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ORIGINAL ARTICLE

Esteban Fernández-Juricic · Alex Kacelnik

Information transfer and gain in flocks: the effects of quality and quantity of social information at different neighbour distances

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Abstract We assessed experimentally how the quality and quantity of social information affected foraging decisions of starlings (*Sturnus vulgaris*) at different neighbour distances, and how individuals gained social information as a function of head position. Our experimental set up comprised three bottomless enclosures, each housing one individual placed on a line at different distances. The birds in the extreme enclosures were labelled "senders" and the one in the centre "receiver". We manipulated the foraging opportunities of senders (enhanced, natural, no-foraging), and recorded the behaviour of the receiver. In the first experiment, receivers responded to the condition of senders. Their searching rate and food intake increased when senders foraged in enhanced conditions, and decreased in no-foraging conditions, in relation to natural conditions. Scanning was oriented more in the direction of conspecifics when senders' behaviour departed from normal. In the second experiment, responses were "dose dependent": receivers increased their searching rate and orientated their gaze more towards conspecifics with the number of senders foraging in enhanced food conditions. In no-foraging conditions, receivers decreased their searching and intake rates with the number of senders, but no variation was found in scanning towards conspecifics. Differences in foraging and scanning behaviour between enhanced and no-foraging conditions were much lower when neighbours were separated farther. Overall, information transfer within starling flocks affects individual foraging and scanning behaviour, with receivers monitoring and copying senders' behaviour mainly when neighbours are close. Information transfer may be related to predation information (responding to the vigilance of conspecifics) and foraging information (responding to the feeding success of conspecifics). Both sources of information, balanced by neighbour distance, may simultaneously affect the behaviour of individuals in natural conditions.

Keywords Birds · Public information · Scanning · Social foraging · Vigilance

Introduction

Conspecific behaviour is a source of information that may directly or indirectly affect the costs and benefits of social foraging (Roberts 1996; Beauchamp 1998; Giraldeau and Caraco 2000). One persistent question in the literature is whether (and if so, to what extent) the behaviour of conspecifics modifies the behaviour of an individual foraging in a group (Krause and Ruxton 2002). The information that is extracted from the performance of conspecifics in a given activity (e.g., foraging, vigilance, breeding, etc., see Danchin et al. 2001) can be broadly defined as social information (Galef and Giraldeau 2001; Giraldeau et al. 2002; Valone and Templeton 2002).

In mammals, there is evidence of social information transfer in foraging groups; namely, the behaviour of dominants may influence the foraging decisions of subordinates (Held et al. 2002). Social information transfer in avian flocks has been assessed from two perspectives (e.g., Bekoff 1996): information about potential predators (e.g., monitoring the vigilance of others) and information about food opportunities (e.g., local enhancement, scrounging, etc.). Although both social information sources are bound to affect animals simultaneously, studies have usually tested each type separately, with disparate results. For instance, experiments in juncos (*Junco hyemalis*) and zebra finches (*Taenopygia guttata*) failed to detect an effect of

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E. Fernández-Juricic (✉) · A. Kacelnik
Department of Zoology,
University of Oxford,
South Parks Road, Oxford, OX1 3PS, UK
e-mail: efernand@csulb.edu

Present address:
E. Fernández-Juricic, Department of Biological Sciences,
California State University,
Peterson Hall 1–109, 1250 Bellflower Blvd., Long Beach,
CA 90840, USA

individuals monitoring the vigilance of conspecifics (Lima and Zollner 1996; Beauchamp 2002). However, redshanks (*Tringa totanus*) would escape from predators only after the simultaneous departure of several conspecifics (Cresswell et al. 2000), implying that in this species individuals respond to the behaviour of neighbours.

The most compelling evidence that individuals modify their behaviour under the influence of conspecifics comes from studies of public information. Public information is defined as a special case of social information in which a forager uses the behaviour of group mates to get an estimate of food availability without sampling the whole patch (Clark and Mangel 1986; Valone 1989; Valone and Templeton 2002). Public information can increase the ability to recognize differences between patches, and equalize patch assessment and patch departure decisions, thereby reducing some costs of social foraging (Valone 1989, 1993). Empirical studies point out that some species (starling *Sturnus vulgaris*, red crossbill *Loxia curvirostra*, and great tit *Parus major*), but not others (blackbird *Turdus merula* and budgerigar *Melopsittacus undulatus*), seem to use public information, and that individuals can recognize conspecifics' successful and unsuccessful foraging behaviour (Krebs and Inman 1992; Valone and Giraldeau 1993; Templeton and Giraldeau 1995a, 1995b, 1996; Templeton 1998; Smith et al. 1999; Marchetti and Drent 2000; Smith et al. 2001).

There is relatively scant evidence as to how the quality and quantity of social information would influence foraging decisions under realistic behavioural clues (e.g., prey consumption on natural substrates, variations in vigilance and foraging patterns of flock-mates) and under different neighbour distances, and how individuals would gain such information. The issue needs to be treated experimentally to remove the confounding effects that social companions exert through modifying the feeding opportunities (namely, local depletion, interference, etc.) and through behavioural responses alone. Here, we present an experimental study in which members of a group are kept apart so that the first route is blocked, with the purpose of exposing the behavioural effects of social companions' foraging conditions. The specific goal of this study is to answer the following questions:

1. Do animals respond to the foraging behaviour of neighbours?
2. Does this response depend on the number of neighbours behaving in a particular way?
3. Is the response to conspecifics' behaviour weakened at increasing neighbour distances within the range of natural flocks?

