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Increasing the costs of conspecific scanning in socially foraging starlings affects vigilance and foraging behaviour

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Social foragers receive and use information both about companions (social information) and about events external to the group, such as presence of potential predators. Scanning behaviour is often incorporated in theoretical models using simplifying assumptions in relation to the trade-off in information gathering between body postures (head-up versus head-down); however, some avian visual systems may allow individuals to scan in both body postures. We studied these issues experimentally, using starlings, *Sturnus vulgaris*, foraging in enclosures on natural fields. We varied the availability of information from conspecifics by placing visual barriers that blocked the view when the subjects were in head-down position and by manipulating the distance between group members. We found that as social information was reduced, starlings spent more time scanning (on and off the ground) and head-up scanning was mainly oriented towards conspecifics. The visual-obstruction effects imply that some information about conspecifics is normally gathered while starlings are foraging head-down. Neighbour distance and visual obstruction negatively affected food-searching rates and intake rates in two ways: (1) the effect of obstruction was mediated mostly through time competition between foraging and scanning on the ground, and (2) the effect of distance was due to a reduction in the rate of prey returns per searching effort while the birds were head-down. We conclude that the head-up posture is only one component of scanning, that the effects of head-down scanning should also be considered in species with ample visual fields, and that scanning in starlings is strongly connected to monitoring other flock members.

Scanning has attracted the attention of investigators dealing with social foraging in birds perhaps because it is an easily identifiable behaviour (raising the head, often from ground-directed foraging, to an upright position) that seems to have clear costs and benefits (Roberts 1996; Treves 2000; Beauchamp 2003). This is only true, however, under the assumption that the observable behaviour (head-up) is linked to its potential informational consequences. Here we focus on the connection between body posture and information gathering by examining the form of the behaviour and its response to some elements of the social environment. Because most scanning studies have analysed how the risk of predation affects scanning behaviour (Lima 1995; Bednekoff & Lima 1998a), whereas relatively little empirical attention has been devoted to the role of conspecific scanning (Bekoff 1996; Treves 2000; but see Coolen et al. 2001), we concentrate on the latter effect.

Animals may monitor conspecifics while foraging because it is advantageous to learn about predators through their vigilance, to gather information about the location of food items (local enhancement), to obtain information about patch quality (public information), to detect opportunities for stealing food from them (scrounging), and to evade aggression or kleptoparasitism (reviewed in Krause & Ruxton 2002). The behaviour that optimizes gathering information about conspecifics is unlikely to be the same as that which optimizes immediate food finding. Some theoretical models assume that conspecific scanning is costly, because individuals divert time that could be spent foraging (head-down) to scan the vigilance behaviour of neighbours (head-up; mutual exclusivity between foraging and vigilance; Ward 1985; Bednekoff & Lima 1998a). Furthermore, some social foraging models treat scanning not in the context of vigilance, but, instead, in the context of different foraging strategies that are also mutually exclusive (e.g. producer/scrounger, Giraldeau & Caraco

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2000). In this case, individuals monitor their neighbours to learn about the opportunities they offer for parasitizing their food findings, but the conflict is still there: animals engaged in gathering information about food items on the substrate cannot simultaneously obtain information from conspecifics about their foraging success.

Interpretations of scanning using the operational definition of 'head-up' are, however, complicated in birds because of their complex visual systems (Fernández-Juricic et al. 2004). For instance, species with wide visual coverage may be capable of scanning for predators not only when head-up but also when head-down (Lima & Bednekoff 1999; Guillemain et al. 2001). Head-down information gathering can reduce the conflict between scanning and foraging activities and questions the operational definition on which most empirical research is based. Furthermore, the configuration of visual systems interacts with ecological conditions to modify the amount of visual information available from both conspecifics and the surroundings, so that not only the nature of visual systems, but the actual situation of the forager in relation to the potential scanning targets must be included in the picture.

The purpose of this study was to investigate experimentally various aspects of conspecific scanning in the social foraging behaviour of the starling, *Sturnus vulgaris*. The starling is a species with relatively ample visual fields that are likely to allow for scanning in both head-up and head-down positions (Martin 1986). We manipulated the conditions for conspecific scanning by varying simultaneously the degree of visual obstruction in the direction of conspecifics (no obstruction and head-down obstruction) and the distance at which the conspecifics were situated (0-m and 3-m separation). We assessed variations in scanning and foraging strategies as a response to varying conditions for information flow while the birds were feeding on a natural substrate. Previous evidence suggests that group foraging in starlings affects different parameters (e.g. predator detection distance, Powell 1974; searching effort, Templeton & Giraldeau 1995a, 1996; foraging success, Smith 2002; propensity to join groups, Vásquez & Kacelnik 2000), but it is still unclear when and how visual information is gathered in this species, and whether conspecifics could be the focus of scanning attention.

