (enclosures were separated by 1 m), and far (enclosures were separated by 3 m). This led to neighbor distances within the range of natural starling foraging flocks (Whitehead, 1994). The enclosures were arranged in a square (Figure 1a). A previous study showed that the sole presence of enclosures restraining physical contact between starlings did not significantly alter searching activity (Smith, 2002). We acknowledge that the structure of the mesh may have slightly reduced the ability of starlings to gather visual information. Nevertheless, this potential source of bias is not likely to have affected our results because we used light wire and because the obstacle was equal in all directions and at all neighbor distances.

Eight (4 males and 4 females) out of the 24 birds served as focal individuals. Each of these experienced two replicates at each level of separation. Therefore, we carried out 48 trials (3 levels of separation \times 8 focal birds \times 2 replicates per focal). The remaining 16 nonfocal birds were randomly assigned daily to complete the four-bird flocks in the trials. Flock composition thus varied from test to test to avoid systematic association between partner birds and experimental treatments or conditions. There were four trials per day, but neither the focal nor the nonfocal birds experienced more than one trial in any one day.

We divided the field in which the experiment took place into six sections, and each focal bird experienced at least one session in each section. The field sections were much larger than the experimental plots, and each experimental plot (a site for one trial) was assigned at random and used only once to avoid any possible depletion effects or systematic variations in food density. A previous study (Whitehead, 1994) found no significant differences in prey distribution and prey abundance within the field used in this study. The experimental plots were covered with plastic for approximately 24 h before each trial.

Birds were food deprived from 1700 h the day before being tested. At the time of testing, we transported birds in soft bags and released them in the enclosures. The observer hid into a tent positioned 5 m away from the focal bird enclosure. We used two video cameras throughout (Figure 1a). The behavior of the focal bird was recorded on a video camera placed 5.3 m from the focal bird's position (hereafter, lateral camera), and a second camera placed at sufficient distance to capture all four birds (between 5 m and 12 m from the center of the flock) served for the analysis of temporal distribution of scans (hereafter, wide-angle camera). We used data from this second camera only for scoring whether the four birds had their heads down or otherwise, as explained later. Based on previous experience with the same setup (Smith, 2002; Whitehead et al., 1995), we used 15-min trials, timed from the first ground-probes by the subjects. We did not conduct trials during high winds or rain.

Data collection

To examine issues related to the behavior of the focal birds, we used a fine level of analysis based on the recordings obtained with the lateral camera, but to deal with the temporal distribution of scans between all members of the flock, we used a coarse level based on the recordings obtained with the wide-angle camera of all four enclosures at a time (Figure 1).

Focal bird behavior

While on the ground (Figure 1b), starlings alternate bouts of foraging (the sum of times with head pointing downward, probing, and feeding) with bouts of scanning (time head up). Scanning, however, is defined as also including the time when birds are off the ground (Figure 1b). We use the term scanning as a descriptive operational definition that reflects times unavailable for direct food finding, but the label does not imply a specific function of all behaviors during these intervals.

To assess the allocation of time among different behaviors, we measured the duration of some states and estimated that of others using an event-recording program. We recorded:

Time head-down: this category is defined as excluding probing and handling prey (seconds).

Probing events: poking into the ground with the beak. We considered a probe each time the bird poked in the same or different location.

Intake events: captures, without differentiation of prey size.

We used the numbers of probes and captures to compute probing and intake rates (in probes per unit of total time and captures per unit of total time, respectively) and foraging efficiency (number of prey items captured per probing attempt). Foraging efficiency aims at examining capture success while controlling for searching effort. We recorded the time when the head was in different positions while the

birds were on the ground. The time hanging from the enclosure walls was simply defined as time off the ground.

To explore their world visually, birds move their heads in different directions (Dawkins, 1995, 2002) because eye movements are very limited (Pratt, 1982). In starlings, the presence of a blind area at the back of the head limits complete visual coverage (Martin, 1986); and as a result, the shape of starling's visual fields defines an area including the front and part of the lateral portions of their heads (Figure 1a), where the probability of detecting objects (e.g., conspecifics, predators) is greater than toward the back. Therefore, we classified head positions as either toward or away from conspecifics (Figure 1a) to have a relative measure of whether the target of attention was external or internal to the flock.

To determine head postures based on bill position while individuals were on the ground, we conducted a preliminary calibration study with an additional third camera placed above the enclosure (this top-view camera was removed for the experimental phase). We used a subject-centered system of coordinates with the origin in the center of the bird's head (Figure 1a). We defined north as the perpendicular to the enclosure's diagonal aiming at the other three conspecifics (Figure 1a). Then, we labeled as "toward" all positions between 270 and 90° clockwise, and defined the complement range between 90 and 270° as "away". Videotapes were analyzed by measuring bill positions recorded by the lateral camera (Figure 1a) relative to the standard positions recorded with it and the top-view cameras during the calibration. To minimize bias, we kept the lateral camera in the same angle in relation to the ground and in the same position relative to the focal bird's enclosure throughout the experiment. The focal bird's head was followed continuously, and each time its bill entered the space defined by one of the two categories (toward or away), the observer hit a key that started recording the time spent in that category until the position of the bill switched to the reciprocal category or to another type of behavior (hanging from the enclosure walls or foraging). We did not include bill positions that were difficult to assign to a particular category (0.9% on the average per trial). Taking into account scanning on and off the ground, we obtained total scanning time (seconds), scanning rate (the number of scanning events per minute), and mean length of scanning bouts.