Our experimental scenario comprised three enclosures placed linearly, with one individual in each (Fig. 1). We modified the behaviour of two individuals (senders) by manipulating their foraging opportunities in the peripheral enclosures, and then assessed the reaction of the focal bird located at the centre of the flock (receiver). We also defined a measure, based on head positions, of the target of the subjects' search for social information (information gain, sensu Smith et al. 2001). We addressed these questions in two experiments.

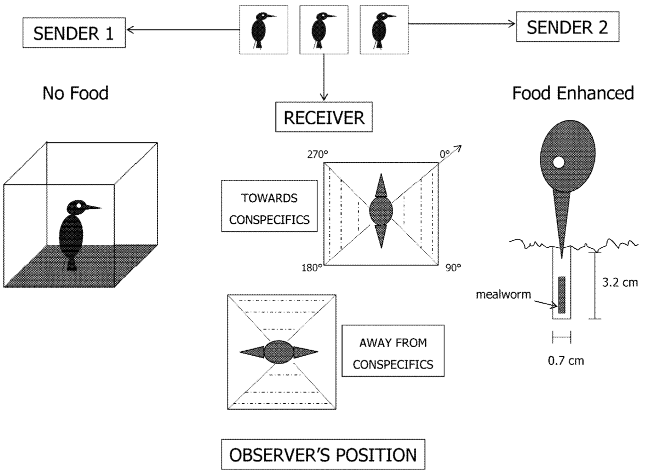

Fig. 1 Experimental set up to assess how the quality and quantity of information transmitted by two senders at the edges of a three-individual flock affected the foraging and scanning behaviour of receivers. Conditions in which food was not available were simulated by placing a dark green piece of wood on the ground (see *sender 1*). Food-enhanced conditions were simulated by burying mealworms in holes (see *sender 2*). Head positions were classified as towards or away from conspecifics based on the location of the bill. The *grey areas to the side of the head* highlight the peripheral visual fields and hence the regions of maximum visual receptivity for targets at the neighbour distances used in this experiment

Predictions

Provided senders and receivers have similar pre-harvest information (Valone 1989), modifying the opportunities for senders' foraging through the manipulation of the food density in their own patches should increase their patch-sample information (Valone 1989).This in turn should affect their foraging and scanning behaviour, leading to changes in the behaviour of receivers that could then be attributed to information flow. In the first experiment, we manipulated the foraging conditions of senders (natural food availability, enhanced food availability, no-foraging allowed) and varied the number of senders in these conditions. The expectation here is for receivers to increase or decrease their foraging effort in parallel with the changes in the foraging conditions of the senders (Valone 1993; Smith et al. 1999). Putative behavioural changes in the receivers mediated by conditions of the senders should be objectively observable, but the mechanism involved is still open to interpretation. It may or may not be possible for receivers to discriminate whether a sender that spends more time with its head up is doing so because there is nothing to eat or because it has perceived an alarming stimulus signalling possible predation risk (Roberts 1996). A second expectation is that the strength of any effect should be mediated through the number of neighbours being observed. Increasing the number of senders in a given condition should decrease the ambiguity of the type of information perceived. We also expected that receivers would spend more time monitoring conspecifics when senders foraged in conditions different from natural, because the more unusual the sender's behaviour, the greater will be the potential information content of their behaviour once this is detected by receivers. In the second experiment, we expected that the greater separation between senders and receivers would lead to a decline in the senders' influence because of a reduction in visibility (Elgar et al. 1984; Pöysä 1994; Lima and Zollner 1996; Beauchamp and Livoreil 1997), which would decrease the chances of a receiver's detecting details of the senders' behaviour. An alternative explanation is that information from more distant group members is less likely to be relevant if resource availability between patches drops sharply with distance.

Methods

General procedures

Experiments were conducted at the University Farm (Wytham, Oxfordshire) between March and April 2001 in a permanent pasture field frequented by wild foraging starlings (Whitehead et al. 1995). We caught and colour-ringed 24 adult individuals from the local population. Seven weeks prior to, and during the experiments, birds were housed in indoor cages (0.9×0.7×0.6 m), under a 12L:12D light cycle (lights on at 0700 hours). 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.

We used three cubic (edge: 0.5 m) bottomless enclosures made of chicken mesh (light wire), and placed them in natural foraging grounds for starlings, which responded well to this situation by foraging in the same general way as when free (see also Whitehead et al. 1995). Enclosures were arranged linearly, with one bird in each (Fig. 1). Previously, it was determined that starlings could monitor neighbours through the enclosures, and that the physical separation between birds did not affect food-searching behaviour (Smith 2002). Enclosures limited the size and shape of experimental plots (0.5×0.5 m). We manipulated the foraging opportunities and amount of food in the enclosures located at the edges of the flock, where individuals acted as senders (Fig. 1). In the central cage (receiver, Fig. 1), no food-manipulation was done, with the focal bird resting on the resources available in the turf (see following discussion). We assessed the foraging and scanning behaviour of receivers when senders foraged under different conditions. Most social information transfer studies have focused on patch departure decisions (Templeton and Giraldeau 1995a, 1995b, 1996; Lima and Zollner 1996; Cresswell et al. 2000), but we tested the consequences of using social information in terms of foraging effort and success within patches while keeping constant time available for foraging (see following discussion).