In a constant foraging setting, if birds do indeed gather some information on their neighbours when their heads are down and they behave to avoid the complete loss of this information (Harkin et al. 2000), when the view from the head-down position is modified by a low-level obstruction, they would be forced to spend longer periods with their heads up and with their gaze towards conspecifics to minimize the loss of this information. Moreover, if a significant function of scanning is to observe these neighbours, when they are moved further away, we should also expect changes in the time spent with the head-up (Pöysä 1994; Proctor et al. 2003) and in gaze orientation. Alternatively, if social information is too costly to obtain, foragers may forego it (Templeton & Giraldeau 1995b, 1996) and rely on their own ability to detect potential predators or assess patch quality. This would still affect scanning budgets (e.g. greater scanning time due to increasing risk of predation), but gaze orientation would not vary with increasing obstruction or neighbour distance. Finally, if individuals have less time available for foraging as social information becomes increasingly costly, both food-searching activity and the rate of food intake would be negatively affected.

METHODS

General Procedures

We conducted the experiment at the University Farm (Wytham, Oxfordshire) between January and February 2001 in a permanent pasture field frequented by wild foraging starlings (Whitehead et al. 1995).

We caught and colour-ringed 24 adult starlings from the local population. Five weeks before, and during, the experiment, birds were housed in indoor cages ($0.9 \times 0.7 \times 0.6$ m), under a 12:12 h light:dark cycle (lights on at 0700 hours). Birds were in visual and auditory contact, with two to three birds per cage. Water and food (turkey starter crumbs; Orlux pellets, Orlux, Roeselare, Belgium; and mealworms, *Tenebrio molitor*) were available ad libitum except during experimental trials and the preceding periods of food deprivation. Birds remained in captivity for 1 year and were released at their original capture sites.

We used bottomless enclosures, placed in normal foraging grounds for starlings. Starlings responded well to this situation and quickly started foraging in the same general way as when free (see also Whitehead et al. 1995; Olsson et al. 2002). A previous study showed that the presence of enclosures restraining physical contact between starlings did not noticeably perturb searching activity (Smith 2002).

Four cubic enclosures (edge: 0.5 m), completely constructed of light chicken mesh, were placed at two levels of separation (0 m and 3 m). This led to interstarling distances within the range observed in natural starling foraging flocks (Whitehead 1994). The enclosures were arranged in a square with one bird in each (Fig. 1a). One of the individuals was the focal bird (Fig. 1a).

We also varied the degree of visual contact between the focal bird and its neighbours with two manipulations (Fig. 1b): no-occlusion and head-down occlusion. In the latter, the two sides of the focal enclosure that faced conspecifics were blocked with wooden partitions with a height of 8 cm to impede head-down scanning only in the direction of the conspecifics. The other two sides were left unaltered, because we were particularly interested in the effects of losing social information (see also Beauchamp 2002). Other authors often opted for blocking subjects' view on all directions (e.g. Templeton & Giraldeau 1995b; Lima & Zollner 1996; Arenz & Leger 1997, 1999; Lima & Bednekoff 1999; but see Harkin et al. 2000). To choose the height of the partitions, we filmed birds while they were foraging in the enclosures with different partition levels, and determined the heights that blocked vision in head-down but not head-up postures, considering individual differences in size. We initially designed the