Temporal distribution of scans between subjects

We assessed whether members of a flock raised their heads at the same time (synchronization), at complementary times (coordination), or at random times with respect to each other. This temporal distribution of scans was analyzed on the whole flock with "snapshots" of the videos taken with the wide-angle camera every 20 s, recording the behavior of all four birds at each snapshot at a coarse level (Figure 1b). We obtained 45 snapshots from every 15-min trial. We used two categories: scanning (on the ground with head up and off the ground) and not scanning, which included all the behaviors directly linked to foraging (Figure 1b).

E.F.J. performed all video analyses after extensive self-training using pilot video tapes. At the time of recording the experimental tapes, there was less than 4% difference between two scorings of the same tape.

Statistical analyses

We used a repeated-measures ANOVA to analyze the influence of neighbor distance on the following dependent variables: time head-down, probing rate, intake rate, foraging efficiency, total time spent scanning, scanning rate, scanning bout length, time spent scanning on the ground, and time spent

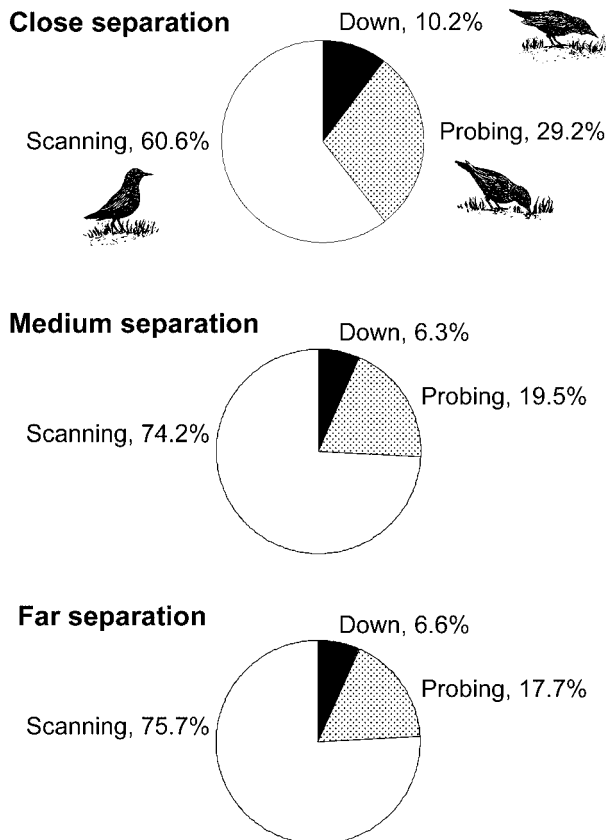


Figure 2

Variation in time budgets of starlings foraging in enclosures at different distances from conspecifics. The proportion of time spent probing was estimated by measuring the average time taken to perform a single event (from random samples within each individual in each treatment), and by multiplying that value by the mean number of probing events per treatment.

hanging from the enclosure walls. The eight randomly chosen focal individuals were tested at each combination of levels of two within-subject factors: neighbor distance (three levels, close, medium, far) and replicate (two levels, first and second). Therefore, each focal bird was tested six times. Both within-subject factors were considered as fixed. Repeated-measures ANOVAs containing factors with more than two levels should meet the sphericity assumption, which requires that the variances (pooled within-groups) and covariances (across subjects) of the repeated measures are homogeneous. We tested for this assumption with the Mauchly sphericity test; in those cases in which the assumption was violated, we reported adjusted results with the Huynh and Feldt correction, which included epsilon factors used to multiply the degrees of freedom of the mean squares for the effect and the error (Myers and Well, 1995). We performed *post hoc* comparisons (Tukey tests) to assess differences between levels of neighbor distance. To assess the simultaneous variations in gaze direction with neighbor distance, we used a MANOVA, with a design similar to the one explained previously, but including two dependent variables: time spent with the head toward and away from conspecifics. In this analysis, we assessed differences in gaze direction at each level of neighbor distance with orthogonal planned comparisons.

The dependent variables describing foraging and scanning performance are interdependent (e.g., foraging efficiency is the ratio of intake rate over probing rate), so that the associated

results cannot be combined for hypothesis testing. In spite of this caveat, we conducted statistical analyses on all of them to achieve quantitative measurements of the effects of neighbor distance along several foraging and scanning dimensions.

Although we randomized the order of treatments during the experiment and avoided days of extreme weather conditions, we assessed the influence of temperature and wind speed on scanning rate, mean scanning bout length, and probing rate and found no significant effects (analyses of covariates from ANCOVA; R^2 varied between 0.01 and 0.06, $F_{2,22}$ varied from 0.17 to 1.41, $p > .25$).

To examine the temporal distribution of scans across subjects, we computed the probability that all four individuals were simultaneously in the head-up state under the assumption of independent or random foraging. This estimate was used as the null hypothesis. To compute the probability of synchronicity under independent behavior, we multiplied the four individual probabilities of each bird being in head-up position in a given snapshot using the fraction of the snapshots in which that individual was head-up, test by test. For each level of neighbor distance (close, medium, far), pairs of one-sided tests were used to test departures toward or against synchronicity, as follows. First, to test if there was less overlapping than random (i.e., a bias toward cooperative coordination), we calculated for each trial the probability that as many or greater occurrences of all four birds being in the head-up position than was actually significant because both predicted and observed values per trial were very small. To overcome this, we combined the results of all the trials, after averaging the results obtained in the two replicates of each focal bird. Under the null hypothesis, the expected p value would be 0.5 (actually slightly greater than 0.5, as the null hypothesis distributions are discrete). We performed a Wilcoxon Signed-Ranks test to determine whether the sample mean of the trials' p values was significantly less than one half.

