



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



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ARTICLE INFO

Article history:

Received 15 July 2013

Initial acceptance 20 August 2013

Final acceptance 19 December 2013

Available online 26 February 2014

MS. number: 13-00587R

Keywords:

foraging

group cohesion

leadership

social network

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

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