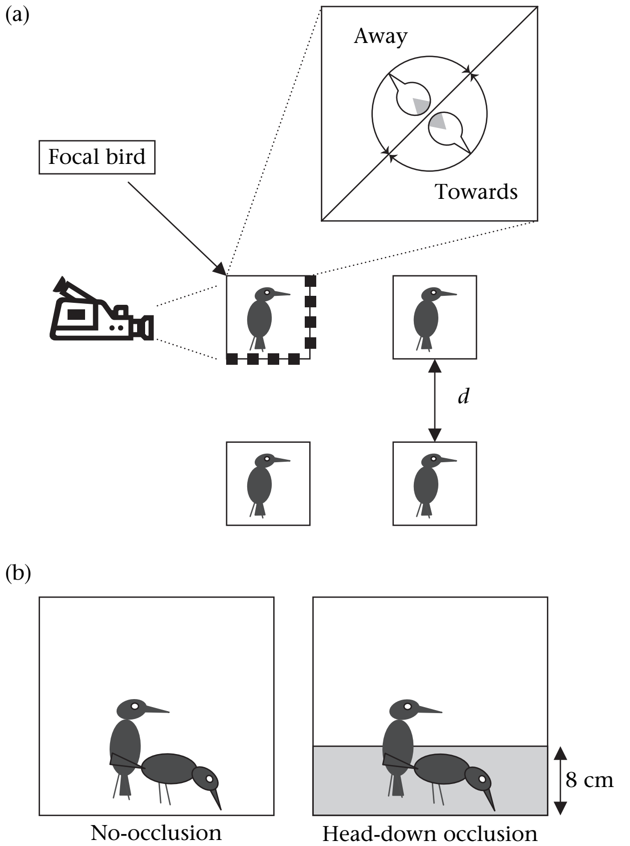

Figure 1. (a) Experimental set-up showing the location of the four bottomless enclosures placed at different distances ($d = 0$ and 3 m), the relative position of the camera recording the behaviour of the focal bird, and the placement of the partitions. Also shown are the positions of the head (towards and away from conspecifics) and the size of the blind area of starlings at the rear of their heads (based on Martin 1986). (b) Levels of conspecific visual obstruction from one of the sides facing neighbours: no-occlusion (without partition) and head-down occlusion (with partition 8 cm tall).

experiment to include two control treatments where conspecifics were absent (three empty cages and one cage with the focal bird) at 0-m and 3-m separation between enclosures. The purpose of including these controls was to ascertain whether any observed behavioural response to the partitions was due to the presence of conspecifics or to the other birds' enclosures per se. However, we interrupted these controls for ethical reasons (see Results).

Eight (four males and four females) of the 24 birds served as focal individuals. A factorial combination of the two levels of visual obstruction and separation was performed (no obstruction × 0 m; no obstruction × 3 m; head-down obstruction × 0 m; head-down obstruction × 3 m). Each focal bird experienced two replicates at each combination of separation and visual obstruction. Hence, we conducted 64 trials (four combinations of visual obstruction and separation × eight focal birds × two replicates per focal bird). 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. There were four trials per day, but neither the focal nor the nonfocal birds experienced more than one trial in any 1 day.

The 14-ha field in which the experiment took place was divided 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 (0.5 × 0.5 m), 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. Previous studies found that prey abundance does not vary significantly between soil cores (80-mm diameter and 150-mm depth) within the field used in this study (Whitehead 1994), and that the natural distribution of prey consumed by starlings (leatherjackets, *Tipula paludosa*, and earthworms, *Lumbricus terrestris*) is patchy (Smith 2002). The experimental plots were covered with mesh wire for approximately 24 h before each trial.

Birds were food deprived from 1700 hours until testing began on the following day. At the time of testing, they were transported in soft bags and released in the enclosures. The observer hid in a tent positioned 5 m from the focal bird enclosure. The behaviour of the focal bird was recorded on a video camera placed 5.3 m from the bird (hereafter, lateral camera). Based on previous experience with a similar set-up (Smith 2002), we used 15-min trials, which started when the subjects began probing. The mean (±SD) latency to commence probing was 87 ± 25 s, but this had no effect on our results given that the trials were timed from the end of this latency. Trial duration was short enough to keep the birds foraging actively (namely, no satiation effects were observed) and to avoid substantial changes in food abundance within trials (Smith 2002). Trials were not performed in high winds or rain.

Behavioural Recordings

The behaviour of focal birds was recorded from videotapes using an event-recording program (JWatcher 0.9; Blumstein et al. 2000). We based our analysis on the following exhaustive categorization of behaviour. A starling could be, at a given moment, in either of two major states: 'on the ground' or 'off the ground' (hanging from the enclosure wall). While on the ground, it could be head-down or head-up, depending on whether its head was below or above its shoulder. The jerky nature of the birds' movement meant that there was no problem in categorizing behaviour between these two categories, with no provision for the head being at shoulder level. While the birds were on the ground with their heads up, their behaviour was categorized in two mutually exclusive categories regarding the direction of their gaze, as explained later. We recorded the number and duration of such scanning events while the bird had its feet on the ground, and later calculated the time spent scanning on the ground (s) and scanning rate on the ground (the number of scanning events per min on the ground). Time spent scanning off the ground (s) was also recorded. When defining our dependent variables for birds on the ground, we followed the usual convention and used the term 'scanning', based on the descriptive operational definition, to describe behaviour when a bird was in the head-up position. However, we also classified times off the ground as scanning because, in this way, the label reflected all the times that were definitely not available for direct food finding. The actual information flow during these different behaviours (including head-down, when some information may be gathered, as we discuss below) was not known and it was in fact the target of our enquiry.