Second, to test whether there was significant departure from random toward synchronization, we repeated this analysis, making the necessary alterations, for the probability that there were as many or fewer occurrences of all four birds in the head-up state. These two separate analyses were necessary because of the discrete nature of the null hypothesis: the number of birds with the head up at any given time could only be an integer between 0 and 4, but the expected number under the null hypothesis is a real number. Notice that this is the only analysis in which the behavior of the nonfocal animals was included.

RESULTS

Overall time budgets of focal birds varied with neighbor distance (Figure 2). Individuals spent a greater proportion of time scanning (on and off the ground) at the expense of foraging time when neighbors were at medium and far distances than when the enclosures were adjacent. This is examined in greater detail in the following sections.

Foraging performance

Time head down (excluding probing and eating) over the 15-min trials decreased significantly with neighbor distance (close, 78.30 ± 20.74 s; medium, 45.01 ± 16.76 s; far, 44.82 ± 21.80 s; Table 1), with a significant reduction between close and medium distances and between close and far distances. Likewise, probing rate dropped with increasing neighbor distance (probing rate; close, 31.75 ± 9.06 probes/min; medium, 20.31 ± 8.29 probes/min; far, 19.04 ± 6.31 probes/min; Table 1). Probing rate decreased significantly from close

Table 1
The effect of neighbor distance on time spent with the head pointing downward, probing rate, intake rate, and foraging efficiency

	<i>F</i> (ϵ)	df	<i>p</i>	Close vs. medium	Close vs. far	Medium vs. far
Time head down (s)						
Neighbor distance	13.59	2, 14	<.001	0.001	0.001	0.999
Replicate	0.05	1, 7	.838			
Interaction	0.62	2, 14	.551			
Probing rate (probes per min) ^a						
Neighbor distance	10.43 (0.59)	1.8, 8.3	<.01	<0.01	<0.01	0.911
Replicate	0.21 (1)	1, 7	.656			
Interaction	0.65 (1)	2, 14	.536			
Intake rate (prey items per min)						
Neighbor distance	10.22	2, 14	<.01	0.067	0.001	0.133
Replicate	0.08	1, 7	.791			
Interaction	0.03	2, 14	.972			
Foraging efficiency (prey items per probe) ^a						
Neighbor distance	4.86 (1)	2, 14	<.05	0.775	<0.05	0.091
Replicate	0.01 (1)	1, 7	.995			
Interaction	0.01 (0.64)	1.3, 9.1	.947			

Also shown are the *post hoc* comparisons (Tukey tests) between distances.

^a Results adjusted with the Huynh-Feldt correction because of a violation of the sphericity assumption (see text for details).

to medium and to far distances (Table 1). Intake rate declined as the distance between the focal bird and its neighbors increased (Table 1; Figure 3a), with a significant reduction between close and far distances. Finally, foraging efficiency also decreased as the distance between individuals increased (Table 1; Figure 3b); the difference being caused by a drop between close and far conditions. We found no significant effect of the replicates or the interactions between neighbor distance and replicate (Table 1). The decline in intake rate with greater separation was due to the combination of lower foraging effort (decline in probing rate) and lower efficiency (decline in captures per probe).

Scanning quantity

Concomitant with the decline in time devoted to foraging, total scanning time increased with neighbor distance (close, 463.98 ± 73.20 s; medium, 526.92 ± 47.45 s; far, 512.28 ± 62.23 s; Table 2). We analyzed total scanning time statistically for completeness, but this result is naturally not independent of that for foraging time presented earlier. The distance effect was mainly due to a steep rise in total scanning time from close to medium and from close to far distances (Table 2). The main component of this scanning effect was the increase in scanning bout length (close, 5.83 ± 2.07 s; medium, 7.88 ± 1.42 s; far, 6.97 ± 2.52 s; Table 2), particularly from close to medium separation because scanning rate (i.e., number of scanning events per min) did not vary significantly with neighbor distance (close, 5.80 ± 1.12 scans/min; medium, 4.92 ± 0.51 scans/min; far, 5.32 ± 1.20 scans/min; Table 2). No effects of the replicates or significant interactions between factors were found (Table 2).

Scanning: visual orientation

Neighbor distance affected the direction of gaze ($F_{2,14} = 16.07, p < .001$; Figure 4). When conspecifics were close to each other, focal birds spent more of their scanning time with the bill pointing away rather than toward conspecifics ($F_{1,7} = 9.93, p < .02$; Figure 4). This pattern was reversed at medium

separation ($F_{1,7} = 26.23, p < .002$; Figure 4). However, at far distance, individuals spent a similar amount of their scanning time with the bill toward and away from conspecifics ($F_{1,7} = 0.01, p = .96$; Figure 4). Neither the interactions between neighbor distance and replicate ($F_{2,14} = 0.97, p = .403$) nor among gaze direction, neighbor distance, and replicate were significant ($F_{2,14} = 0.5, p = .617$).

Scanning time on the ground (including scanning toward and away from conspecifics) varied significantly with neighbor distance (neighbor distance, $F_{2,14} = 4.31, p < .05$; replicate, $F_{1,7} = 0.07, p = .804$; interaction, $F_{2,14} = 0.97, p = .03$; close, 428.83 ± 18.15 s; medium, 466.72 ± 28.93 s; far, 398.19 ± 26.56 s), the difference being determined mainly by a significant drop from medium to far distances (Tukey test, $p < .05$). The other contrasts were not significant ($p > .05$).

