



Food reduction has a limited effect on following relations in house sparrow flocks



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Forming foraging groups may help to improve protection from predators, foraging efficiency and exchange of information, but to benefit from these advantages, animals need to maintain group cohesion. Several studies have investigated how social status or behavioural and physiological traits promote leadership and followership in various species, but the potential role of ecological factors in modulating social cohesion of foraging groups has received less attention. We used social network analysis to investigate how a temporary shortage of food affects within-group following behaviour in house sparrow, *Passer domesticus*, flocks and which individual characteristics influence birds' positions in the following networks. To test this, we observed nine captive house sparrow flocks, composed of 12 individuals each, in three consecutive sessions, in which the food availability was altered. We found that food reduction did not modify the following network structure and that individuals had consistent positions within the flocks, as males and adults were followed more often than females and juveniles, respectively. However, short-term food reduction affected individuals' following behaviour according to their age: adults increased their following rates during food scarcity, whereas the opposite trend was found in juveniles. This pattern also remained after the re-establishment of initial conditions, suggesting that ecological changes can also induce individual-level lasting effects. Our study provides empirical evidence that food reduction does not affect the global social structure of house sparrow flocks but nevertheless individuals respond differently to ecological changes according to their age.

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In many animal species interactions between group mates play an important role in resource exploitation, social learning, disease or information transmission (Krause & Ruxton, 2002). Social relations, consequently, can ultimately affect individual survival and/or reproductive success (e.g. see in Oh & Badyaev, 2010; Otterstatter & Thomson, 2007). Animals' decisions about with whom to interact and in what manner translate into a dynamic network of social relationships that also determines how the group as a social unit will function. The effect of social interactions at the group level is often studied in collective movements and consensus decision making within the framework of social network theory, which provides sufficient analytical tools to examine how leaders and influential group members acquire their status in the network of interacting individuals (e.g. Bode, Franks, & Wood, 2012; Bode, Wood, & Franks, 2011; Lusseau, 2007; Sueur, Deneubourg, & Petit,

2012; Sueur & Petit, 2008). The main question here is whether all individuals contribute equally to the decision or the maintenance of social cohesion, or whether group members differ from each other in the amount of influence they exert on their group (King, Johnson, & Van Vugt, 2009). Many studies have examined how differences in social network positions are related to attributes such as motivation (e.g. Rands, Cowlshaw, Pettifor, Rowcliffe, & Johnstone, 2003), temperament (e.g. Johnstone & Manica, 2011; Pike, Samanta, Lindström, & Royle, 2008), dominance (e.g. Šárová, Špinká, Panamá, & Šimeček, 2010) or knowledge (e.g. Nagy, Ákos, Biro, & Vicsek, 2010). We can assume that if these attributes can vary within individuals over short timescales (e.g. motivation), positions can be expected to change or fluctuate over time, while in other societies positions can be more stable and certain individuals become more influential for an extended period of time or have constantly greater influence on collective movements or decision making than others (Leblond & Reeb, 2006).

Ecological factors such as predation pressure and food distribution are known to shape the evolution of animal aggregations

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(Krause & Ruxton, 2002), but how such environmental factors alter the social structure of a group has been investigated less often (but see Webster, Atton, Hoppitt, & Laland, 2013). Although it is known that food scarcity affects social relations by increasing aggression among group members (e.g. Hodge, Thornton, Flower, & Clutton-Brock, 2009; Polo & Bautista, 2002), how this may modulate the cohesion and stability of a social system is less obvious. Several studies have shown a potential link between aggression and affiliative relationships (Barton, Byrne, & Whiten, 1996; Dey, Reddon, O'Connor, & Balshine, 2013; Lea, Blumstein, Wey, & Martin, 2010) or found that increased predation threat (Kelley, Morrell, Inskip, Krause, & Croft, 2011), climatic factors (Cross et al., 2004; Sundaesan, Fischhoff, Dushoff, & Rubenstein, 2007) or density of conspecifics (Buhl et al., 2006; Moussaïd, Perozo, Garnier, Helbing, & Theraulaz, 2010) affected collective movements or altered existing social structure. However, we know little about how social cohesion within a group changes on a shorter timescale. Are some social relations more prone to be affected by environmental variation, while others can be expected to be consistent? This question is important to investigate as environmental perturbations are common in nature, but their effect on social interactions is not well known.

In this study, we investigated how a temporary shortage of food affected two aspects of social behaviour, namely aggressive interactions on a feeder and within-group following of other individuals to the feeder, in captive house sparrow flocks. More specifically, we tested how (1) the frequency of different interactions/events that were related to foraging, (2) the structure of the social networks that were constructed from pairwise following events to the feeder and (3) individual positions within these networks changed after a short-term food reduction and were affected by individual characteristics such as age and sex. Furthermore, we also examined how (4) different measures of prominence (relative importance of individuals' positions in their following network) correlated with each other and with aggression in the sparrow flocks. We considered pairwise following events to the feeder to be movement initiations that facilitate and maintain social cohesion within the flock, and positions within the constructed following networks to be indicators that reflect the level of influence individuals can exert on maintaining cohesion in their group. By answering the above questions, we aimed to explore the consequences of a short-term environmental perturbation on the social structure of following events and individuals' roles within the sparrow flocks. The house sparrow is a highly gregarious (e.g. Hoi, Tost, & Griggio, 2011), small passerine species; birds form flocks during the nonbreeding season that may vary in size from a few birds to several hundred individuals (Summer-Smith, 1963). As flock members perform various activities together such as foraging, roosting and dustbathing, and frequently compete for resources with each other, this species has been the model organism of many behavioural studies (Anderson, 2006). We predicted that if a lower amount of food generated a higher frequency of aggressive interactions between group mates, increased aggression could also alter initial positions and prominence in the following networks. To reach general conclusions about the effect of food limitation on the social structure of the sparrow flocks and on individual network positions, we observed and analysed within-group social interactions in many replicate flocks in our study.

METHODS

Study Subjects

The house sparrows originated from a population of 304 individuals kept in 17 outdoor aviaries located at the Konrad Lorenz Institute for Ethology (KLIVV), Vienna, Austria. Of these individuals

208 were juveniles born in captivity during the breeding season in 2011 and kept in 10 aviaries, whereas the remaining 96 individuals were adults from previous breeding seasons and were kept in seven other aviaries (for more details see Griggio, Biard, Penn, & Hoi, 2011; Griggio & Hoi, 2010). These outdoor aviaries, measuring approximately 2 × 3.9 m and 2.6 m high, were equipped with a feeding table (0.46 × 0.46 m, 0.50 m from the ground), roosting trees and several perches. Ad libitum food was provided consisting of a mixture of millet, canary seed, wheat and sunflower seeds, apple slices and millet spray. In addition, a water dish on the ground was also available for drinking and bathing. Nestboxes were installed in each aviary as shelter during the night.