Birds' visual fields often include two areas of high concentrations of photoreceptors (foveae) in each eye, enabling lateral and frontal visual attention (Martin & Katzir 1999). Head movements help in positioning the image of an attention target in either fovea because eye movements in birds are very limited (Pratt 1982; Wallman & Letelier 1993). With this limitation, in starlings, head positioning does give an indication of the target of attention, because the presence of a blind area at the back of the head limits complete visual coverage (Martin 1986). Thus, a starling's visual field includes the area to the front and alongside part of the lateral portions of its head (Fig. 1a) where the probability of detecting objects (e.g. conspecifics, predators) is greater than it is towards the back of the head. Several studies have used head orientation as an adequate estimator of gaze (e.g. Land 1999; Franklin & Lima 2001; Dawkins 2002). Therefore, to have a relative measure of whether the target of attention was external or internal to the flock, we classified head positions as either towards or away from conspecifics (Fig. 1a).

To determine head positions based on bill positions using videotapes, we conducted a preliminary calibration study with an additional camera placed above the enclosure (this top-view camera was removed for the experiment). We used a subject-centred system of coordinates with the origin in the centre of the bird's head (Fig. 1a). We defined north using the diagonal of the square formed by the four enclosures that passed through the focal bird's enclosure. On this diagonal, 0° indicated the direction of the conspecifics. Regardless of the position of the focal bird within its enclosure, it was classified as facing towards the flock if its bill fell within the range of 270–90°, and away from the flock if it fell in the remaining directions (see Fig. 1a). Videotapes recorded by the lateral camera (Fig. 1a) were analysed by measuring bill positions relative to the standard positions recorded during the calibration. To minimize bias, we kept the lateral camera at 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 (towards 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 behaviour (head-down or hanging from the enclosure walls). We did not include bill positions that were difficult to assign to a particular category (on average, 1.7% of the time per trial). Because, according to our definitions, time scanning away and towards conspecifics added up to total scanning time while on the ground, we only present results for the scanning towards conspecifics.

While the bird was head-down, we recorded food-searching events (poking into the ground, whether it was in a new site or in the site of a previous poke) and intake events (without considering prey sizes). The numbers of searching and capture events were used to compute food-searching rate and intake rate. To tease apart the energetic consequences of both visual obstruction and neighbour distance, we examined these foraging-dependent variables as a function of two components of trial time. We first present the results as a function of total time on the ground, namely excluding the time the birds spent obviously not foraging (e.g. hanging from the enclosure walls), because this overall effect is what may be energetically most relevant. However, this analysis hides the mechanisms by which some of these effects occur. We then examined foraging activity during the time the birds were seeking food with their heads down, removing the time off the ground as before but also removing the time on the ground head-up.

E.F.J. performed all video analyses after extensive self-training in analysing pilot videotapes. At the time of recording the experimental tapes, the difference between two scorings of the same tape for each of the main variables was less than 5%.

In a preliminary study, we found no effect of ambient temperature and wind speed on time spent scanning, scanning rate, searching rate and intake rate for starlings foraging in similar experimental conditions. During the experiment, wild starlings never approached the experimental set-up.

Statistical Analyses

The partial results of the two control treatments (with empty cages) were not included in the statistical analyses because of the radically different behaviour observed under these conditions (see Results). We used a repeated measures ANOVA to analyse the influence of visual obstruction and neighbour distance on the following dependent variables: time spent scanning on and off the ground, scanning rate, percentage of scanning time with the head pointing towards conspecifics, food-searching rate (while on the ground and while head-down) and intake rate (while on the ground and while head-down). The eight randomly chosen focal individuals were tested at each combination of levels of three within-subject factors: visual obstruction (two levels: without occlusion, head-down occlusion), neighbour distance (two levels: 0 m, 3 m) and replicate (two levels: first and second). Therefore, each focal bird was tested eight times. All within-subject factors were entered as fixed effects (Myers & Well 1995).

RESULTS

The behaviour of starlings in the control treatment (three empty enclosures and one enclosure with the focal bird) was entirely different from that observed in the other experimental situations. The birds spent most of the trial time very agitated, scanning ($\bar{X}\pm$SE: 0 m: 839.12 ± 23.89 s; 3 m: 849.83 ± 15.01.26 s) and flying within the enclosures (0 m: 8.36 ± 1.04 events/min; 3 m: 9.83 ± 0.77 events/min). Movements were so fast that head positions could not be determined. Flights started and ended on the ground or involved very frequent movements between enclosure sides. These types of flights did not occur when starlings foraged near other starlings. Foraging activity was almost nil and restricted to a few probes (0 m: 0.04 ± 0.02 events/min; 3 m: 0.07 ± 0.06 events/min). We considered these behavioural patterns to be indicators of stress, and after six samples, we decided to interrupt this treatment due to a concern for the welfare of the animals and the lack of significance of any potential data collected under these circumstances. Consequently, we only used treatments where focals were foraging in groups.