Time spent off the ground (hanging from the enclosure walls) increased significantly as foragers were farther apart (Huynh-Feldt correction, neighbor distance, $F_{1,8,12.3} = 4.53, \epsilon = 0.88, p < .05$; replicate, $F_{1,7} = 0.36, \epsilon = 1, p = .566$; interaction, $F_{1,1,7.9} = 0.07, \epsilon = 0.56, p = .829$; Figure 5), with significant differences between close and far separation (Tukey test, $p < .05$; other contrasts $p > .05$).

Scanning: temporal distribution across individuals

We examined the temporal distribution of scanning to detect any departure from randomness in the degree of synchrony of head-up positions. The *p* values for each trial showing whether there were as many or fewer occurrences of the four birds in the head-up posture are presented in Appendix A. Under the null hypothesis, the combined *p* value should not differ from .5. If the estimated combined *p* value falls significantly below .5, the implication is that scanning is synchronized, whereas if it is > .5, scanning is less synchronous than random, and the birds would be coordinating their scanning.

Close neighbor distance

Following the procedure detailed in the statistical analysis section, the 95% confidence interval obtained for the

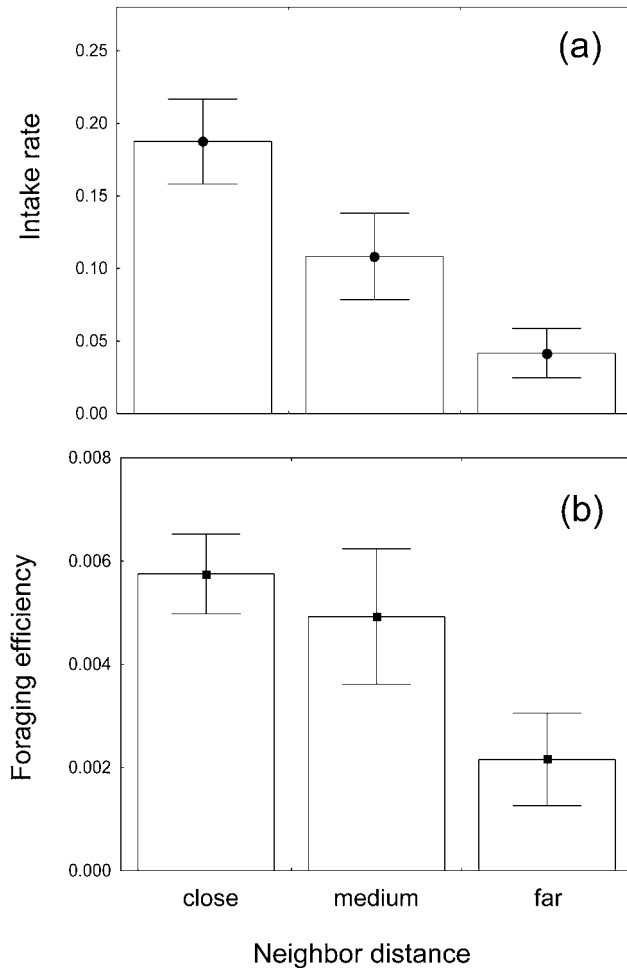


Figure 3
Variation in (a) intake rate (number of prey items captured per min) and (b) foraging efficiency (number of prey items captured per probing attempt) with neighbor distance (close, medium, and far).

probability that all four individuals would have their head up was 0.003–0.151 per trial, clearly rejecting the null hypothesis of independent scanning behavior. Thus, there is strong evidence ($W = 0$, $p = .014$, $n = 8$) that at close distance individuals synchronized their scanning. This is consistent with either some degree of intraflock communication or with external cues making all of the birds look up at the same time. To deal with this latter possibility, we considered a further null model of foraging behavior, in which external cues caused all four individuals to be in the head-up position a proportion q of the time, while $1 - q$ of the time they foraged independently. We fitted the best model of this form for each trial based on least squares differences between actual and expected frequencies of zero to four birds being in the head-up posture (see Appendix B for further details). We compared the theoretical proportion of all heads up versus actual proportion of all heads up after taking into account the best fitting q and found that the synchronized pattern just failed to be significant ($W = 30$, $p = .054$, $n = 8$).

Medium and far neighbor distances

At medium and far separations between enclosures, the 95% confidence intervals for the probabilities that all four birds

Table 2

The effect of neighbor distance on total time spent scanning, mean scanning bout length, and scanning rate

	$F(\epsilon)$	df	p	Close vs. medium	Close vs. far	Medium vs. far
Total time spent scanning (s)						
Neighbor distance	6.8	2, 14	<.01	<0.01	<0.05	0.695
Replicate	0.51	1, 7	.5			
Interaction	1.19	2, 14	.331			
Scanning bout length (s)						
Neighbor distance	4.72	2, 14	<.05	<0.05	0.232	0.395
Replicate	1.82	1, 7	.218			
Interaction	1.48	2, 14	.261			
Scanning rate (scans per min)						
Neighbor distance	2.37	2, 14	.129			
Replicate	3.67	1, 7	.097			
Interaction	0.55	2, 14	.589			

Also shown are the *post hoc* comparisons (Tukey tests) between distances.

being in the head up position were 0.289–0.557 ($W = 9$, $p = .234$, $n = 8$) and 0.285–0.539 ($W = 8$, $p = .183$, $n = 8$), respectively, indicating no significant difference from the random foraging expectation.