In the sender's enclosures, we simulated three conditions: natural food availability, no-foraging conditions, and enhanced food availability. In natural conditions (N), senders foraged in non-manipulated ground, so that their food availability was the same as the receiver's. No-foraging conditions (Z) were created by placing a thin (0.03 m) piece of wood (0.55 m long×0.55 m wide) on the ground of the sender's enclosures (Fig. 1). Under this condition, senders spent all of their time in what we classify as scanning because there was no possibility of probing.

We enhanced food availability (E) by digging holes and burying 35 mealworms in the experimental plot (Fig. 1). Senders were trained to increase food searching when presented with 2–3 mealworms left on the turf at the beginning of the trials, and had no difficulty in finding the buried prey. This training was necessary to keep active levels of sender's food searching in different experimental conditions, particularly when neighbour distance was modified. Previous studies that assessed the abundance of prey consumed by starlings (mainly, leatherjackets *Tipula paludosa* and earthworms *Lumbricus terrestris*) in 80-mm diameter and 150-mm depth soil cores concluded that its distribution was patchy in natural conditions (Whitehead 1994; Smith 2002). Consequently, a sender's finding of a food item should modify the receiver's estimate of its own food availability (Valone 1989). We divided the senders' enclosures in a grid of 5×5 cells. We randomly buried mealworms in 10 out of the 25 cells available. We then created a patchy distribution by placing 1–4 mealworms in each hole such that the mean number of mealworms per hole would be lower than the variance. Therefore, in enhanced conditions senders had at their disposal the natural availability of prey plus the 35 mealworms buried in the experimental plots.

Two experiments were conducted. In the first experiment, all enclosures were placed adjacent to each other (0 m separation). Treatments varied as to foraging conditions of senders (N, Z, E) and the number of senders (one, two) in enhanced or no-foraging conditions. We employed five treatments that were named with a combination of two letters (NN, ZZ, EE, NE, NZ), indicating the conditions faced by the right and left sender, respectively. When conditions between senders differed in the same trial (NE or NZ), we randomised the location of the condition at the right and left of the receiver. In the second experiment, we assessed the effects of senders foraging in two conditions (ZZ and EE) at two distances (0 and 3 m) between enclosures. This led to inter-starling distances within the range of natural foraging flocks (Whitehead 1994). We treat the flow of social information as unidirectional (from senders to receivers) because the physical conditions of receivers did not change throughout any of the experimental conditions.

Eight (4 males and 4 females) out of the 24 birds served as focals (receivers). Each receiver experienced two replicate trials under each treatment. In the first experiment, we carried out 80 trials (5 treatments×8 receivers×2 replicates per receiver), whereas in the second experiment, we conducted 64 trials (4 treatments×8 receivers×2 replicates per receiver). The remaining 16 non-focal birds (senders) were randomly assigned daily to complete the three-bird 'flocks' in the trials. Flock composition thus varied from test-to-test to avoid systematic association between senders and experimental treatments. There were 4 trials per day, but neither the receivers nor the senders experienced more than 1 trial in any 1 day. Experimental plots were covered with mesh wire for approximately 24 h before each trial. The 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 (defined as the site occupied by one enclosure, hence measuring 0.5×0.5 m), and each experimental plot was assigned at random and used only once to avoid any possible depletion effects or systematic variations in food density for receivers.

Birds were food deprived from 1700 hours the day before being tested. At the time of testing, they were transported in soft bags to the enclosures. The observer hid in a tent positioned 5 m away from the enclosure of the receiver. Within the tent, one video camera recorded the behaviour of the receiver, and another camera, the behaviour of senders. In the latter case, our intention was to assess whether senders increased their foraging behaviour from natural to enhanced conditions. To that end, we selected eight senders at random, and for each individual, we randomly recorded 2 trials in each condition (N and E) in the following treatments EE, NN, and EN in the first experiment. In the second experiment, we followed a similar approach, and recorded senders' behaviour in EE conditions to find out whether their foraging behaviour varied between 0 and

3 m. Based on previous experience with a similar set up (Smith 2002), we used 15-min trials, timed from the first probes by the receivers. Trials were not performed in high winds or rain.

Behavioural recordings

The behaviour of focal birds was recorded from videotapes using an event-recording programme (Jwatcher 0.9). We based our analysis on the following categorization of behaviour. A starling could be in 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, respectively. This classification uses a descriptive rather than a functional criterion, as birds could potentially gather social information relative to predation and foraging both on and off the ground. Since our interest here is the allocation of behaviour between activities leading predominantly to food gathering or information gathering (scanning), we define the time on the ground as foraging time and create the category of "scanning" from the sum of time on the ground with head up plus time hanging from the enclosure walls.

While the bird was head down, we recorded probing events (poking into the ground in a new site) and intake events (without considering prey sizes). The numbers of probing and capture events in relation to the time on the ground were used to compute probing and intake rates (in number of events per min).

While the birds were with their heads up on the ground, we defined a measure of social information gain based on head positions. Different head positions in birds usually indicate different scanning targets, since eye movements in birds are very limited (Pratt 1982). Conspecific and predator monitoring in birds is generally accomplished with the peripheral visual field, and food handling with the binocular field (Maldonado et al. 1988; Martin 1993). Operationally, we assumed that the probability of gaining (or at least seeking) information about an object (e.g., conspecific, predator, etc.) increased at each side of the starling's bill (peripheral visual fields), but decreased at the front and back of its head (Fig. 1, see Martin 1986; Dawkins 1995). The binocular visual field is generally used when an object is at very close range (<10 cm), and after an object is first detected with the peripheral field (Dawkins 2002). The blind area at the rear of the starling's head justifies this operational simplification (Martin 1986). Several studies have used head orientation as an adequate estimator of gaze (e.g., Land 1999; Franklin III and Lima 2001; Dawkins 2002). Therefore, to have a relative measure of whether the target of attention was internal or external to the flock, we classified head positions as either towards or away from conspecifics (Fig. 1).

