Animal Behaviour 132 (2017) 201–208

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Friends give benefits: autumn social familiarity preferences predict reproductive output

Gregory M. Kohn*

Psychological and Brain Sciences, Indiana University, Bloomington, IN, U.S.A.

ARTICLE INFO

Article history:
Received 29 March 2017
Initial acceptance 1 May 2017
Final acceptance 22 June 2017

MS. number: A17-00283

Keywords:
brown-headed cowbird
familiarity
fission–fusion dynamics
reproduction
social dynamics
social network
social niche

Fission–fusion dynamics create social instability, as individuals must adjust to changes in group size and composition. In many social species, group changes are associated with increases in aggression, stress responses and individual mortality. It has been hypothesized that fission–fusion processes select for strong bonds between familiar individuals that provide a predictable social environment across group changes. In the present study, I explored whether familiar social networks remain predictable across periods of social instability in brown-headed cowbird, *Molothrus ater*, flocks, and whether females who sustain stronger autumn familiarity preferences show higher reproductive output during the spring. During autumn, the organization of familiar social networks remained predictable across a series of introductions with novel flocks. Familiar individuals were able to maintain their relationships with each other despite large-scale group perturbations. During the spring, I found that autumn familiarity preference was the only predictor of reproductive output, with female cowbirds that sustained the strongest familiarity preferences laying more eggs than other females. These findings suggest that familiarity preferences have a cascading influence on later reproductive performance, and that the social dynamics of fission–fusion groups select for a familiarity-based social organization.

Most social vertebrates inhabit fission–fusion groups where group size and composition change over short timescales. Such changes create social instability, as individuals modify established behavioural routines in response to novel conspecifics (Aureli et al., 2008; Couzin, 2006). Social instability is often associated with increases in aggression, greater stress responses and higher incidents of mortality, especially among females (Capitanio, Mendoza, Lerche, & Mason, 1998; Marler, 1976; Sapolsky, 1983). Consistent differences in the frequency, content and selectivity of individual social interactions have been observed in a wide range of vertebrates. Some social vertebrates reduce the costs of social instability by consistently interacting with familiar individuals across group changes (Silk, 2007). In the present study, I explored whether such consistent differences in autumn social interaction preferences are associated with reproductive benefits during the breeding season in female brown-headed cowbirds, *Molothrus ater*.

Individuals depend on a diverse range of social interactions to facilitate and sustain life in a group. Nevertheless, studies investigating the social contributions to reproduction often focus on interactions between mates, with only a few studies investigating within-group interactions outside breeding periods (Arnberg, Shizuka, Chaine, & Lyon, 2015; Firth & Sheldon, 2016; Shizuka et al., 2014). In some social mammals, females construct predictable social networks by maintaining strong bonds with familiar females. Such bonds are thought to have adaptive value, as stronger bonds between familiar females are associated with fewer aggressive interactions, lower stress levels and higher reproductive success (Cameron, Setsaas, & Linklater, 2009; Capitanio et al., 2008; Silk, 2007). Like mammals, many bird species inhabit year-round social groups where changes in social composition are associated with increased rates of aggression, higher stress and lower reproductive output (Guibert et al., 2010; Riedstra & Groothuis, 2002; Zayan, 1991). Therefore, the ability to maintain predictable familiar relationships with others across group changes provides advantages that can ultimately reflect differences in fitness (Emery, Seed, von Bayern, & Clayton, 2007).

As obligate brood parasites, brown-headed cowbirds (hereafter cowbirds) do not exhibit parental care. The range of the cowbird extends from northern Canada during the spring and summer to Central America in the winter. In autumn and winter, cowbirds form large mixed-age and mixed-sex flocks that forage and roost together. These flocks dissipate in spring as cowbirds form

* Correspondence: G. M. Kohn, Department of Psychological and Brain Sciences, Indiana University, 1101 E. 10th Street, Bloomington, IN 47405, U.S.A.
E-mail address: gmkohn@indiana.edu.

http://dx.doi.org/10.1016/j.anbehav.2017.08.013
0003-3472/

monogamous pairs, where males compete with other males over access to females, and females maintain home ranges where they inspect, defend and deposit eggs in host nests (Darley, 1982; Friedmann, 1929; Ortega, 1998; Yokel, 1989). Cowbirds are generalist brood parasites and have been observed to parasitize over 220 species. Thus, unlike many altricial species, where clutch size is often limited, the number of eggs a female cowbird deposits in host nests is a significant aspect of each pair's reproductive success.

The organization of autumn cowbird flocks reflects the maintenance of strong social preferences in females. In mixed-age, mixed-sex flocks, females show strong age- and sex-based social preferences, preferentially interacting with females of similar age (Gros-Louis, White, King, & West, 2003; Kohn, King, Scherschel, & West, 2011). In response to the fusion of two novel flocks, females also exhibit significant preferences for familiar conspecifics, while males do not (Kohn, Gwendŵr, Magdaleno, King, & West, 2015). As responses to novel and juvenile conspecifics are more likely to be aggressive, strong female social preferences have been hypothesized to limit disruptive interactions and create a more predictable social environment (Freed-Brown, King, Miller, & West, 2006). If selection favours the construction of predictable social environments, then stronger social preferences should confer advantages to an individual's ability to survive and reproduce in the group. Nevertheless, across many species little is known about the consistency of individual social preferences and their association with later fitness.