Experimental Set-up

We observed nine experimental flocks from October 2011 to March 2012, which were formed by allocating juveniles and adult birds from the outdoor aviaries. Each flock consisted of 12 individuals (six males and six females), taken randomly from at least four different outdoor aviaries (mean ± SE = 5.20 ± 0.36). The adult:juvenile ratio differed between the flocks: two flocks contained 12 adults, three flocks contained eight adults and four juveniles (two young males and two young females), one flock contained 11 juveniles and one adult male, and three flocks were composed entirely of young individuals. Flock size, sex and age ratios were within the range of natural variation occurring in free-living flocks of house sparrows (Barnard, 1980; Caraco & Bayham, 1982; Sodhi, 1992). As following behaviour has previously been found to be affected by kinship in house sparrows (Tóth et al., 2009a), we used pedigree information to form flocks preferably from individuals that were not related to each other (although in two flocks one pair of siblings occurred).

Each experimental flock was moved to one indoor aviary measuring 6.60 × 3.30 m and 2.25 m high. The aviary was equipped with a roosting tree, several perches, a water dish and a central feeder, which was the only source of food. Commercial food for granivorous passerines was provided on the feeder but its amount differed between observation sessions (see below). Other than natural light from several windows, artificial light was also provided with 12:12 h light:dark periods. The indoor aviary room was maintained at a temperature of about 20–22 °C. We measured body mass (±0.1 g) prior to the transfer to the experimental aviary and also at the end of the experiment. All birds were banded with a metal ring and a unique combination of coloured rings for individual identification during the observations. Upon release into the indoor aviary, birds were allowed to become familiar with the environment of the experimental aviary for 2 days, during which we fed them ad libitum. Behavioural observations started on the following day. Of 120 birds, one individual was accidentally included in two different flocks, which raises the problem of statistical dependence between these flocks. However, as analyses from whichever of the two flocks was excluded yielded qualitatively the same results, we chose to present our results based on the highest possible sample size, that is, data collected in nine flocks.

Ethical Note

Prior to conducting the experiment, we had decided to suspend the experimental trial if a bird became hurt or appeared stressed, but we never observed any sign of injury or stress. We also checked the birds' health before allocating them to the experimental flocks. After the study, we released individuals back into their original outdoor aviaries. In one of the 10 flocks we initially set up, two females died during the experiment for unknown reasons; this flock was therefore excluded from the analyses. This mortality rate

(two of 120) does not exceed the natural level of mortality (Anderson, 2006). All the birds had access to the feeder during the experiment. Several individuals lost weight during the study (on average 0.5 g) but regained this weight after the study. For a subsample of individuals we recorded the weight also 1 week after the experiment ended (subsample of 46 individuals: weight before the experiment \pm SD = 27.05 \pm 2.0 g; weight 1 week after the experiment \pm SD = 27.19 \pm 2.19 g, paired *t* test: $t_{45} = 0.597$, $P = 0.55$). In the following breeding season, the birds made several successful breeding attempts, suggesting that the housing conditions were appropriate and that the experimental birds remained healthy (Griggio et al., 2011; Griggio & Hoi, 2010). Capture, housing and handling of birds were in accordance with the relevant Austrian laws and were licensed by the government of Vienna (MA 22) licence number 424/2011. The experiments reported in this paper comply with current laws on animal experimentation in Austria and the European Union. This study was approved by the institutional ethics committee and the national authority according to § 8ff of Law for Animal Experiments *Tierversuchsgesetz – TVG*, licence number GZ 68.205/0220-II/3b/2012.

Behavioural Observations

In seven of the nine flocks, birds were observed for 12 consecutive days, divided into four different sessions each 3 days long. In the other two flocks, birds were observed for 8 consecutive days and each session lasted for 2 days. In session 1 ('Before treatment'), 300 g of seeds was supplied on the feeder (in a metallic bowl), simulating an environment with *ad libitum* food availability. This specific amount of food was nearly twice the usual daily intake. In session 2 ('Treatment'), the amount of food provided was reduced to 80 g, and this was usually consumed by the end of the day; by doing so we produced an environment with limited resources. Feeding conditions were otherwise identical to the other sessions. This set-up aimed to stimulate intense competition among flock members for food. In session 3 ('After treatment'), 300 g of seeds was supplied again on the feeder, re-establishing the initial set-up. This session was included to verify whether a potential change in social structure persisted or whether the original social dynamics were re-established in the studied flocks.

Flocks were observed daily, in the morning between 0745 and 1245 (mean duration of observation \pm SE: 3.86 \pm 0.03 h/flock; Appendix Table A1), and in the afternoon between 1330 and 1700 (1.72 \pm 0.05 h/flock). The feeder was inserted into and removed from the aviary at the beginning and at the end of both observation periods; by doing so, we prevented feeding beyond the observation time. Observations, made directly by D.B., took place from a hide 2 m away through a one-way glass, during which three different 'events' on the feeder were recorded: one individual following another to the feeder, aggressive interactions on the feeder and occasions when an individual arrived at the feeder by itself ('arriving alone'). A following event occurred when an individual arrived at the feeding place and was followed by one or more group mates. The former individual was described as the 'initiator' and the latter(s) as the 'follower(s)'. We included only those following events to the feeder in which the follower bird followed the initiator within 5 s (Tóth et al., 2009a; Tóth & Griggio, 2011). For each aggressive interaction, which ranged from intentional movements/displacements to chases across the aviary, we noted the identity of the participants and the result of the interaction (winner versus loser), their initial position before, and final position immediately after, the interaction. To examine when individuals were not able to act as initiators (i.e. failed initiations), we also recorded all the feeding trips they made to the feeder when they were not followed by any group member. As individuals could visit the feeder any time

by themselves and irrespective of the behaviour of their flockmates throughout the study, we regarded the observed following events to be movement initiations contributing to social cohesion within the flocks rather than explicit leader–follower interactions.

Network Construction

Using the collected data we constructed social networks to examine the following patterns within the nine sparrow flocks in detail. The precision with which one can estimate the structure of any society depends on the number of observations, and thus on the duration of data collection (Whitehead, 2008). However, differences in precision may also mask the effect of treatment in repeated measures set-ups; in such cases, identical observation effort is desirable at least within the investigated social unit. As originally the length of observation time differed both within and between flocks, we selected the shortest session for each flock and reduced the number of observations in the other two sessions accordingly (Appendix Table A1). In this way, we obtained identical observation time for each flock, that is, the duration of observation did not differ between sessions within a flock, but could differ between flocks. Next, we constructed social networks based on following events from data collected in each session for each flock. Only those following events in which both participants were unambiguously identified were considered. In the constructed networks individuals were represented by nodes that were connected to each other by edges. An edge was present between two nodes if at least one following event occurred between the respective individuals during a given session and the direction of the edge was taken from the 'follower' towards the 'initiator' (Fig. 1). The frequency with which one bird followed the other was reflected by the weight of the edge between the two adjacent nodes. With this method, we built weighted directed networks: 'weighted' because the weight of the edge represented the frequency of interactions between a pair of nodes in a given session, and 'directed' as edges were asymmetric, always pointing from followers towards initiators (thus, an edge pointing from individual A to individual B was not identical to an edge pointing from B to A). We used weighted networks for the analysis of within-flock following events instead of applying a threshold value for constituting an edge between adjacent nodes, because we presumed that not only the topology of particular nodes, but also the intensity of the connections between nodes may provide useful information about the social structure of the sparrow flocks (Barrat, Barthélemy, Pastor-Satorras, & Vespignani, 2004).