To determine head positions based on bill positions, we conducted a preliminary calibration study with an additional camera placed above the enclosure (this top-view camera was removed for the experiment). We employed a subject-centred system of coordinates with the origin at the centre of the bird's head (Fig. 1). We defined 0° as the diagonal to the receiver's enclosure aiming away and to the right of the observer (Fig. 1) and then used the angular position of the bill to classify the direction of maximum perception (peripheral visual fields). Hence, we labelled as "towards conspecifics" all bill positions between 90° and 180° and between 270° and 360° clockwise, and defined as "away from conspecifics" the remaining directions. This classification of head positions improves on previous studies (e.g., Fernández-Juricic et al. 2004a) by focussing on the zones of maximum receptivity (showed in grey in Fig. 1) within the visual fields of starlings (Martin 1986). Videotapes were analysed by measuring bill positions recorded by the lateral camera hid in the tent relative to the standard positions recorded with it and the top-view camera 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 angles 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 (foraging or hanging from the enclosure walls). We did not include bill positions that were difficult to assign to a particular category (0.77% of the time on average per trial). With this information, we calculated time scanning towards and away conspecifics (s).

We also recorded time spent scanning off the ground, defined as all the time hanging from the enclosure walls (s), as an indicator of time the receivers spent in positions from which they could perceive stimuli not accessible while foraging (e.g., distant conspecifics, potential predators, etc.). We were not able to record head positions while starlings were off the ground. We present the scanning time towards conspecifics, away from them, and off the ground as percentages of the total time spent in these three scanning positions. E. Fernández-Juricic performed all video analyses after extensive self-training analysing pilot video tapes. At the time of recording the experimental tapes there was less than 5% difference between two scorings of the same tape.

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

Statistical analyses

General linear models were used to analyse the effects of sender's foraging condition, number of senders, and neighbour distance on the following response variables: probing rate, intake rate, percentage of time scanning towards conspecifics, percentage of time scanning away from conspecifics, and percentage of time scanning hanging from the enclosure walls.

In the first experiment, we entered foraging condition as a fixed factor, and averaged the two replicates of each animal to obtain a single score per subject. To analyse the behaviour of senders we contrasted two conditions: natural and enhanced. For receivers, sender's foraging conditions included five levels: ZZ, ZE, EE, NE, and NZ. We assessed differences among these levels according to the three questions posed in the Introduction using contrast analysis (Day and Quinn 1989) in the following way: (1) To determine whether receivers reacted differently to sender's foraging conditions, we analysed differences between EE and NN, and between ZZ and NN. (2) To determine whether the number of senders in manipulated foraging conditions affected receivers' behaviour, we performed two analyses; one for enhanced conditions by comparing NE and EE, and another for no-foraging conditions by comparing NZ and ZZ.

In the second experiment, to assess the behaviour of senders and the response of receivers under different sender's foraging conditions at different neighbour distances, we included two fixed factors in our model: foraging condition (two levels, ZZ and EE) and neighbour distance (two levels, 0 and 3 m). Replicates of each individual were averaged to obtain a single score. For senders, we analysed variations between neighbour distances in enhanced conditions. For receivers, we assessed differences between enhanced and no-foraging conditions at the two levels of separation between neighbours. Specific differences between levels were analysed with contrast analysis (Day and Quinn 1989). All statistical analyses were conducted with STATISTICA 6.0.

Results

Experiment 1

Senders' behaviour

Senders increased their foraging activity from natural to enhanced food conditions. Probing rate (means±SE; N,

Table 1 Variations in the foraging behaviour of senders (probing and intake rates) between two treatments: natural and enhanced food availability (experiment 1), and 0- and 3-m separation between neighbours under enhanced food availability (experiment 2). Results from general linear models

Senders	*F*	*df*	*P*
Experiment 1			
Probing rate			
Intercept	50.24	1, 14	<0.001
Treatment	11.82	1, 14	<0.01
Intake rate			
Intercept	36.17	1, 14	<0.001
Treatment	3.98	1, 14	<0.03
Experiment 2			
Probing rate			
Intercept	168.19	1, 14	<0.001
Treatment	0.16	1, 14	0.695
Intake rate			
Intercept	74.50	1, 14	<0.001
Treatment	0.04	1, 14	0.844

4.32±0.40 probes/min; E, 14.88±0.53 probes/min) and intake rate (N, 0.22±0.11 captures/min; E, 0.39±0.18 captures/min) were significantly higher in enhanced conditions (Table 1).

Receiver's behaviour: did receivers respond differently to the foraging conditions of senders?

Receivers did respond to the conditions under which senders fed. Probing rate increased in enhanced (EE) ($F_{1,35}$=6.72, P<0.02), and decreased in no-foraging (ZZ) conditions ($F_{1,35}$=6.82, P<0.02), in relation to natural (NN) conditions (Fig. 2a). Food intake increased from no-foraging to natural conditions ($F_{1,35}$=5.39, P<0.05, Fig. 2b), and from natural to enhanced conditions ($F_{1,35}$=4.56, P<0.05, Fig. 2b).