DISCUSSION

We studied how foraging behavior of individual starlings responded to the proximity of conspecifics (a proxy for natural flock density) when physical interference was excluded and group size was constant. We found that as neighbor distance varied, a number of foraging parameters varied as well, and so did qualitative and quantitative aspects of what the birds did when they interrupted foraging by raising their heads. The main results were (1) individual searching activity, and food consumption per unit of searching effort increased with density; (2) time spent scanning and scanning bout length decreased with density; (3) scanning orientation (head position during head ups on the ground) was random with respect to the companions' location at large separation between foragers, toward the companions at medium separation, and away from the companions at close distance; (4) time spent off the ground decreased with density; and (5) the temporal pattern of scanning was not significantly different from random at medium and far distances but was significantly biased toward synchronization at close distance.

To elaborate about the functional and ecological significance of these findings, we must relate them to some other mechanisms uncovered by previous work in the same species. Vásquez and Kacelnik (2000) showed in a laboratory experiment that starlings choose to forage close to other starlings even if this entails a loss in feeding rate. However, under more natural conditions (Smith, 2002; this study), intake rate is actually enhanced by being near others. This enhancement is mediated by more than one mechanism. Starlings allocate greater foraging effort when others are near, probably because of a decrease in the time devoted to individual scanning (Beauchamp and Livoreil, 1997; Caraco, 1979; Figure 2). However, we found that they also get more food per unit of

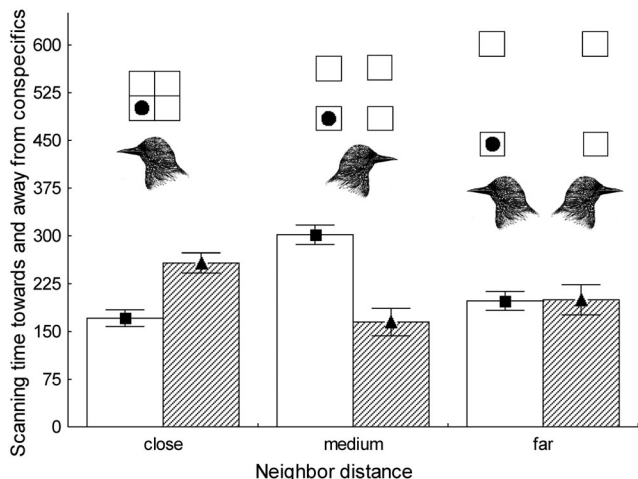


Figure 4 Scanning time (seconds) on the ground in different bill positions: toward (open bars) and away (filled bars) from conspecifics. Also shown is the relative position of the focal bird with respect to conspecifics in each treatment.

effort spent, an observation not reported previously. This may be partly due to using information from conspecifics about patch location (local enhancement; Smith, 2002) and about patch quality (public information; Templeton and Giraldeau, 1995, 1996), but it must also involve some additional reason, because in the present experiment intake rate increased with density even though we did not allow for local enhancement to take place. One possible mechanism may be deeper probing when density increases, as the proximity of flock members may reduce the perceived risk of predation (through dilution; Roberts, 1996), and individuals can modify their prey-searching method as a result. Another alternative explanation is that faster probing at high flock density may be a strategy in which the rate of work is increased above the optimum to preempt greater (perceived) competition (scramble competition; Clark and Mangel, 1986). Real depletion competition was excluded in our experiment because of the physical separation between birds, but it cannot be dismissed as a potentially important factor in natural flocks of starlings.

Foraging benefits may be the functional explanation for the presence of social attraction in starlings, which means that they actively seek the proximity of conspecifics instead of sharing a spot only because of high resource availability. However, the fact that starlings forage more efficiently when others are nearby raises the question of why they forage at a submaximal rate and submaximal profitability per unit of effort when foraging alone (Smith, 2002). This may be related to predation risks, as it has been shown (Powell, 1974) that starlings foraging alone have greater latency for detecting a potential predator than those foraging in groups. Future experimental studies should pursue the integration of mechanistic and functional analyses of social foraging.

As in other studies (Beauchamp and Livoreil, 1997; Pöysä, 1994; Roberts, 1988; Rolando et al., 2001), scanning time increased with neighbor distance. This seems to involve both monitoring other flock members and vigilance for external predators. As individuals get farther apart, getting information from conspecifics is more difficult (Pöysä, 1994), and the advantages of dilution of predation risk may decrease because each individual can be singled out by a predator more easily (Bednekoff and Lima, 1998b). In our experiments, scanning bouts lengthened and interscan intervals decreased (duration of feeding bouts) with neighbor distance. Shorter interscan

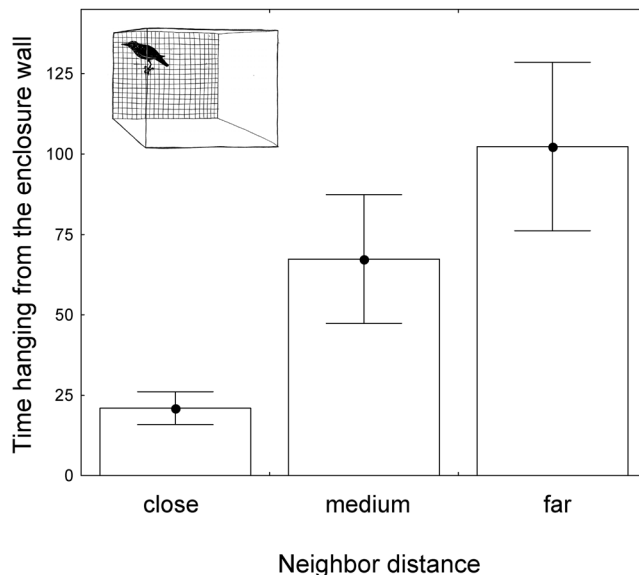


Figure 5 Variation in the amount of time hanging from the enclosure walls (seconds) with neighbor distance (close, medium, and far).