Using the relevant functions of the package 'tnet' (Opsahl, 2009), run with the R 2.15.3 Statistical Program (R Development Core Team, 2013), we calculated several network metrics to characterize the structure of the observed following networks and the position of the individuals within them: weighted reciprocity, weighted transitivity, in-degree (k_{in}), out-degree (k_{out}), in-strength (s_{in}) and out-strength (s_{out}). Weighted reciprocity was calculated for each individual as the sum of the weights of reciprocal edges (i.e. edges that ran in both directions between two adjacent nodes) divided by the sum of the weights of all outgoing edges:

$$\text{weighted reciprocity}_i = \frac{\sum_{1 \leq j \leq N-1} \min(w_{ij}, w_{ji})}{\sum_{1 \leq j \leq N-1} w_{ij}},$$

where $\sum \min(w_{ij}, w_{ji})$ is the sum of following events that occurred mutually (therefore symmetrically) between individual 'i' and its flockmates, N is the number of individuals in the flock, and $\sum (w_{ij})$ is the total number of occasions individual 'i' followed others (which equals s_{out} for individual 'i'). Its value reflects the proportion of following events that were reciprocated by a given initiator and

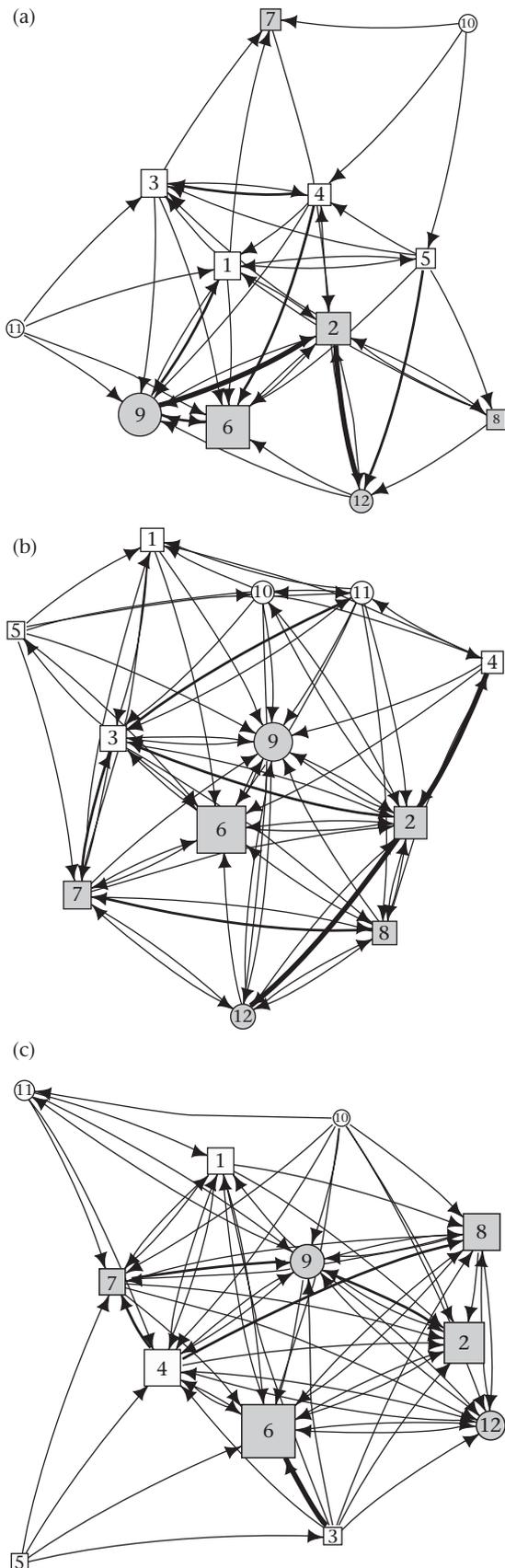


Figure 1. Examples of the following networks (for Flock 5) constructed for the three observation sessions: (a) Before treatment; (b) Treatment; (c) After treatment. Individuals are represented by nodes with sex indicated by colour (males: grey; females:

thus the prevalence of mutual following events in the flocks. Transitivity is the proportion of transitive triples (if individual A directs a tie to individual B and B directs a tie to C, then A also directs a tie to C) in a network, indicating the tendency of nodes to form clusters or tightly connected groups (Junker & Schreiber, 2008). Its generalization, proposed by Opsahl and Panzarasa (2009), also takes the weights of the edges into account by attributing values to the triplets calculated from edge weights present in given triplets. The in-degree of a node is the number of direct edges a given node receives from its neighbours (i.e. number of followers), whereas its out-degree is the number of edges a node directly sends to other nodes in the network (i.e. number of followed group mates; Wasserman & Faust, 1994). The in-strength of a node is the sum of the weights of its incoming edges (i.e. frequency of being an ‘initiator’), while its out-strength is the sum of the weights of its outgoing edges (i.e. frequency of being a ‘follower’). These standard measures take only direct connections into account; we used them to describe group-level social structure and to characterize prominence in the following networks in each observation session. We also calculated a group-level centralization index ($C_{in-strength}$) to assess the level of centralization in each session in our flocks (Sueur et al., 2012). To be able to apply Sueur et al.’s (2012) method to weighted directed networks, we used the in-strength of the nodes (instead of eigenvector centrality) in each network and calculated the index as the maximal in-strength value in a given network minus the average in-strength of all other nodes in that particular network, and divided by the maximal in-strength value. The greater the difference in in-strength between the most prominent individual and the rest of the group, the higher the value of this index will be, that is, the network can be considered to be more centralized. It would equal 1 in a star network, where only the central node receives connections from other nodes, and would be zero in an equal network, where all nodes are connected to all other nodes with the same strength. To estimate the consistency of node strength across sessions in the flocks, we calculated the sum of variances of individual ranks (SV) for in- and out-strength according to Wilson, Krause, Dingemans, and Krause (2013):

$$SV(R) = \sum_{1 \leq i \leq N} \text{variance}(R_{i,1}, \dots, R_{i,K}),$$

where R is the matrix of ranks, $R_{i,1}$ is the node strength rank of individual i in network 1, N is the number of individuals and K is the number of networks. Ranks were obtained from the order of the values of in- and out-strength, respectively, in each flock. We compared these sums of variances of individual ranks to that calculated from equivalent random networks (see below) in each flock to test whether variations in node strength in the following networks across sessions were different from random.