The percentage of scanning time towards conspecifics increased in enhanced ($F_{1,35}$=32.67, P<0.001) and no-foraging conditions ($F_{1,35}$=4.46, P<0.05) in relation to natural conditions (Fig. 3a). The percentage of scanning time away from conspecifics showed the reversed pattern, decreasing in enhanced ($F_{1,35}$=9.98, P<0.01) and no-foraging conditions ($F_{1,35}$=12.57, P<0.01) relative to natural conditions (Fig. 3b). No significant variation was found in the percentage of scanning time hanging from the enclosure walls between no-foraging and natural conditions ($F_{1,35}$=1.14, P=0.292, Fig. 3c), and between enhanced and natural conditions ($F_{1,35}$=2.24, P=0.143, Fig. 3c).

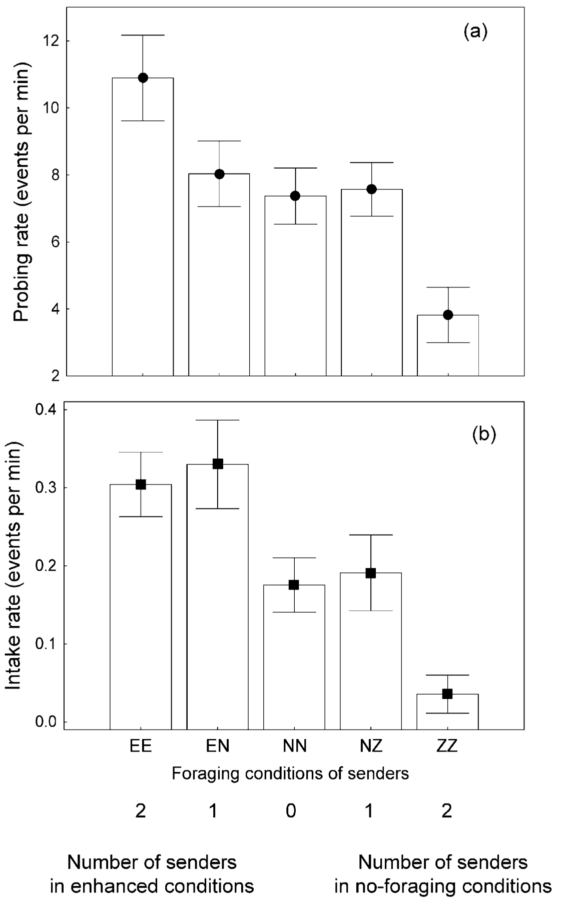

Fig. 2 Experiment 1. Foraging behaviour of receivers (**a** probing rate, events per min; **b** intake rate, events per min) as a function of the foraging conditions of senders: *NN*, *ZZ*, *EE*, *NE*, *NZ* (each letter indicates the conditions faced by the right and left sender, respectively, Fig. 1). *N*, natural food availability; *Z*, no-foraging; *E*, enhanced-food availability

Receiver's behaviour: was receiver's response dependent on the number of senders?

Receivers' probing rate increased with the number of senders in enhanced food conditions (NE vs EE, $F_{1,35}$=4.43, P<0.05, Fig. 2a). However, intake rate ($F_{1,35}$=0.18, P=0.670, Fig. 2b) did not increase significantly with the same variable. The percentage of scanning time towards conspecifics increased with the number of senders in enhanced conditions ($F_{1,35}$=11.97, P<0.01, Fig. 3a), whereas, scanning away from conspecifics decreased ($F_{1,35}$=4.33, P<0.05, Fig. 3b). The percentage of scanning time hanging from the enclosure walls did not vary significantly with the number of senders in enhanced conditions ($F_{1,35}$=0.26, P=0.612, Fig. 3c).

The number of senders in no-foraging conditions affected the foraging behaviour of receivers by decreasing probing (NZ vs ZZ, $F_{1,35}$=7.61, P<0.01, Fig. 2a) and intake rates ($F_{1,35}$=6.65, P<0.02, Fig. 2b). The percentage of scanning time towards conspecifics did not vary significantly with the number of senders ($F_{1,35}$=0.51,