The degree of visual obstruction and neighbours' distance caused significant changes in the amount and form of scanning. Scanning time on the ground increased from slightly greater than 50% of the total time of a trial (900 s) with no-occlusion to approximately 70% of the total time for the head-down occlusion (Table 1, Fig. 2). However, neighbours' distance did not noticeably affect scanning on the ground (Table 1, Fig. 2). On the other hand, time spent scanning off the ground (hanging from the enclosure walls) was higher when neighbours were positioned at 3 m than at 0 m, but did not vary with the degree of visual occlusion (Table 1, Fig. 2).

Scanning rate on the ground was higher under head-down occlusion conditions compared with no-occlusion conditions (Table 1, Fig. 3a). However, neighbour distance did not exert a significant influence on scanning rate. Both visual obstruction and neighbour distance affected the direction of gaze, but their interaction was not significant (Table 1). Starlings spent a greater percentage of their scanning time on the ground with the head towards conspecifics with head-down visual occlusion and with increasing neighbour distance (Table 1, Fig. 3b).

Table 1. The effects of conspecific visual obstruction (VO) and neighbour distance (ND) on time scanning on the ground, time scanning off the ground (hanging from the enclosure walls), scanning rate on the ground, and percentage of total scanning time with the head towards conspecifics

	F	df	*P*
Time scanning on the ground			
Visual obstruction	48.32	1, 7	<**0.001**
Neighbour distance	1.01	1, 7	0.350
Replicate	0.02	1, 7	0.988
VO∗ND	0.44	1, 7	0.529
Time scanning off the ground (log-transformed)			
Visual obstruction	0.70	1, 7	0.429
Neighbour distance	12.41	1, 7	**0.009**
Replicate	0.27	1, 7	0.615
VO∗ND	0.21	1, 7	0.660
Scanning rate on the ground			
Visual obstruction	6.29	1, 7	**0.041**
Neighbour distance	0.66	1, 7	0.442
Replicate	0.06	1, 7	0.816
VO∗ND	0.537	1, 7	0.487
Percentage of total scanning time with the head towards conspecifics			
Visual obstruction	7.73	1, 7	**0.027**
Neighbour distance	21.11	1, 7	**0.003**
Replicate	0.04	1, 7	0.851
VO∗ND	1.86	1, 7	0.215

Significant results are marked in bold.

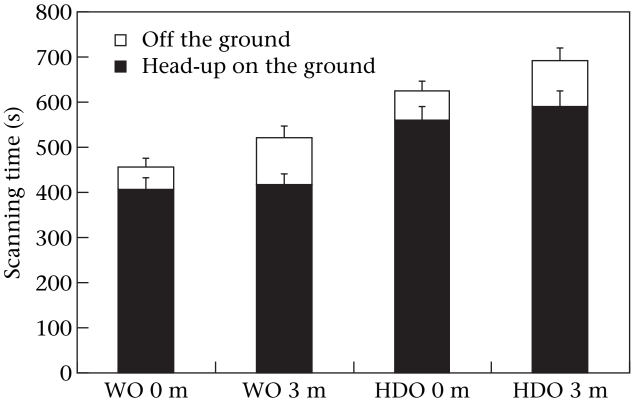

Figure 2. Effects of conspecific visual occlusion (WO: without occlusion; HDO: head-down occlusion) and neighbour distance (0 m and 3 m) on scanning time on the ground and off the ground. Figure shows means + SE (*N* = 8).

Increasing the costs of conspecific scanning also affected foraging behaviour in different ways (Fig. 4a–d). After excluding the time the birds spent off the ground, intake rate per unit of time on the ground decreased when the degree of visual obstruction towards conspecifics increased and with increasing separation between foragers (Table 2, Fig. 4a). Food-searching rate per unit of time on the ground decreased in head-down occlusion in relation to no-occlusion conditions (Fig. 4b), thus explaining part of the intake reduction. However although distance had an effect on intake, it had no noticeable effect on food-searching behaviour (Table 2, Fig. 4b). This decrease in food-searching rate is probably due to the time spent scanning head-up. When time scanning head-up was excluded and only head-down time was considered, we found no significant effect of visual obstruction or neighbour distance on food-searching rate (Table 2, Fig. 4d). On the other hand, even after the effect of scanning head-up was removed, there was an effect on food intake: intake rate per unit of time head-down decreased with neighbour distance, but not with visual obstruction (Table 2, Fig. 4c). We did not find any effect of replicate or interaction between visual obstruction and neighbour distance on any of the response variables studied.