Statistical Analyses

First, we used all observations (see Appendix Table A1) to test whether the frequency of the observed events (number of times individuals arrived alone/h, number of times individuals followed others to the feeder/h, number of aggressive interactions on the feeder/h) differed between sessions in the flocks. For this, we applied linear mixed-effect (LME) models with ‘flock’ as a random factor and

white) and age indicated by shape (adults: squares; juveniles: circles); the size of the nodes is proportional to individuals’ in-strength (i.e. the total number of times an individual is followed by other group mates). Asymmetric curved edges (lines) indicate that following events were not exclusively mutual; the widths of the lines are proportional to the edge weights (i.e. number of occasions one individual followed a particular other one). Graphs were generated using a Kamada-Kawai algorithm with 9999 iterations (‘igraph’ package; Csárdi & Nepusz, 2006).

included 'observation time' and 'session' as potential predictors; this method is an equivalent for repeated measures analysis in R (Pinheiro & Bates, 2000). A similar approach was applied (but using the reduced number of observations [Appendix Table A1], as in all further analyses) to test group-level differences in the calculated network measures between sessions. We used the variance of weighted reciprocity, weighted transitivity, variance of node degree (i.e. in- and out-degree), variance of node strength (i.e. in- and out-strength) and the calculated centralization index as dependent variables, and included 'flock' as a random factor and 'observation time' and 'session' as potential explanatory variables in the LME models. Variance of in-strength was square-root transformed to improve its fit to a normal distribution. A significant effect of session on any of the above measures would indicate that the social structure of the following networks was changed by the food manipulation treatment. We also tested the consistency of network positions by comparing the sum of variances of individual ranks calculated for in-strength and out-strength across the three sessions between the observed and equivalent random networks. For that, we used two-tailed randomization tests with 9999 iterations. Equivalent random networks were generated by randomly reassigning the observed ties among the same number of dyads in each session and each flock. Our null model was created based on the simple assumption that interactions (with a given intensity) are equally likely between any pair of nodes. We defined an observed value to be significantly different from random if it fell within the top or bottom 2.5% of the distribution for the statistic obtained from the generated random networks (Edgington, 1995).

In the individual-level analysis, we investigated the relationship between node strength and node degree, and those between node strength and the number of 'arriving alone' events, number of aggressive interactions and their success (as a crude proxy of dominance rank; calculated as the number of times an individual won divided by the number of aggressive interactions in which the individual participated; Liker & Barta, 2001, 2002). For that, we applied Spearman correlation tests in each session, with 'flock' used for stratification, and calculated simulated *P* values from 4999 iterations ('coin' R package; Hothorn, Hornik, van de Wiel, & Zeileis, 2008). We also tested, using LME models, how individual node strength (i.e. in-strength and out-strength) changed between sessions and how it was affected by characteristics such as age and sex. Here, 'individual' was included as a random factor, whereas 'flock', 'session', 'sex', 'age' and the interaction of the latter two with 'session' were potential predictors. Both dependent variables were square-root transformed to improve their fit to a normal distribution. As measures derived from relational data violate the assumption of independence in classical statistical analyses (James, Croft, & Krause, 2009), here we calculated simulated *P* values (from 4999 iterations) for model selection and also for the predictors in the final models using the 'pgirmess' R package (Giraudeau, 2006). In all LME model fitting (both group- and individual-level) we used a backward removal procedure, starting with the full models containing all main effects and the interaction term, then dropped the predictor with the highest *P* value in each step until only $P \leq 0.05$ effects remained (if there were any) in the final models. We also calculated eta squares (η^2) as effect sizes and their 95% confidence interval to estimate the variance explained by each predictor in the final models (Cohen, 1988; Nakagawa, 2004). The requirements of LMEs were checked by plot diagnosis. All tests were two tailed with α set to 0.05.

RESULTS

Group-level Analysis

We found that a temporary shortage of food had no effect on the frequency of birds following others to the feeder ($F_{2,16} = 0.634$,

$P = 0.544$) or on the frequency of birds arriving alone ($F_{2,16} = 0.474$, $P = 0.631$), but it significantly increased the frequency of aggressive interactions on the feeder ($F_{2,16} = 23.60$, $\eta^2 = 0.75$ [CI: 0.41–0.84], $P < 0.001$; Fig. 2). Observation time had no effect on any of the above variables (all $P > 0.769$), indicating that the slight differences in the sampling periods between and within flocks did not significantly influence the frequency of the observed measures. Parameter estimates of the random effect in the final models are shown in Appendix Table A2.

We found no significant differences in any of the investigated network measures between sessions (Table 1). The lack of change in the variation of the calculated metrics suggests that the food manipulation treatment did not modify the structure of the following networks in our sparrow flocks. Also, flocks did not become more/less centralized, but remained intermediate throughout the study, that is, none of the individuals gained disproportionately high prominence in their flocks. Parameter estimates of the random effect ('flock') in the final models are shown in Appendix Table A2. In accordance with the above results, we found that in-strength ranks varied significantly less in all flocks, whereas out-strength ranks showed significantly less variation than expected by chance in six of nine flocks (and the same trend was found in an additional flock; Table 2). This finding also indicates that individuals had a consistent position within their flocks (at least in terms of being followed by other flockmates), and this was not affected abruptly by the food manipulation treatment and the increased aggression that resulted.

Individual-level Analysis

Node strength and node degree measures were strongly and positively correlated in the studied networks: in-strength was correlated with in-degree and out-strength with out-degree in all three sessions (Table 3). This suggests that more prominent individuals (birds that had been followed more often) had many different followers, while individuals that followed others more frequently followed more birds as well. On the other hand, the two node strength measures did not correlate with each other significantly in any of the sessions (Table 3), that is, prominent individuals themselves did not follow others more frequently. In-strength was also positively correlated with the frequency of birds arriving alone in all sessions and with the number of aggressive interactions in the

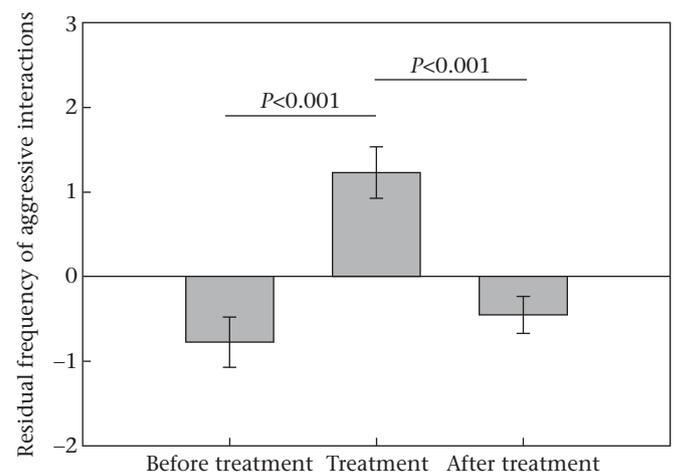


Figure 2. Frequency of aggressive interactions before, during and after the food reduction treatment. Means are shown \pm SE. *P* values were obtained from Tukey post hoc tests ('multcomp' R package; Hothorn et al., 2008). The dependent variable is plotted as residuals from the final LME model fitted without 'session'.