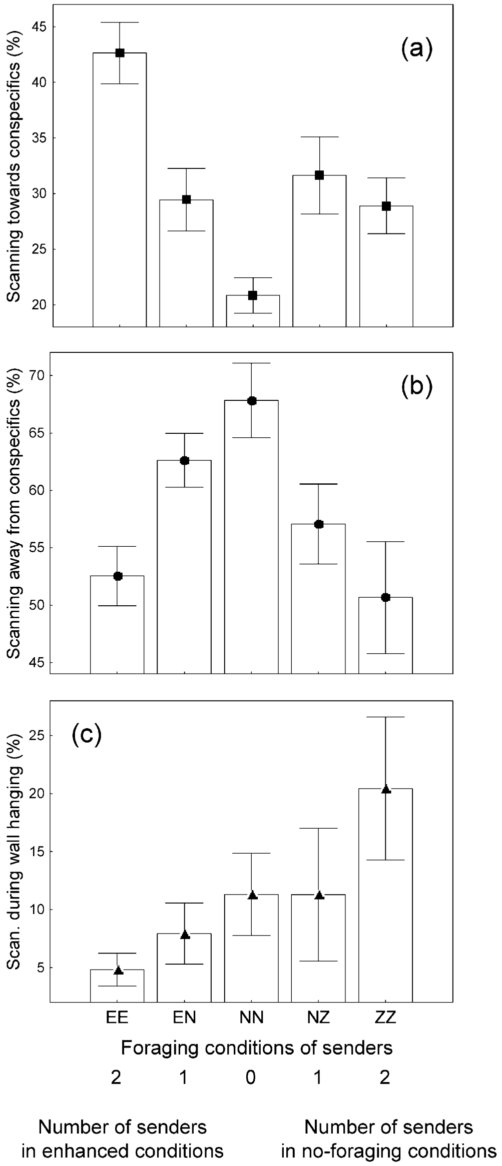

Fig. 3 Experiment 1. Scanning behaviour of receivers (**a** percentage of scanning time towards conspecifics; **b** percentage of scanning time away from conspecifics; **c** percentage of scanning time hanging from the enclosure walls). Treatments as in Fig. 2

P=0.478, Fig. 3a). Likewise, the percentage of scanning time away from conspecifics ($F_{1,35}$=1.74, P=0.195, Fig. 3b) and the percentage hanging from the enclosure walls ($F_{1,35}$=2.22, P=0.142, Fig. 3c) remained similar with the number of senders.

Experiment 2

Senders' behaviour

Although foraging activity was slightly higher when neighbours were close (0 m) than far (3 m), we found no significant differences in probing rate (0 m, 16.12±0.92 probes/min; 3 m, 15.01±1.12 probes/min) and intake rate (0 m, 0.773±0.095 captures/min; 3 m, 0.725±0.103 captures/min) between these distances in enhanced food conditions with the sample sizes used (Table 1).

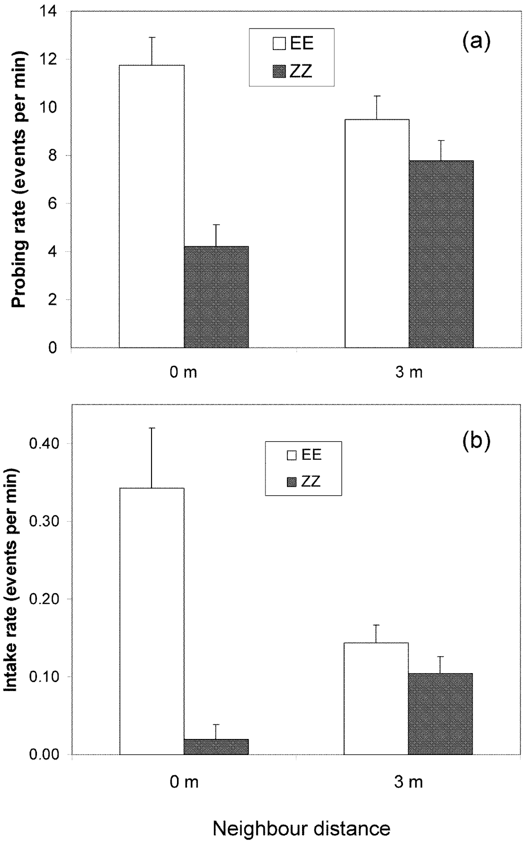

Fig. 4 Experiment 2. Foraging behaviour of receivers (**a** probing rate, events per min; **b** intake rate, events per min) under two treatments: foraging conditions of senders (*ZZ* and *EE*) and distance to senders (0 and 3 m). Sender's foraging conditions were named with a combination of two letters: *Z*, no-foraging; *E*, enhanced-food availability (Fig. 1)

Receiver's behaviour: was the response to the foraging conditions of senders weakened at increasing neighbour distances?

The second experiment replicated certain effects found in experiment 1 (a variation in indices of foraging and scanning behaviour modified in opposite directions when the foraging conditions of senders were enhanced or reduced), but the results of experiment 2 indicated that these differences were much lower when neighbours were separated farther. Most foraging and scanning responses were affected by the interaction between sender's foraging condition and neighbour distance (Table 2). Probing rate decreased steeply from enhanced to no-foraging conditions at 0 m ($F_{1,28}$=28.88, P<0.001, Fig. 4a), whereas at 3 m, the difference between conditions was not significant ($F_{1,28}$=1.51, P=0.228, Fig. 4a). Receiver's

Table 2 Variations in the foraging (probing and intake rates) and scanning (towards conspecifics, away from conspecifics, and while hanging from the enclosure walls) behaviour of receivers under different foraging conditions of senders (enhanced-food availability and no-foraging) and distance to senders (0 and 3 m). Results from general linear models

Receiver	*F*	*df*	*P*
Probing rate			
Intercept	283.07	1, 28	<0.001
Sender's foraging condition (C)	21.81	1, 28	<0.001
Distance (D)	0.42	1, 28	0.517
C×D	8.58	1, 28	<0.01
Intake rate			
Intercept	50.19	1, 28	<0.001
Sender's foraging condition (C)	17.79	1, 28	<0.001
Distance (D)	1.78	1, 28	0.193
C×D	10.83	1, 28	<0.01
Percentage of scanning time towards conspecifics			
Intercept	541.03	1, 28	<0.001
Sender's foraging condition (C)	5.44	1, 28	<0.03
Distance (D)	13.60	1, 28	<0.001
C×D	16.23	1, 28	<0.001
Percentage of scanning time away from conspecifics			
Intercept	975.41	1, 28	<0.001
Sender's foraging condition (C)	1.81	1, 28	0.189
Distance (D)	0.26	1, 28	0.611
C×D	0.17	1, 28	0.683
Percentage of scanning time hanging from the enclosure walls			
Intercept	25.31	1, 28	<0.001
Sender's foraging condition (C)	13.42	1, 28	<0.01
Distance (D)	7.43	1, 28	<0.03
C×D	9.93	1, 28	<0.01

intake rate increased in enhanced conditions when individuals were close ($F_{1,28}$=29.19, P<0.001, Fig. 4b); but this effect waned when individuals were located farther apart ($F_{1,28}$=0.43, P=0.517, Fig. 4b).

