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.

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.

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 × 21.4 × 3.4 m), one small subsection (11 × 3 × 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

in the aviary. All nests were supplied with yoghurt-covered raisins as decoy eggs. A decoy egg was added every day to each nest until the nest contained three decoy eggs. Each day, all nests were checked for the presence of cowbird eggs laid during the morning. After 8 days in one area, each nest was moved to a different location within the aviary. All nests were video-monitored to determine the identity of laying females by using Geovision software (http://www.geovision.com.tw/).

2013 Novel Introduction Experiment

Baseline period

On 2 October 2013, birds were separated into the four aviaries (Aviaries 1–4) within the large aviary complex. Two flocks previously housed in the auxiliary aviary complex were moved into Aviary 1 and Aviary 3 within the large aviary complex. All birds separated into Aviary 1 (10 females, 7 males) and Aviary 2 (5 females, 8 males), and in Aviaries 3 (11 females, 7 males) and 4 (6 females, 7 males) had never previously interacted. All birds were allowed to acclimate to the new surroundings from 2 October to 19 October. From 2 October to 19 October 2013, two observers conducted a total of 107 7-minute observation blocks (Aviary 1: 29 blocks; Aviary 2: 25 blocks; Aviary 3: 29 blocks; Aviary 4: 24 blocks).

First introduction

On 20 October, the partitions separating Aviaries 1 and 2 as well as Aviaries 3 and 4 were opened, allowing the pairs of flocks to interact and to form Aviaries 1–2 and 3–4, respectively. From 20 October to 28 October 2013, two observers conducted a total of 328 7-minute observation blocks (Aviary 1–2: 164 blocks; Aviary 3–4: 164 blocks). Introductions were conducted so that the resulting flocks had similar sex ratios, with Aviary 3–4 having only two more females than males and Aviary 1–2 having equal number of males and females. Across both autumn introductions there were no significant differences in age of the individuals (mean age: Aviary 1–2: 6.12 years old; Aviary 3–4: 6.15 years old; Wilcoxon two-sample test: $W = 481$, $P = 0.82$.

Second introduction

On 4 November, birds originally from Aviary 2 were moved into Aviary 3–4 and birds originally from Aviary 4 were moved into Aviary 1–2. From 4 November to 17 November 2013, a total of 306 blocks were recorded between two observers (Aviary 1–2: 138 blocks; Aviary 3–4: 138 blocks).

Breeding season egg collection

On 1 April, all partitions between the neighbouring aviaries were removed and all birds were allowed to freely interact. On 1 May, six video-monitored decoy nests were installed in each aviary. From 2 May to 7 July, nests were checked each morning, eggs were collected and the identity of the laying females recorded.

Analysis

Predictability of familiar social networks

To assess the predictability or flexibility of familiar social networks across the two introductions, I performed social network analysis in R using the statnet and asnipe packages (Farine, 2013; Handcock, Hunter, Butts, Goodreau, & Morris, 2008). While previous analysis has shown that female cowbirds prefer familiar over novel conspecifics (Kohn et al., 2015), this analysis examined whether cowbirds maintain consistent dyadic familiar relationships across novel group mergers. Group perturbations can reorganize familiar networks by changing the relationships between

familiar conspecifics. Flexible familiar networks reflect the tendency of individuals to change which familiar conspecifics they interact with, and how often they interact with them across group changes. Predictable, or robust, familiar networks reflect the tendency of individuals to interact with the same familiar conspecifics at similar frequencies across group changes.

To assess the predictability of the familiar social network structure across the three introductions, I used multiple regression quadratic assignment procedure (MRQAP) models for weighted networks with double semipartialling procedure to control for the influence of collinearity between dependent variables (Dekker, Krackhardt, & Snijders, 2007). This procedure is analogous to the classic regression, except here a dependent matrix is regressed against a series of predictor matrices. Because dyadic connections within social network data are not independent, the MRQAP permutes the order of the dependent matrix in order to create a null distribution that randomizes who interacts with whom while preserving the overall structural features of the network. The analysis investigated the predictability of the social network across the two novel introductions. Here the dependent matrix was the social network observed in the second introduction, and the predictor was the social network observed in the first introduction. Significant effects indicate that the organization of the social network observed during the baseline period had a significant influence on the social network observed during the first introduction.