Table 1
Mean \pm SD of the following network measures investigated in the three sessions and the estimated effect of the food manipulation treatment (i.e. 'session') obtained from the fitted LME models

Dependent variable	Sessions (mean \pm SD)			F	df	P
	Before treatment	Treatment	After treatment			
Variance of weighted reciprocity	0.07 \pm 0.03	0.07 \pm 0.03	0.08 \pm 0.02	1.03	2,16	0.380
Weighted transitivity	0.66 \pm 0.07	0.66 \pm 0.09	0.67 \pm 0.11	0.10	2,16	0.903
Variance of in-degree	7.40 \pm 2.86	8.31 \pm 2.48	9.08 \pm 3.09	1.32	2,16	0.295
Variance of out-degree	4.77 \pm 3.02	3.50 \pm 1.09	4.11 \pm 1.78	1.13	2,16	0.345
Variance of in-strength*	8.46 \pm 1.51 (73.67 \pm 26.80)	9.74 \pm 4.33 (111.51 \pm 101.46)	9.50 \pm 2.92 (97.91 \pm 54.76)	0.98	2,16	0.398
Variance of out-strength	39.93 \pm 16.74	35.98 \pm 26.02	45.17 \pm 33.79	0.55	2,16	0.587
Centralization index	0.67 \pm 0.08	0.68 \pm 0.05	0.69 \pm 0.07	0.72	2,16	0.504

* Square-root transformed (values in parentheses were calculated from the untransformed data).

third session, but not with their success. Out-strength was not correlated with any of these variables in all sessions (Table 3). These results indicate that prominence in in-strength and out-strength in the sparrow flocks have more or less distinct meanings and do not measure the 'same' feeding activity.

We found that sex and age significantly affected in-strength in the flocks (sex: $F_{1,104} = 18.25$, $\eta^2 = 0.15$ [CI: 0.04–0.27], $P < 0.001$; age: $F_{1,104} = 11.26$, $\eta^2 = 0.10$ [CI: 0.02–0.21], $P < 0.001$); males and adult birds were followed more frequently than females and juveniles, respectively (Fig. 3a, b). Flock or treatment (either by itself or in interaction with sex or age) had no significant effect on in-strength (all $P > 0.1428$). Out-strength was also significantly affected by sex as females followed other group mates more frequently than males (sex: $F_{1,104} = 10.75$, $\eta^2 = 0.09$ [CI: 0.01–0.21], $P = 0.001$; Fig. 3c). Furthermore, we found a significant effect of the interaction between age and treatment: older birds followed others more often during the 'Treatment' and 'After treatment' sessions, whereas the opposite trend was found in juveniles (treatment*age: $F_{2,205} = 3.38$, $\eta^2 = 0.03$ [CI: 0–0.09], $P = 0.040$; Fig. 3d). Flock also had a significant effect on out-strength ($F_{8,205} = 3.37$, $\eta^2 = 0.12$ [CI: 0.02–0.17], $P = 0.002$), indicating that flocks differed from each other in the extent to which individuals followed their group mates to the feeder. Parameter estimates of the random effect in the final models are shown in Appendix Table A2.

DISCUSSION

In this study we investigated how a temporary shortage of food affected two types of social interactions during foraging in house sparrow flocks. We found that although the frequency of aggressive interactions was increased by the treatment, food limitation did not modify the structure of the following networks and individuals kept their position within their flock or at least positions were more consistent than expected by chance. We also showed that males and adult birds were followed more often to the feeder than females and juveniles, respectively. On the other hand, females and

juveniles followed others more often than males and adults. Prominence in the following networks (i.e. how frequently a bird was followed by other group mates, which also reflects its influence on group cohesion) was correlated with the number of failed initiations (i.e. arriving alone) in all sessions, but was related to the rate of aggressive interactions only in the third session. Short-term food reduction affected an individual's following behaviour only according to its age: adults increased their following rates during food scarcity, whereas the opposite trend was found in juveniles. This pattern also remained after the re-establishment of initial conditions, suggesting that ecological changes may induce mid-term effects at the individual level. Overall, our results indicate that house sparrow flocks exhibit an intermediately centralized social regime, in which an individual's position is determined by intrinsic characteristics such as sex and age.

We found consistent differences between the sexes in both in-strength and out-strength as males were followed more often to the feeder than females, and females followed others more frequently than males, which may be because of behavioural inequalities associated with foraging. As the number of failed initiations was positively correlated with the number of times they were followed, males could simply visit the feeder more often and therefore elicited following behaviour at a higher frequency from other group mates. Females, on the other hand, could prefer following others to the food patch, a tendency that could manifest even without the presence of a realistic predation hazard. Similar inequalities were found between adults and juveniles, too. Earlier studies on free-ranging sparrows showed that both males and females, and adults and juveniles, differed in the level of risk taking during foraging (Breitwisch & Hudak, 1989; Sodhi, 1992); our results corroborate these findings and suggest that such differences have a potential influence on an individual's role in maintaining group cohesion. Consistency in prominence revealed by the analysis of sum of variances of individual ranks, together with the lack of change in the group-level network metrics between sessions, further indicates that short-term perturbations do not affect these

Table 2
The sum of variances of individual ranks calculated for in-strength and out-strength across the three sessions in the observed and equivalent random networks

Flock	Observed sum of variances in in-strength ranks	Random equivalents (mean \pm SD)	P	Observed sum of variances in out-strength ranks	Random equivalents (mean \pm SD)	P
1	74.50	140.73 \pm 24.48	0.010	53.50	140.94 \pm 24.84	0.001
2	31.50	141.10 \pm 24.70	<0.001	55.92	141.10 \pm 24.48	0.001
3	33.25	140.94 \pm 24.66	<0.001	92.33	141.02 \pm 24.56	0.059
4	49.17	139.61 \pm 24.21	0.001	134.08	140.00 \pm 24.35	0.774
5	68.50	140.39 \pm 24.35	0.006	55.75	140.72 \pm 24.52	0.002
6	51.08	140.21 \pm 24.68	0.001	69.83	140.62 \pm 24.30	0.007
7	86.42	139.90 \pm 24.49	0.043	81.33	139.98 \pm 24.66	0.029
8	57.33	139.25 \pm 24.19	0.002	97.50	138.72 \pm 24.39	0.116
9	40.08	139.76 \pm 24.33	<0.001	77.92	140.13 \pm 24.58	0.020

In the randomization tests P values were obtained from 9999 iterations.

Table 3

Correlations between in-strength and out-strength, and their relationship with node degree and the observed number of events on the feeder

	Before treatment			Treatment			After treatment		
	r_s	Z	P	r_s	Z	P	r_s	Z	P
In-strength vs out-strength	0.25	1.75	0.083	−0.05	−1.73	0.083	0.01	−1.10	0.282
In-strength vs in-degree	0.94	9.14	<0.001	0.93	9.07	<0.001	0.96	9.23	<0.001
Out-strength vs out-degree	0.84	7.93	<0.001	0.78	7.55	<0.001	0.85	8.16	<0.001
In-strength vs arriving alone	0.59	6.04	<0.001	0.61	6.71	<0.001	0.64	6.48	<0.001
Out-strength vs arriving alone	0.12	1.16	0.246	−0.12	−1.26	0.216	−0.08	−1.15	0.254
In-strength vs aggressive interactions	0.14	0.80	0.426	0.21	1.76	0.084	0.24	2.04	0.041
Out-strength vs aggressive interactions	0.10	0.09	0.928	0.02	−0.79	0.441	0.19	1.49	0.139
In-strength vs success in aggression*	0.03	0.23	0.822	−0.01	−0.10	0.915	−0.10	−1.14	0.251
Out-strength vs success in aggression*	0.01	0.16	0.882	−0.03	0.04	0.968	0.06	0.50	0.626

Spearman correlation coefficients were calculated from unstratified data, whereas test statistics and *P* values were obtained using Spearman correlation tests with flock used for stratification ('coin' R package; Hothorn et al., 2008). Significance levels were computed via Monte Carlo simulation with 4999 iterations. Significant *P* values are shown in bold.