The percentage of scanning time towards conspecifics increased significantly in enhanced conditions at 0 m ($F_{1,28}$=20.24, P<0.001, Fig. 5a), but did not differ between enhanced and no-foraging conditions at 3 m ($F_{1,28}$=1.44, P=0.241, Fig 5a). The percentage of scanning time away from conspecifics did not vary with sender's foraging conditions and distance (Table 2, Fig. 5b). Finally, the percentage of time scanning hanging from the enclosure walls increased when receivers were in no-foraging conditions at 0 m ($F_{1,28}$=23.22, P<0.001, Fig. 5c), but no difference was found between enhanced and no-foraging conditions at 3 m ($F_{1,28}$=0.13, P=0.721, Fig. 5c).

Discussion

We found that (1) starlings tended to behave in parallel with the foraging and scanning behaviour of conspecifics, (2) this response intensified with the number of conspecifics displaying a certain behaviour, and (3) this response dwindled with greater separation between conspecifics. These results confirm that there is social information transfer within starling foraging flocks. These effects have usually been assumed in theoretical and empirical studies but rarely tested in semi-natural scenarios (but see Templeton and Giraldeau 1995b; Smith et al. 2001). Our results are also novel in that we empirically assessed the within-patch consequences of social information use controlling for foraging area, neighbour distance, and group size. We also determined a measure of public information gain based on the visual system of starlings. We discuss these findings with reference to previous research.

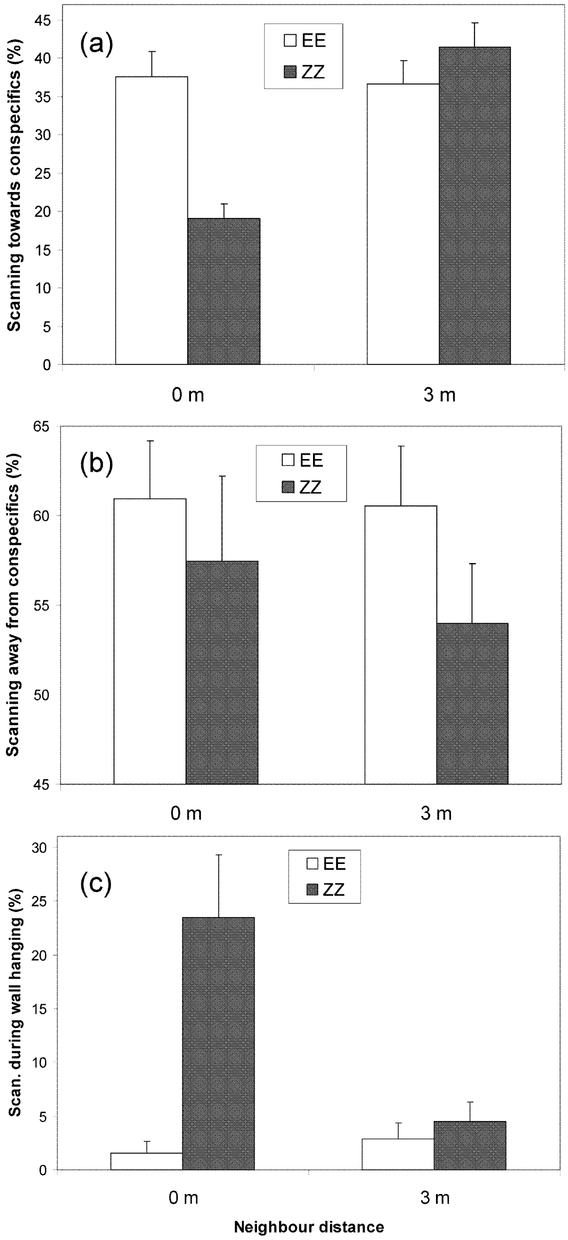

Fig. 5 Experiment 2. Scanning behaviour of receivers (**a** percentage of scanning time towards conspecifics; **b** percentage of scanning time away from conspecifics; **c** percentage of scanning time hanging from the enclosure walls). Treatments as in Fig. 4

When senders increased their searching effort and foraging success in enhanced food conditions, receivers raised their foraging activity accordingly. Detecting a conspecific finding a prey item (e.g., higher intake rate) may promote an increase in the receivers' attribution of value to its own experimental plot (Valone 1993; Smith et al. 1999), given some spatial correlation of food density and despite receiver's foraging grounds not having been enriched. Future studies should differentiate between receivers being sensitive to either increased foraging effort, increased rate of captures, or increase rate of captures per unit of effort. These subtle differences are relevant, as starlings appear to recognize unsuccessful foragers with particular searching behaviours (Templeton and Giraldeau 1996; Templeton 1998). An alternative interpretation, which also considers the use of social information, is that the response of receivers may have been elicited by scramble competition effects at small neighbour distances (Clark and Mangel 1986; Beauchamp 2003). However, we controlled for group size and for the physical contact between neighbours, which could increase competition levels. Furthermore, the time frame of our observations was not likely to affect depletion of natural resources (Smith 2002).