intervals may enhance predator detection (reducing the time available for a predator to make a surprise attack; Hart and Lendrem, 1984), whereas longer scanning bouts may increase the accuracy of assessing far-off objects such as predators or other foragers (Bertram, 1980; Metcalfe, 1984; Roberts, 1988; Pöysä, 1994).

The data on head orientation and time off the ground are also informative in relation to the trade-off between scanning for information internal or external to the flock. In interpreting these data we assume that detection probabilities are lower at the rear of the starling's head (blind area; Martin, 1986). As neighbor distance decreased, focal subjects oriented their heads less toward the inside of the flock and more away from it, while at the same time they spent less time hanging from the enclosure walls and more on the ground. These two results may be expressions of the same social attraction mechanism mentioned above. When other starlings are close by, the visual field of this species (Martin, 1986), allows foragers to monitor companions using peripheral vision. This may let them allocate visual attention to targets outside the flock. However, as distance increased to that of a loose flock (medium separation between enclosures), they gazed more in the direction of other flock members and spent more time at the available elevation. We were not able to measure head orientations while the birds were on the walls, but because scanning time off the ground increased as a function of neighbor distance, part of the goal of wall hanging might be to monitor conspecifics. From a starling's height, seeing another starling across a grazing field becomes progressively difficult with distance. This may explain the joint observation that at the far distance head orientation while standing on the ground was random with respect to the flock, but hanging from the enclosure wall was maximal.

Another thread to consider is the temporal organization of scanning. At high density, our subjects synchronized their head raising, a trait that is somewhat paradoxical in functional terms because it reduces detection coverage per unit of vigilance time. A similar synchronized pattern was found in large flocks of ostriches and greater rheas (Bertram, 1980; Fernández et al., 2003), but these studies did not manipulate neighbor distance nor did they control for group size. In starlings, this

synchronization disappeared and tended toward randomness at greater separations. Synchronization may be also described as copying (Deneubourg and Goss, 1989; Quenette and Gerard, 1992), and since this is more difficult when other flock members are not easy to monitor, it is not surprising that separation caused synchronization to drop.

One tentative explanation for scan copying relates to the mechanisms that initiate head raising. Suppose that one bird raises its head spontaneously after some time probing the ground to scan for danger. A neighbor seeing it through peripheral vision can keep its head down while benefiting from the former's vigilance, leading to coordination (under the collective detection argument). However, suppose instead that the first bird's head raising was not a spontaneous scan but a response to a suspicious stimulus in its peripheral vision. The peripheral vision of its neighbors would let them see the head movement and would favor their own head raising to examine the cause of the former's alarm. This would lead to a wave of copying or synchronization. If foragers cannot discriminate spontaneous versus stimulus-driven head rising, the tendency to synchronization may beat the collective detection safety process at close neighbor distances.

The logic of starling social foraging is far from understood as yet, but our study illustrates the need to resist the temptation of considering any simple hypothesis as strengthened by rough observations such as the changes in rate of scanning as a function of natural or experimental group size. First, group density, rather than size, seems to reflect the mechanisms governing the relationships between social foragers. Second, identifying head raising exclusively with antipredator vigilance is ill advised, as the head-up posture may well be an adaptation for conspecific as much as for predator monitoring. Finally, experimental manipulations that expose the mechanisms that

APPENDIX A

Individual *p*-values for one sided tests to determine whether all four birds in a trial were less likely than expected to have their heads up at the same time given their individual frequencies of being in the head up position together with the assumption of independent foraging (second column) or more likely than expected (third column). Note that the two *p*-values generally sum to greater than 1 because of the discrete nature of the distribution of counts of "all four birds in the head up position."

Neighbor distance	<i>p</i> -value (≤)	<i>p</i> -value (≥)
Close	0.997	0.0075
Close	0.9985	0.004
Close	0.942	0.0925
Close	0.9995	0.001
Close	0.998	0.005
Close	0.8805	0.1725
Close	1	0.001
Close	0.767	0.2935
Medium	0.5195	0.6345
Medium	0.285	0.815
Medium	0.3005	0.821
Medium	0.6975	0.402
Medium	0.417	0.743
Medium	0.16	0.9375
Medium	0.5505	0.6155
Medium	0.4525	0.6655
Far	0.356	0.79
Far	0.3445	1
Far	0.156	0.914
Far	0.417	0.8315
Far	0.469	0.6925
Far	0.285	0.9015
Far	0.7215	0.4825
Far	0.5155	0.7515

control the behavior of group members offer a way to help understand the functional and ecological significance of foraging aggregations.