* Individuals for which success in aggressive interactions could not be calculated because of the lack of observed interactions were omitted from the calculation of Spearman correlation coefficients.

differences in the sparrow flocks. Nevertheless, in the long term individuals' positions within their flock are likely to change as they get older. In accordance with this, we also found that in the period of increased competition (caused by the food reduction) adults followed their group mates to the feeder more often, compared to juveniles, which may be regarded as a behavioural response to the environmental change that can be acquired through learning. For instance, the frequency of using a scrounging tactic has previously been found to be related to social learning in house sparrows (Katsnelson, Motro, Feldman, & Lotem, 2008).

Following other group mates to the feeding place and the resulting spatial proximity can be beneficial in terms of reducing predation risk (e.g. owing to a dilution effect; Edenbrow et al., 2011; Krause & Ruxton, 2002), but also in terms of facilitating social learning (Coussi-Korbel & Frigaszy, 1995) or increasing foraging

success (Ward & Zahavi, 1973). This latter can be especially relevant in societies in which individuals use various foraging tactics to obtain food (Giraldeau & Caraco, 2000). The house sparrow has long been a model species for studying producer–scrounger tactics during foraging (e.g. Lendvai, Liker, & Barta, 2006; Liker & Barta, 2002; Tóth et al., 2009b). In this context, followers as potential scroungers may use initiators as producers to find exploitable food patches. In a previous study, Rohwer and Ewald (1981) suggested that dominant foragers may specifically use subordinates as food finders, implying that dominants may follow other, subordinate group mates more frequently during foraging. Here, we had a limited possibility to test this idea as we could not calculate reliable dominance ranks, owing to the low number of pairwise aggressive interactions in our flocks (which is in line with the findings of other studies on similarly small feeding flocks of house sparrows:

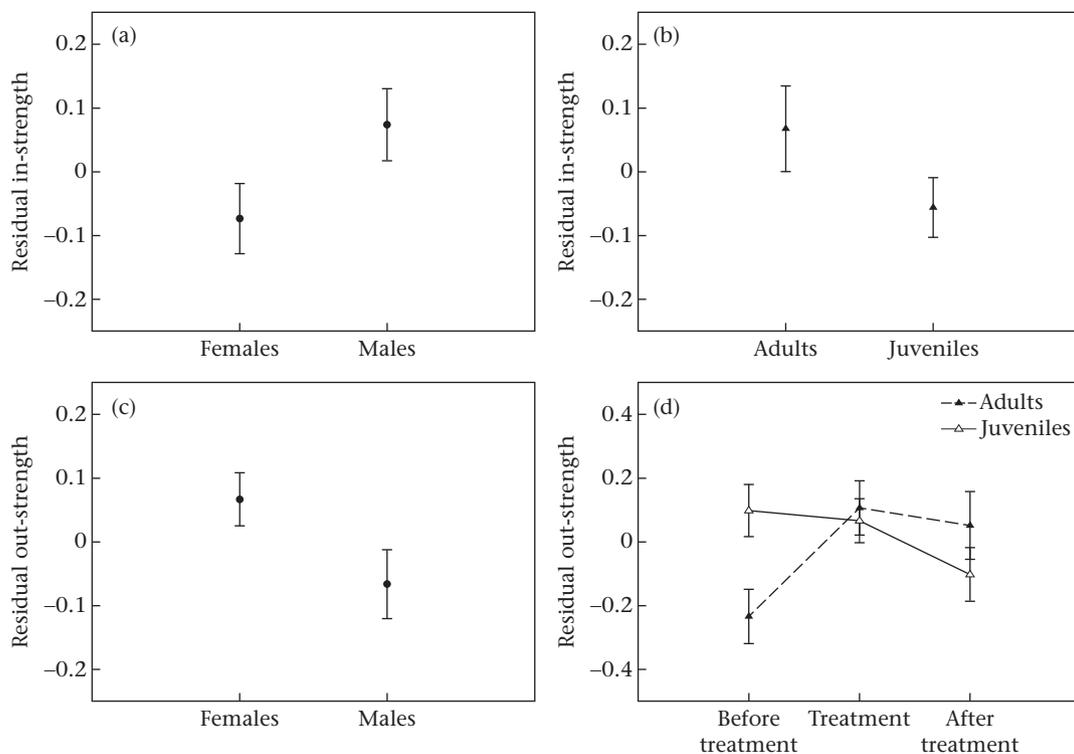


Figure 3. Effects of 'sex', 'age' and 'session' on the two prominence measures in the individual-level analyses. Means are shown \pm SE. Dependent variables are plotted as residuals from the final LME models without the examined factor or interaction (together with its main effects). (a) Sex difference in in-strength, (b) age difference in in-strength, (c) sex difference in out-strength, (d) the effect of 'age' and 'session' on out-strength.

Barnard, 1980; Caraco & Bayham, 1982; Breitwisch & Hudak, 1989). Instead, we examined whether in- and out-strength were correlated with the number of aggressive interactions and their success on the feeder. We found that the number of aggressive interactions was weakly positively correlated ($r_s = 0.24$) with in-strength, and only in the third session. This means that individuals that were followed more often to the feeder also participated in more aggressive interactions after the initial conditions were re-established; we currently have no clear explanation for this delayed effect of the food reduction treatment. Success in these interactions, on the other hand, was not correlated with either prominence measure in any sessions. We argue that these findings provide little support for the idea that dominants follow subordinates to the feeder, although we also acknowledge that they cannot disprove it either. Therefore, a general conclusion about the relationship between dominance/scrounging and following behaviour should not be drawn from our study or only with extreme caution. An alternative interpretation of our results might be that more dominant birds are indeed likely to follow others more often as prominence in the following networks was related to the rate of aggressive interactions in at least one session. We believe, however, that our interpretation is more conservative for several reasons. First, we had insufficient information at hand to assess dominance relationships between dyads reliably, because of the limited number of aggressive interactions in the flocks. Second, we did not explicitly investigate the use of foraging tactics in our study, that is, whether or not following behaviour actually resulted in scrounging on the feeder. Third, our experimental set-up was designed for investigating changes in the flock's social structure based on the highest possible number of observations, and not for testing Rohwer and Ewald's (1981) hypothesis. Using a more complicated set-up in which only a limited number of individuals possess the knowledge of a foraging skill (e.g. in Franz & Nunn, 2009) or location of food patches (e.g. in Webster et al., 2013), it would be possible to examine the spread of information among birds through following events in the flocks and thus evaluate how beneficial following other individuals could be in a complex environment. With the help of network-based diffusion analysis (Franz & Nunn, 2009; Hoppitt, Boogert, & Laland, 2010), a powerful and versatile technique for investigating the effect of social factors in information transmission, the potential role of aggressive interactions in within-group following behaviour could also be unambiguously explored.