DISCUSSION

When visual information from conspecifics was limited, birds compensated by increasing scanning time, changing scanning location from on to off the ground, and gazing towards conspecifics a greater proportion of the scanning time. Moreover, a reduction in time available to foraging

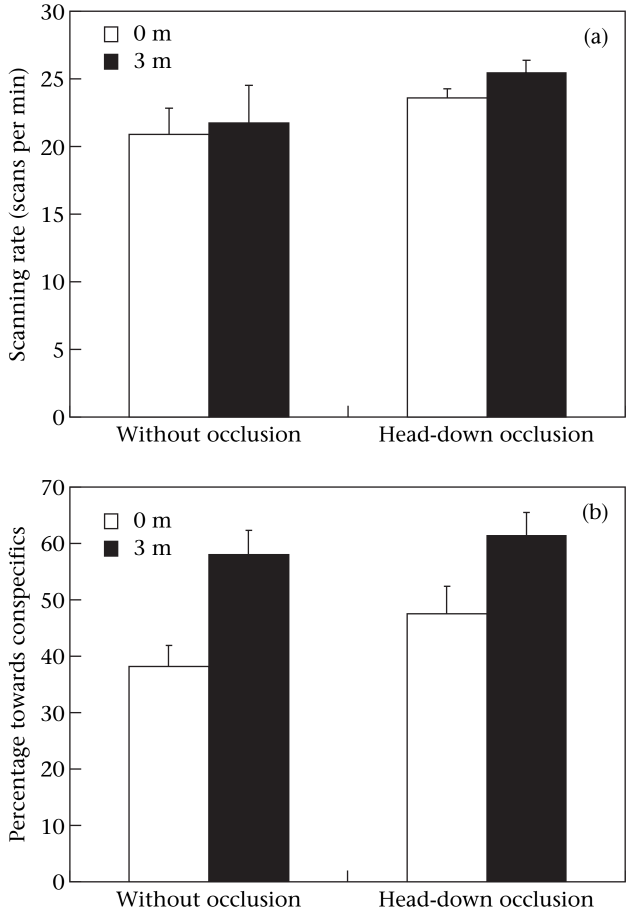

Figure 3. Effects of conspecific visual occlusion (without occlusion and head-down occlusion) and neighbour distance (0 m and 3 m) on (a) scanning rate on the ground and (b) percentage of total scanning time on the ground spent with the head pointing towards conspecifics (see text for details). Figure shows means + SE ($N = 8$).

reduced foraging success. This suggests that various behavioural mechanisms govern the interactions between consumers according to the availability of social information.

Previous studies suggested that the lack of a group-size effect (e.g. reduction in vigilance with flock size) could be associated with the increase in conspecific scanning in larger groups (Catterall et al. 1992) or in monitoring the presence of aggressive dominant heterospecifics in multispecies flocks (Valone & Wheelbarger 1998). Moreover, evening grosbeaks, *Coccothraustes vespertinus*, foraging in linear (versus circular) arrays spend more time scanning, change head and body positions more often, and show less coordination in head movements, suggesting that individuals attempt to monitor conspecific behaviour in conditions where that information is difficult to obtain (Bekoff 1995). The increase in scanning that we observed when head-down vision was blocked from conspecifics could, on first examination, be interpreted to have been caused by individuals responding to the enclosures as much as to conspecifics due to obstruction effects. However, this is unlikely because we interrupted the control experiments with empty enclosures precisely because the effect of no conspecifics in the nonfocal cages was too dramatic and seemed to provoke distress. When conspecifics were present in the enclosures, focal individuals behaved qualitatively as they do in normal social situations.

When head-down vision was blocked, starlings increased both scanning time and scanning rate. An increase in head-up scanning with head-down occlusion in all directions has been shown experimentally in dark-eyed juncos, *Junco hyemalis* (Lima & Bednekoff 1999), the teal *Anas crecca* and the shoveler *Anas clypeata* (Guillemain et al. 2001). However, our study is the first to show that the effect is elicited by blocking exclusively the view of other flock members. Furthermore, scans became more oriented towards conspecifics with obstruction than when no obstruction was present, perhaps as a compensation for the loss of information that otherwise would have been gathered in the head-down posture. This suggests that even while their heads are down, starlings seem to pay attention to conspecifics. Although head-down scanning may not result in as much information as that in head-up postures (Lima & Bednekoff 1999), it may be enough to detect changes in the position and motion of flockmates, and to organize short-term decisions such as whether to keep foraging or to raise the head to increase the quality/quantity of information. This finding challenges the validity of the assumption of mutually exclusive vigilance and feeding behaviours on which most vigilance models are based (e.g. Ward 1985), and the assumption of some social foraging models, by which individuals cannot search for food and monitor the behaviour of conspecifics at the same time (Giraldeau & Beauchamp 1999; but see Vickery et al. 1991).