APPENDIX B

When perusing the group scan feed data, we noticed that there was a strong peak in the head up probability density data for all four birds being in the head-up posture. One hypothesis considered, as an explanation for this observation was that there were external cues driving all four birds to be in the "head up" posture. Although there are numerous possible ways in which external cues could perturb otherwise independent foraging, we considered a single simple null model of the effect of external cues. This model assumed that external cues caused all four individuals to be in the head up position a proportion *q* of the time, whilst 1 - *q* of the time they foraged independently. We fitted the best model of this form for each trial based on least squares differences between actual and expected frequencies of zero to four birds being in the head up posture as follows.

Let *p_i* be the average probability that bird *i* was in the head up position over the *n* measurements taken on a given trial (*n_{head up}*/*n*). Setting *q_{max}* = *n* × min_{*i*} {*p_i*}, we allowed *q* to range from 0 to *q_{max}* in integer steps. At each step, the null probability that *j* birds were in the head up posture was calculated in the following way. For each bird, a new probability of being in a head up posture whilst foraging independently was calculated by the formula (*n_{head up}* - *q*)/(*n* - *q*) and this was then used to calculate the probability density, *P(j)*, of the number of birds in the head up position for the *n* - *q* measurements in which the birds "were not reacting to an external cue." The expected frequency, *E(j, q)* of *j* birds being in the head up position simultaneously was then given by:

$$E(j, q) = \begin{cases} (n - q)P(j) & j \neq 4 \\ (n - q)P(4) + q & j = 4 \end{cases}$$

For each trial the best fitting *q* was deemed to be the *q* for which the sum of the squared deviations of *E(j, q)* from the observed number of cases of the birds being in the head up posture, *M(j)*, was minimized. That is the *q* for which the sum:

$$\sum_{j=0}^4 [E(j, q) - M(j)]^2, \quad 0 \leq q \leq q_{max}$$

is minimized. The best fitting *q* was then subtracted from *M(4)* and the new distribution of observed values disregarding those "caused by external cues" was then tested against the null distribution (*n* - *q*)*P(j)* for "independent" foraging by the procedure outlined in the statistical analysis section.

We thank Dave Stephens, Jeff Stephens, Marlene Zuk, and two anonymous referees for critically reviewing the manuscript, Becs Smith for fruitful discussions about social foraging in starlings and for allowing us to refer to her unpublished work, Michael Morecroft and Michele Taylor (Environmental Change Network) for providing us the weather information, and Gabriela Sincich for illustrations. E.F.J. was funded by Consejo Nacional de Investigaciones Cientificas y Tecnicas and "la Caixa" Foundation. The research was partly supported by grant BBSRC 43/S13483 and by a fellowship from the Institute for Advanced Studies (Berlin) to A.K.

REFERENCES

Beauchamp G, 1998. The effect of group size on mean food intake rate in birds. *Biol Rev* 73:449-472.
 Beauchamp G, Livoreil B, 1997. The effect of group size on vigilance