In conclusion, our results demonstrate the utility of social network analysis as a method to investigate the modulating effect of ecological factors on the social organization of foraging groups. Our study provides empirical evidence that food reduction does not affect the social structure of within-group following behaviour in house sparrow flocks, but nevertheless individuals respond differently to food reduction according to their age.

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References

Anderson, T. R. (2006). *Biology of the ubiquitous house sparrow: From genes to populations*. Oxford, U.K.: Oxford University Press.

- Barnard, C. J. (1980). Factors affecting flock size mean and variance in a winter population of House Sparrows (*Passer domesticus* L.). *Behaviour*, 74, 114–127.
- Barrat, A., Barthélemy, M., Pastor-Satorras, R., & Vespignani, A. (2004). The architecture of complex weighted networks. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 3747–3752.
- Barton, R. A., Byrne, R. W., & Whiten, A. (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, 38, 321–329.
- Bode, N. W. F., Franks, D. W., & Wood, A. J. (2012). Leading from the front? Social networks in navigating groups. *Behavioral Ecology and Sociobiology*, 66, 835–843.
- Bode, N. W. F., Wood, A. J., & Franks, D. W. (2011). The impact of social networks on animal collective motion. *Animal Behaviour*, 82, 29–38.
- Breitwisch, R., & Hudak, J. (1989). Sex differences in risk-taking behavior in foraging flocks of house sparrows. *Auk*, 106, 150–153.
- Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R., et al. (2006). From disorder to order in marching locusts. *Science*, 312, 1402–1406.
- Caraco, T., & Bayham, M. C. (1982). Some geometric aspects of house sparrow flocks. *Animal Behaviour*, 30, 990–996.
- Cohen, J. (1988). *Statistical power analysis for the behavioural sciences*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, 50, 1441–1453.
- Cross, P. C., Lloyd-Smith, J. O., Bowers, J. A., Hay, C. T., Hofmeyr, M., & Getz, W. M. (2004). Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger national park. *Annales Zoologici Fennici*, 41, 879–892.
- Csárdi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695.
- Dey, C. J., Reddon, A. R., O'Connor, C. M., & Balshine, S. (2013). Network structure is related to social conflict in a cooperatively breeding fish. *Animal Behaviour*, 85, 395–402.
- Edenbrow, M., Darden, S. K., Ramnarine, I. W., Evans, J. P., James, R., & Croft, D. P. (2011). Environmental effects on social interaction networks and male reproductive behaviour in guppies, *Poecilia reticulata*. *Animal Behaviour*, 81, 551–558.
- Edgington, E. S. (1995). *Randomization tests*. New York: Marcel Dekker.
- Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1829–1836. <http://dx.doi.org/10.1098/rspb.2008.1824>.
- Giraldeau, L.-A., & Caraco, T. (2000). *Social foraging theory*. Princeton, NJ: Princeton University Press.
- Giraudeau, P. (2006). 'pgirmess': Miscellaneous functions for analysis and displays of ecological and spatial data. Version 1.5.1. Retrieved from: <http://giraudeau.pagesperso-orange.fr/#pgirmess>.
- Griggio, M., Biard, C., Penn, D. J., & Hoi, H. (2011). Female house sparrows 'count on' male genes: experimental evidence for MHC-dependent mate preference in birds. *BMC Evolutionary Biology*, 11, 44.
- Griggio, M., & Hoi, H. (2010). Only females in poor condition display a clear preference and prefer males with an average badge. *BMC Evolutionary Biology*, 10, 261.
- Hodge, S. J., Thornton, A., Flower, T. P., & Clutton-Brock, T. H. (2009). Food limitation increases aggression in juvenile meerkats. *Behavioral Ecology*, 20, 930–935.
- Hoi, H., Tost, H., & Griggio, M. (2011). The effect of breeding density and male quality on paternity-assurance behaviours in the house sparrow, *Passer domesticus*. *Journal of Ethology*, 29, 31–38.
- Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, 263(4), 544–555.
- Hothorn, T., Hornik, K., van de Wiel, M. A., & Zeileis, A. (2008). Implementing a class of permutation tests: the coin package. *Journal of Statistical Software*, 28, 1–23.
- James, R., Croft, D. P., & Krause, J. (2009). Potential banana skins in animal social network analysis. *Behavioral Ecology and Sociobiology*, 63, 989–997.
- Johnstone, R. A., & Manica, A. (2011). Evolution of personality difference in leadership. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 8373–8378.
- Junker, B. H., & Schreiber, F. (2008). *Analysis of biological networks*. Hoboken, NJ: J. Wiley.
- Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. (2008). Early experience affects producer–scrounger foraging tendencies in the house sparrow. *Animal Behaviour*, 75, 1465–1472.
- Kelley, J. L., Morrell, L. J., Inskip, C., Krause, J., & Croft, D. P. (2011). Predation risk shapes social networks in fission-fusion populations. *PLoS One*, 6, e24280.
- King, A. J., Johnson, D. D. P., & Van Vugt, M. (2009). The origins and evolution of leadership. *Current Biology*, 19, R911–R916.
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, U.K.: Oxford University Press.
- Lea, A. J., Blumstein, D. T., Wey, T. W., & Martin, J. G. A. (2010). Heritable victimization and the benefits of agonistic relationships. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 21587–21592.
- Leblond, C., & Reeb, S. (2006). Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*). *Behaviour*, 143, 1263–1280.
- Lendvai, Á. Z., Liker, A., & Barta, Z. (2006). The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. *Animal Behaviour*, 72, 747–752.
- Liker, A., & Barta, Z. (2001). Male badge size predicts dominance against females in house sparrows. *Condor*, 103, 151–157.