Increasing neighbour distance intensified the effects of visual obstruction by increasing time spent scanning off the ground as well as the percentage of scanning time on the ground towards conspecifics. Greater separation between foragers may pose higher predation risks per unit of predator attack, because individuals could be singled out by predators more easily (Bednekoff & Lima 1998b). Our animals spent the time off the ground in the only elevated position they could achieve in the enclosures (i.e. hanging from the enclosures themselves). We believe that, at least in part, this is another expression of greater scanning effort, where starlings may be gathering information from conspecifics relative to predation risk (e.g. presence of a potential predator in the surroundings). Information flowing from conspecifics at eye level is increasingly difficult to obtain at greater neighbour distances across a grazing field (see also Pöysä 1994; Lima & Zollner 1996; Rolando et al. 2001). Therefore, increasing scanning with distance may somewhat compensate for the loss of information due to separation (Roberts 1996).

Foraging activity decreased with decreasing availability of social information. When starlings foraged alone in control treatments, foraging activity was severely disrupted. Similar low rates of foraging activity in solitary conditions have been reported elsewhere (Olsson et al. 2002; Smith 2002), and are probably responses to higher risk of predation. In social conditions, foraging activity varied in different ways. Neither visual obstruction nor neighbour distance affected food-searching rate while

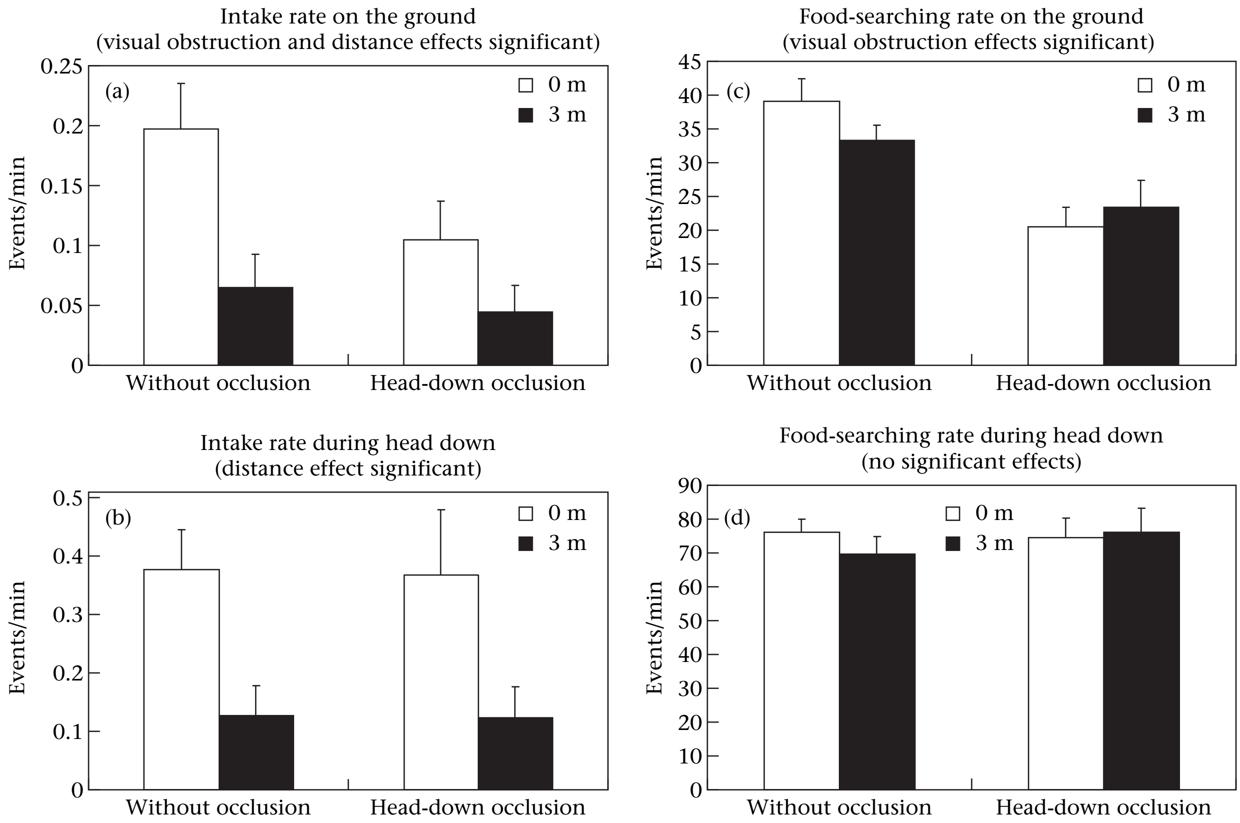

Figure 4. Effects of conspecific visual occlusion (without occlusion and head-down occlusion) and neighbour distance (0 m and 3 m) on intake rate (a) on the ground and (b) during head-down, and food-searching rate (c) on the ground and (d) during head-down. Values are means + SE ($N = 8$). See Table 2 for ANOVA results.

Table 2. The effects of conspecific visual obstruction (VO) and neighbour distance (ND) on intake rate and food-searching rate considering time on the ground (excluding time hanging from the enclosure walls) and time head-down

	F	df	*P*
Intake rate (on the ground)			
Visual obstruction	5.61	1, 7	**0.049**
Neighbour distance	29.07	1, 7	**0.001**
Replicate	0.05	1, 7	0.824
VO∗ND	3.75	1, 7	0.093
Food-searching rate (on the ground)			
Visual obstruction	49.41	1, 7	<**0.001**
Neighbour distance	0.59	1, 7	0.467
Replicate	2.97	1, 7	0.128
VO∗ND	5.44	1, 7	0.052
Intake rate (during head-down)			
Visual obstruction	0.02	1, 7	0.902
Neighbour distance	19.55	1, 7	**0.003**
Replicate	0.02	1, 7	0.895
VO∗ND	0.01	1, 7	0.943
Food-searching rate (during head-down)			
Visual obstruction	0.65	1, 7	0.445
Neighbour distance	0.20	1, 7	0.670
Replicate	0.01	1, 7	0.947
VO∗ND	1.87	1, 7	0.213

Significant results are marked in bold.