- and feeding rate in spice finches (*Lonchura punctulata*). *Can J Zool* 75:1526–1531.
- Bednekoff PA, Lima SL, 1998a. Randomness, chaos and confusion in the study of antipredator vigilance. *Trends Ecol Evol* 13:284–287.
- Bednekoff PA, Lima SL, 1998b. Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proc R Soc Lond B* 265:2021–2026.
- Bekoff M, 1995. Vigilance, flock size, and flock geometry: information gathering by western evening grosbeaks (Aves, Fringillidae). *Ethology* 99:150–161.
- Bekoff M, 1996. Cognitive ethology, vigilance, information gathering, and representation: who might know what and why? *Behav Process* 35:225–237.
- Bertram BCR, 1980. Vigilance and group size in ostriches. *Anim Behav* 28:278–286.
- Caraco T, 1979. Time budgeting and group size: a test of theory. *Ecology* 60:618–627.
- Catterall, CP, Elgar MA, Kikkawa J, 1992. Vigilance does not covary with group size in an island population of silvereyes (*Zosterops lateralis*). *Behav Ecol* 3:207–210.
- Clark CW, Mangel M, 1986. The evolutionary advantages of group foraging. *Theor Popul Biol* 3:45–75.
- Coolen I, Giraldeau L-A, Lavoie M, 2001. Head position as an indicator of producer and scrounger tactics in a ground feeding bird. *Anim Behav* 61:895–903.
- Dawkins MS, 1995. How do hens view other hens? The use of lateral and binocular visual fields in social recognition. *Behaviour* 132:591–606.
- Dawkins MS, 2002. What are birds looking at? Head movements and eye use in chickens. *Anim Behav* 63:991–998.
- Deneubourg JL, Goss S, 1989. Collective patterns and decision-making. *Ethol Ecol Evol* 1:295–311.
- Elcavage P, Caraco T, 1983. Vigilance behaviour in House Sparrow flocks. *Anim Behav* 31:303–312.
- Elgar MA, 1989. Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biol Rev* 64:13–33.
- Elgar MA, Burren PJ, Posen M, 1984. Vigilance and perception of flock size in foraging house sparrows (*Passer domesticus* L.). *Behaviour* 90:215–223.
- Erichsen JT, 1979. How birds look at objects (PhD thesis). Oxford: University of Oxford.
- Fernández GJ, Capurro AF, Reboreda JC, 2003. Vigilance and group size in greater rheas: individual and collective detection effects. *Ethology* 109:413–425.
- Fretwell SD, Lucas JHJ, 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor* 19:16–36.
- Giraldeau L-A, Caraco T, 2000. Social foraging theory. Princeton, New Jersey: Princeton University Press.
- Giraldeau L-A, Lefebvre L, 1986. Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Anim Behav* 34:797–803.
- Goss-Custard JD, Cayford JT, Lea SG, 1999. Vigilance during food handling by Oystercatchers *Haematopus ostralegus* reduces the chances of losing prey to kleptoparasites. *Ibis* 141:368–376.
- Green PA, 1998. Head orientation and trajectory of locomotion during jumping and walking in domestic chicks. *Brain Behav Evol* 51:48–58.
- Hart A, Lendrem DW, 1984. Vigilance and scanning patterns in birds. *Anim Behav* 32:1216–1224.
- Kacelnik A, Krebs JR, Bernstein C, 1992. The ideal free distribution and predator-prey populations. *Trends Ecol Evol* 7:50–5.
- Krause J, Ruxton GD, 2002. Living in groups. Oxford: Oxford University Press.
- Land MF, 1999. The roles of head movement in the search and capture strategy of a tern (Aves, Laridae). *J Comp Physiol A* 184:265–272.
- Lima SL, Bednekoff PA, 1999. Back to the basis of antipredatory vigilance: can nonvigilant animals detect attack? *Anim Behav* 58:537–543.
- Lima SL, Zollner PA, 1996. Anti-predatory vigilance and the limits of collective detection: visual and spatial separation between foragers. *Behav Ecol Sociobiol* 38:355–363.
- Martin FR, Katzir G, 1999. Visual fields in short-toed eagles, *Circus gallicus* (Accipitridae), and the function of binocularity in birds. *Brain Behav Evol* 53:55–66.
- Martin GR, 1986. The eye of a passeriform bird, the European Starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics. *J Comp Physiol A* 159:545–557.
- McNamara JM, Houston AI, 1992. Evolutionary stable levels of vigilance as a function of group size. *Anim Behav* 43:641–658.
- Metcalf NB, 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? *Anim Behav* 32:981–985.
- Metz KJ, Prior KA, Mallory M, 1991. Do cattle egrets gain information from conspecifics when foraging? *Oecologia* 86:57–61.
- Myers JL, Well AD, 1995. Research design and statistical analysis. Rahway, New Jersey: Lawrence Erlbaum Associates.
- Olsson O, Bruun M, Smith HG, 2002. Starling foraging success in relation to agricultural land-use. *Ecography* 25:363–372.
- Powell GVN, 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim Behav* 22:501–505.
- Pöysä H, 1987. Feeding-vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. *Behaviour* 103:108–122.
- Pöysä H, 1994. Group foraging, distance to cover and vigilance in the teal, *Anas crecca*. *Anim Behav* 48:921–928.
- Pratt DW, 1982. Saccadic eye movements are coordinated with head movements in walking chickens. *J Exp Biol* 97:217–223.
- Quenette P-Y, Gerard J-F, 1992. From individual to collective vigilance in wild boar (*Sus scrofa*). *Can J Zool* 70:1632–1635.
- Roberts SC, 1988. Social influences on vigilance in rabbits. *Anim Behav* 36:905–913.
- Roberts G, 1996. Why individual vigilance declines as group size increases. *Anim Behav* 51:1077–1086.
- Rolando A, Caldoni R, De-Sanctis A, Laiolo P, 2001. Vigilance and neighbor distance in foraging flocks of red-billed choughs, *Pyrrhocorax pyrrhocorax*. *J Zool* 253:225–232.
- Smith JW, Benkman CW, Coffey K, 1999. The use and misuse of public information by foraging red crossbills. *Behav Ecol* 10:54–62.
- Smith R, 2002. Together for better or worse: why starlings forage in groups (PhD thesis). Oxford: University of Oxford.
- Stillman RA, Caldow RWG, Goss-Custard JD, Alexander MJ, 2000. Individual variation in intake rate: the relative importance of foraging efficiency and dominance. *J Anim Ecol* 69:484–493.
- Sutherland WJ, 1996. From individual behaviour to population ecology. Oxford: Oxford University Press.
- Templeton JJ, Giraldeau L-A, 1995. Patch assessment in foraging flocks of European starlings—evidence for the use of public information. *Behav Ecol* 6:65–72.
- Templeton JJ, Giraldeau L-A, 1996. Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. *Behav Ecol Sociobiol* 38:105–114.
- Tinbergen JM, 1981. Foraging decisions in starlings (*Sturnus vulgaris* L.). *Ardea* 69:1–67.
- Tregenza T, 1995. Building on the ideal free distribution. *Adv Ecol Res* 26:253–307.
- Treves A, 2000. Theory and method in studies of vigilance and aggregation. *Anim Behav* 60:711–722.
- Vásquez RA, Kacelnik A, 2000. Foraging rate versus sociality in the starling *Sturnus vulgaris*. *Proc R Soc Lond B* 267:157–164.
- Valone TJ, 1989. Group foraging, public information, and patch estimation. *Oikos* 56:357–363.
- Valone TJ, Wheelbarger AJ, 1998. The effect of heterospecifics on the group-size effect in white-crowned sparrows (*Zonotrichia leucophrys*). *Bird Behav* 12:85–90.
- Ward P, 1985. Why birds in flocks do not coordinate their vigilance periods. *J Theor Biol* 114:383–385.
- Whitehead SC, 1994. Foraging behaviour and habitat use in the European starling, *Sturnus vulgaris*, in an agricultural environment (PhD thesis). Oxford: University of Oxford.
- Whitehead SC, Wright J, Cotton PA, 1995. Winter field use by the European starling *Sturnus vulgaris*: habitat preferences and the availability of prey. *J Avian Biol* 26:193–202.