In cowbird flocks, the consistency of social interactions varies by sex. In females, differences in the frequency of social interactions and the strength of social preferences are consistent over time and across contexts (Kohn et al., 2011). In response to fission–fusion group changes, some females remain more sociable than others, and more frequently approach and direct affiliative displays towards conspecifics (Kohn, King, Dohme, Meredith, & West, 2013a; Kohn et al., 2011). Females are also consistent in their preference to interact with familiar and same-sex conspecifics (Kohn et al., 2015), with some females maintaining stronger preferences for familiar individuals when novel flocks are combined. Males show greater plasticity in their social preferences than females, with individual differences in male familiarity preferences being significantly less repeatable than females across group changes (Kohn et al., 2015).

While social preferences are central to cowbird social organization (Gros-Louis et al., 2003; Kohn et al., 2011, 2015), it is unknown how individual variation in familiarity preferences predicts later reproductive output. In familiar autumn flocks, the frequency of interactions predicts later reproductive performance, with more sociable females developing courtship skills sooner (Kohn, King, Dohme, Meredith, & West, 2013b) and producing more eggs as adults (Kohn et al., 2013a). Nevertheless, flocks composed entirely of familiar individuals are likely uncommon, as cowbirds form large flocks with resident and migratory individuals (Ortega, 1998). In such flocks individuals navigate interactions with familiar and novel conspecifics (Friedmann, 1929), and previous studies have shown that females show stronger social preferences during fusion events with novel flocks than during fusion events with flocks of familiar conspecifics who have been separated (Kohn et al., 2015). These findings suggest that female cowbirds recognize novel individuals and adjust their social preferences in their presence.

I hypothesized that social instability selects for strong and consistent preferences for familiar conspecifics. The present study follows up on Kohn et al.'s (2015) study, where four flocks of familiar individuals experienced a series of two introductions with novel flocks during autumn. Here, I investigated whether the social networks created by familiar individuals remained predictable across these novel introductions, and whether females with stronger autumn familiarity preferences showed greater reproductive output the following spring. Across autumn introductions, I used social network models to investigate whether familiar individuals rewired or maintained connections with other familiar conspecifics. The following spring all four flocks were combined in a large aviary complex, and the number of eggs each female laid in decoy host nests was recorded. I used permuted regression models to explore whether consistent individual differences in social preferences and frequency of interactions across autumn introductions predicted the number of eggs a female laid the following breeding season.

METHODS

Subjects

All individuals in this study were brown-headed cowbirds, *M. ater ater*. The average age was 6 years in autumn 2012 (age range 1–12 years). All individuals were caught in Indiana or Pennsylvania, U.S.A., and fitted with uniquely coloured leg bands. All bird were fed daily the standard Bronx Zoo diet for blackbirds, along with a millet and canary seed mixture that was available ad libitum.

Aviaries

I used a single large aviary complex to conduct the novel introductions used in this experiment. The large aviary complex consisted of four aviaries each with identical dimensions ($9.1 \times 21.4 \times 3.4$ m), one small subsection ($11 \times 3 \times 3.4$ m) and three indoor enclosures. An auxiliary aviary complex contained two aviaries of identical dimensions to the aviaries in the large complex but was both visually and acoustically separate from the large aviary complex. The auxiliary complex was used to house birds before the introductions. Partitions between neighbouring aviaries could be opened or closed. Each subsection of the aviary contained a covered feeding station, water bowls and foliage, and provided cowbirds significant degrees of freedom to engage or avoid conspecifics.

Behavioural Observations

I utilized a scan-sampling procedure: the entire flock was scanned and behaviours were recorded as they were observed. During scan sampling all behaviours were recorded using voice recognition technology described in detail by White, King, and Duncan (2002). When used in combination with voice recognition technology, scan sampling can accurately acquire a more comprehensive data set than focal sampling (White & Smith, 2007). During scan sampling, I recorded individual approach behaviour. An approach was scored when one individual approached another within a 30 cm radius around their body and the recipient of the approach did not withdraw for 1 s. Such a definition reflects the ability of an individual to initiate close proximity, without initiating a withdrawal. All observations were conducted between 0700 and 1030 hours. Two observers conducted all scan sampling in this study and reliability between the two observers was high at 83% (intraclass correlation coefficient $= 0.83$, $F_{1,29} = 10.9$, $P < 0.0001$).

Egg Collection

During the spring, video-monitored decoy nests were used to record the number of eggs each female laid. Six decoy nests were installed in each of the four large subsections of the aviary complex. Each nest was mounted on a forked perch attached to a backboard that contained a video camera and was installed on posts or bushes