- Liker, A., & Barta, Z. (2002). The effects of dominance on social foraging tactic use in house sparrows. *Behaviour*, 139, 1061–1076.
- Lusseau, D. (2007). Evidence for social role in a dolphin social network. *Evolutionary Ecology*, 21, 357–366.
- Moussaïd, M., Perozo, N., Garnier, S., Helbing, D., & Theraulaz, G. (2010). The walking behaviour of pedestrian social groups and its impact on crowd dynamics. *PLoS One*, 5, e10047.
- Nagy, M., Ákos, Z., Biro, D., & Vicsek, T. (2010). Hierarchical group dynamics in pigeon flocks. *Nature*, 464, 890–893.
- Nakagawa, S. (2004). A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology*, 15, 1044–1045.
- Oh, K. P., & Badyaev, A. V. (2010). Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *American Naturalist*, 176, E80–E89.
- Opsahl, T. (2009). *Structure and evolution of weighted networks* (Unpublished doctoral dissertation). U.K.: University of London.
- Opsahl, T., & Panzarasa, P. (2009). Clustering in weighted networks. *Social Networks*, 31, 155–163.
- Otterstatter, M. C., & Thomson, J. D. (2007). Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies. *Oecologia*, 154, 411–421.
- Pike, T. W., Samanta, M., Lindström, J., & Royle, N. J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2515–2520.
- Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-effects models in S and S-Plus*. New York: Springer.
- Polo, V., & Bautista, L. M. (2002). Daily body mass regulation in dominance-structured coal tit (*Parus ater*) flocks in response to variable food access: a laboratory study. *Behavioral Ecology*, 13, 696–704.
- R Development Core Team. (2013). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved from: <http://www.R-project.org>.
- Rands, S. A., Cowlshaw, G., Pettifor, R. A., Rowcliffe, J. M., & Johnstone, R. A. (2003). Spontaneous emergence of leaders and followers in foraging pairs. *Nature*, 423, 432–434.
- Rohwer, S., & Ewald, P. W. (1981). The cost of dominance and advantage of subordination in a badge signaling system. *Evolution*, 35, 441–454.
- Šárová, R., Špinká, M., Panamá, J. L. A., & Šimeček, P. (2010). Graded leadership by dominant animals in a herd of female beef cattle on pasture. *Animal Behaviour*, 79, 1037–1045.
- Sodhi, N. S. (1992). Sex and age differences in risk-taking behavior in house sparrows. *Condor*, 94, 293–294.
- Sueur, C., Deneubourg, J.-L., & Petit, O. (2012). From social network (centralized vs. decentralized) to collective decision-making (unshared vs. shared consensus). *PLoS One*, 7, e32566.
- Sueur, C., & Petit, O. (2008). Shared or unshared consensus decision in macaques? *Behavioural Processes*, 78, 84–92.
- Summer-Smith, J. D. (1963). *The house sparrow*. London, U.K.: W. Collins.
- Sundaresan, S. R., Fischhoff, I. R., Dushoff, J., & Rubenstein, D. I. (2007). Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager. *Oecologia*, 151, 140–149.
- Tóth, Z., Bókony, V., Lendvai, Á. Z., Szabó, K., Péntzes, Z., & Liker, A. (2009a). Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. *Behavioural Processes*, 82, 173–177.
- Tóth, Z., Bókony, V., Lendvai, Á. Z., Szabó, K., Péntzes, Z., & Liker, A. (2009b). Effects of relatedness on social-foraging tactic use in house sparrows. *Animal Behaviour*, 77, 337–342.
- Tóth, Z., & Griggio, M. (2011). Leaders are more attractive: birds with bigger yellow breast patches are followed by more group-mates in foraging groups. *PLoS One*, 6, e26605.
- Ward, P., & Zahavi, A. (1973). The importance of certain assemblages of birds as 'information-centers' for food-finding. *Ibis*, 115, 517–534.
- Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications*. New York: Cambridge University Press.
- Webster, M. M., Atton, N., Hoppitt, W. J., & Laland, K. N. (2013). Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *American Naturalist*, 181(2), 235–244.
- Whitehead, H. (2008). Precision and power in the analysis of social structure using associations. *Animal Behaviour*, 75, 1093–1099.
- Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: a key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology*, 67, 163–173.

Appendix

Table A1

Number of interactions/events recorded throughout the study

Flock	Session	All observations				Reduced number of observations			
		Arriving alone	Following	Aggression	Observation time (h)	Arriving alone	Following	Aggression	Observation time (h)
1	BEF	58	164	67	17.97	55	137	58	15.91
	TR	54	192	92	17.25	46	174	87	15.91
	AFT	38	197	44	15.91	38	197	44	15.91
2	BEF	61	156	19	16.54	61	156	19	16.54
	TR	64	208	37	17.27	60	197	36	16.54
	AFT	86	200	17	16.91	81	191	17	16.54
3	BEF	51	176	6	16.36	51	176	6	16.36
	TR	43	202	61	16.99	43	200	59	16.36
	AFT	73	127	13	17.34	69	122	13	16.36
4	BEF	59	90	4	14.58	59	90	4	14.58
	TR	55	116	57	15.10	54	106	55	14.58
	AFT	41	137	18	15.57	37	131	17	14.58
5	BEF	52	159	15	17.42	51	141	13	16.32
	TR	50	163	40	17.54	45	151	38	16.32
	AFT	49	147	15	16.32	49	147	15	16.32
6	BEF	43	126	8	13.65	43	126	8	13.65
	TR	21	151	55	15.08	20	138	53	13.65
	AFT	50	168	45	17.05	41	132	42	13.65
7	BEF	64	141	28	17.61	64	141	28	17.61
	TR	60	101	45	17.79	60	97	45	17.61
	AFT	57	117	14	17.72	57	115	14	17.61
8	BEF	44	99	11	12.55	42	97	11	12.39
	TR	44	93	23	12.39	44	93	23	12.39
	AFT	40	72	14	12.48	38	71	13	12.39
9	BEF	35	110	12	11.10	35	108	9	10.89
	TR	42	108	37	11.06	42	105	36	10.89
	AFT	37	102	24	10.89	37	102	24	10.89

BEF indicates the 'Before treatment', TR the food manipulation 'Treatment' and AFT the 'After treatment' sessions. 'Arriving alone' refers to birds arriving alone at the feeder, 'Following' to birds following other individuals to the feeder and 'Aggression' to aggressive interactions at the feeder. See text for an explanation of 'Reduced number of observations'.

Table A2

Estimated parameters of the random effects in the final LME models (both from the group-level and individual-level analyses)

	Dependent variable	Predictor(s) in the final model	Random factor	Between-group estimate (SD) [95% CI]	Within-group estimate (SD) [95% CI]
Group-level analyses	Frequency of feeding alone	—	Flock	0.36 [0.14–0.94]	0.58 [0.42–0.80]
	Frequency of aggressive interactions	Session	Flock	0.73 [0.39–1.38]	0.67 [0.47–0.94]
	Frequency of following	—	Flock	1.40 [0.73–2.67]	1.33 [0.96–1.85]
	Variance of weighted reciprocity	—	Flock	0.01 [0.01–0.03]	0.02 [0.01–0.03]
	Weighted transitivity	—	Flock	0.07 [0.04–0.13]	0.06 [0.04–0.08]
	Variance of in-degree	—	Flock	1.75 [0.80–3.81]	2.24 [1.61–3.10]
	Variance of out-degree	—	Flock	1.12 [0.43–2.91]	1.80 [1.30–2.50]
	Variance of in-strength*	—	Flock	2.37 [1.28–4.40]	2.06 [1.48–2.85]
	Variance of out-strength	—	Flock	18.92 [9.89–36.19]	18.17 [13.11–25.19]
	Centralization index	—	Flock	0.04 [0.02–0.09]	0.05 [0.04–0.07]
Individual-level analyses	In-strength*	Sex+Age	Individual	1.00 [0.85–1.19]	0.84 [0.76–0.92]
	Out-strength*	Flock+Sex+Age×Session	Individual	0.59 [0.48–0.74]	0.72 [0.65–0.79]

* Square-root transformed.