When senders' foraging was restricted (no-foraging condition), receivers decreased their foraging activity in spite of having natural food at their disposal. These results should be interpreted with caution due to the extreme conditions that senders faced, since they were not allowed to forage normally. Two alternative functional explanations can be suggested, one related to foraging information and the other to predation information. On the one hand, receivers may have misused public information decreasing their searching for food because senders did not spend time doing so (Smith et al. 1999; Valone 1993). This assumes that receivers attributed properties of neighbours' patches to their own patches. This is similar to the findings that individuals leave their patch when conspecifics spend little time foraging (Smith et al. 1999) or their foraging is not successful (Templeton and Giraldeau 1996). However, we did not allow birds to depart, but let individuals stay in the enclosure for a fixed amount of time.

Another interpretation is that the drop in receiver's foraging behaviour when both senders were not allowed to forage may be related to the transmission of an alarm message (e.g., a potential predator in the surroundings). Starlings appear to rely on the scanning behaviour of conspecifics when escaping from dummy predators (Powell 1974). In our study, receivers increased intake rate when senders changed from no-foraging to natural conditions, suggesting that when senders forage normally receivers may perceive a reduced risk of predation (e.g., less scanning time by senders), allowing them to increase food searching activity. We could distinguish the foraging information and collective vigilance effects with our design. However, both mechanisms involve social information and are bound to concurrently affect the foraging and scanning dynamics of groups in natural conditions (Bahr and Bekoff 1999), probably playing an important role in the decision making to join or leave flocks (Drent and Swierstra 1977; Inglis and Isaacson 1978).

Previous studies conducted on artificial food patches have demonstrated that starlings used the searching behaviour of conspecifics to estimate the quality of patches (Krebs and Inman 1992; Templeton and Giraldeau 1995a) and to approach or avoid neighbours according to the quality of public information provided (Templeton and Giraldeau 1995b, 1996; Templeton 1998). We found that such responses are mediated by allocating a greater fraction of scanning time to gazing towards conspecifics, likely to acquire social information. Greater attention towards conspecifics was observed whenever senders departed from some normal baseline behaviour (e.g., increased foraging or scanning behaviour). Estimating information gain based on head-positions could be used to assess the amount of social information necessary to make scanning and foraging decisions in groups or the relative value of personal and conspecific scanning under different ecological and social conditions (see also Coolen et al. 2001). However, empirical tests do need to consider the species-specific differences in the configuration of visual fields before defining the targets of scanning (Fernández-Juricic et al. 2004b).

Previous studies suggested that animals seem to use the number or proportion of individuals as clues to make foraging decisions (Drent and Swierstra 1977; Inglis and Isaacson 1978; Thompson 1983; Metz et al. 1991). In this study, we found that the responses to conspecifics intensified with the number of senders, particularly in no-foraging conditions, causing a sharp decline in foraging behaviour. In enhanced conditions, probing rate increased with the number of senders; but we could not detect a concomitant increase in intake rate likely because our tests did not have enough power to detect differences due to small sample size. These results are similar to those found in an experiment with crossbills, which started using public information when surrounded by two conspecifics instead of only one (Smith et al. 1999), but in our experiment starling response was gradual.

The intensity of the receiver's response towards senders between enhanced and no-foraging conditions was lowered when neighbours were farther apart. When neighbours were more distant, the costs of using social information about food availability may have increased due to distance effects (Pöysä 1994; Proctor et al. 2003; e.g., seeing a conspecific across a grazing field becomes progressively difficult due to reduced visual contrast and increased light attenuation), with animals resorting to personal information to make foraging decisions (Valone 1989, 1993; Templeton and Giraldeau 1995a, 1995b). Furthermore, if receivers increase or decrease their foraging effort in parallel to that of receivers as an adaptive response to spatial correlation of food density, then the significance of a sender's foraging conditions for the receiver should decline as distance increases, because the information is simply less valuable to indicate the receiver's own opportunities.

Our results indicate that starlings adjust their foraging and scanning budgets according to both the quality and the quantity of information gathered from conspecifics, and that the stronger effects take place at small neighbour distances. We suggest that flock cohesion in this species may be maintained through a trade-off between neighbour distance, that may determine the ease with which a certain behaviour is transmitted and gathered visually across the flock, and the behaviour of flock-mates, which may modify the response of individuals. This mechanism could lead to copying conspecific behaviour when neighbours are close, and to behaving independently from conspecifics when neighbours are far apart (Fernández-Juricic et al. 2004a).

The use of social information is bound to be common in contexts other than those usually ascribed to foraging (Valone and Templeton 2002); for instance, mate choice copying (Nordell and Valone 1998; Galef and White 2000), breeding habitat selection (Danchin et al. 2001; Doligez et al. 2002), predator attacks (Roberts 1997; Cresswell et al. 2000), and aggressive encounters (Kennedy and Gray 1994, but see Koops and Abrahams 1999). Social information should therefore be studied in broad contexts, because in natural conditions, individuals face a wide array of problems (foraging, predation, intra-specific competition, etc.). It is clearly important to find some way of measuring the intensity of the effects and the factors that promote or restrict social information flow. Detailed examination of gaze orientation and of searching effort and success in finding resources may be productive in areas in the future.

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