birds were head-down; but distance did affect intake rate in this posture, which was higher when birds were foraging closer to neighbours. This result suggests a change in starling foraging behaviour that could be mediated by a variety of different mechanisms (see also Smith 2002). For instance, when enclosures were adjacent and without visual occlusion, we observed that when a neighbour found a prey item near the edge of the enclosure, the focal bird rushed to that side and started probing eagerly. Thus, focal birds may have benefited from the sampling of all three neighbours when choosing a probing region. This mechanism could not operate at 3 m because sampling plots were separated and information about conspecifics' foraging success would have been useless. An alternative explanation is that birds probed more confidently (perhaps deeper) when they were in a state of greater perceived safety in denser flocks. We would have expected to observe the same effect as a function of obstruction, but this was not the case.

On the other hand, we found a significant effect of obstruction, but not of neighbour distance, on food-searching rate per unit of time on the ground. This effect is likely to be mediated by time spent scanning head-up, because it disappeared when head-up scanning was excluded from the denominator (see above). Faster food searching when neighbours are visible (e.g. no obstruction) is unlikely to be an adaptation for scramble competition (hastening consumption to outpace the competitors' effect on the prey, Clark & Mangel 1986), because the time frame of depletion in this situation appears to be vastly shorter than the time frame of individual patch visits or trials such as ours (Smith 2002). Although distance did not affect search rate, both obstruction and neighbour distance modified intake rate per unit of time on the ground. Combined with the previous results, the effect of obstruction seems to be mediated mostly through time competition between foraging and scanning on the ground, whereas the effect of neighbour distance is due to the prey returns per searching effort while the birds are head-down.

In summary, we found that behaviours that compete with food gathering (scanning on and off the ground) increased as information from conspecifics foraging nearby was reduced, and this, together with the direction of gaze, indicates that flock members are important targets of attention for foraging starlings. Some information about neighbours is probably collected not only when head-up, but also when head-down (the loss of this information with low-level obstructions caused starlings to increase efforts to see over the obstruction). Overall, models based on excessively simple assumptions such as taking the head-up posture as a full measure of scanning, or taking scanning as either predation or foraging driven rather than a complex combination of both are useful heuristic tools to formalize questions, but may be misleading if their logic is used to make predictions to be tested against real behaviour (Bednekoff & Lima 2002; Fernández-Juricic et al. 2004), whether in experimental or natural conditions.

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