I used post hoc Mantel tests and structural correlation coefficients to calculate the strength and direction of the correlation between the social networks in the first and second introduction (Butts & Carley, 2001). Predictable familiar relationships reflect positive structural correlation coefficients, while changing familiar relationships reflect a negative structural correlation coefficient. To assess the significance of structural correlation coefficients, I used a conditional uniform graph test (cugtest in statnet). This test uses a Monte Carlo procedure for determining whether observed network metrics are significant based on a bootstrapped distribution of the strength of ties (how often two individuals interacted) between individuals drawn from the observed social networks. Each cugtest in the analysis used 10 000 repetitions.

Autumn social niches and spring reproductive output

To assess how autumn social behaviour influenced spring egg production, I performed a permuted linear regression model using the lmPerm package (Wheeler, 2010). I conducted two models, one with all females included ('all female model') and the one restricted only to laying females ('laying female model').

Both models contained the number of eggs a female produced during the breeding season as the dependent variable. I calculated three aspects of autumn social behaviour to use as explanatory variables in the model. Previous studies have shown that each of these three measures exhibits high between-individual repeatability over time and across contexts (Kohn et al., 2013b, 2015, 2013a). The first variable was the total number of approaches each female initiated towards all other conspecifics during both introductions. The second variable was a female's social familiarity preference or the proportion of approaches directed towards familiar conspecifics out of the total number of approaches across the two autumn introductions. The third variable was the female's same-sex preference, which measured the proportion of approaches directed towards female conspecifics by the total number of approaches across the two introductions. In addition to these variables, I included the individual's age along with the original baseline aviary conditions to uncover any influences of age and aviary.

All permuted linear models were simplified through the selection of terms based on minimizing the Akaike's information criteria (AIC) using both drop1 and step functions in R. Variance inflation factors (VIF) were used to assess multicollinearity. VIFs were calculated for both the saturated models and for each resulting model during model simplification. In none of the presented models did the VIFs for any factor exceed 3. I conducted post hoc analysis between explanatory variables and eggs laid using Spearman's correlations, with 95% confidence intervals calculated using resampling techniques.

Ethical Note

All work was conducted under ASAB/ABS guidelines and approved by the Institutional Care and Use Committee of Indiana University (08-018). Animals were collected with federal permit number (MB767881-0) using a funnel trap that was checked multiple times per day. Birds were immediately moved to a larger holding aviary ($9.1 \times 21.4 \times 3.4$ m) after capture. No potentially harmful or invasive manipulations were used in this study and handling was kept at a minimum in order to reduce stress. The experimental manipulations were designed to mimic fission−fusion dynamics observed in the wild, and the large aviaries provided significant space for individuals to choose to interact or not and escape from aggressive interactions. After the completion of this study all the birds were maintained in the laboratory to be used in further experiments.

RESULTS

Predictability of Familiar Networks across Introductions

Familiar social networks exhibited consistent structure across the two introductions. All MRQAP models were significant and explained 13−46% of the variance in the structure of the networks observed during the second introduction (Table 1). For each MRQAP model, the network observed during the first introduction was a significant explanatory factor for the network observed during the second introduction (Table 1). Post hoc tests showed a positive structural correlation coefficient that was significant across Aviaries 2, 3 and 4 but did not reach significance for the Aviary 1 (Table 1, Fig. 1).

Egg Production and Autumn Social Behaviour

The minimal model for all females explained 38% of the variance in the number of eggs produced ($F_{1,22} = 13.31$, $P = 0.001$), while the model on laying females explained 37% of the variance ($F_{1,11} = 6.417$, $P = 0.027$). Both models contained a significant influence of familiarity preference on the number of eggs laid (all females: estimate = 40.04, iterations = 5000, $P < 0.0001$; laying females: estimate = 37.3, iterations = 5000, $P = 0.033$). All other explanatory factors were removed from the models during simplification. Females that had stronger autumn familiarity preferences were more likely to lay more eggs during the breeding season (all females: $r_S = 0.54$, $N = 24$, $P = 0.007$, 95% CI = 0.14−0.76, laying females: $r_S = 0.66$, $N = 13$, $P = 0.001$, 95% CI = 0.28−0.77; Fig. 2).

To examine familiarity preferences further, I separated preferences for familiar females and familiar males. Across all females, there was a significant correlation between autumn familiar female preferences and number of eggs laid ($r_S = 0.54$, $N = 24$, $P = 0.007$, 95% CI = 0.17−0.79), but only a tendency for male familiarity preferences to correlate with number of eggs laid ($r_S = 0.37$, $N = 24$, $P = 0.07$, 95% CI = 0.01−0.68). When I restricted the analysis to laying females, there was a significant correlation between female and male familiar preferences and number of eggs laid (male: $r_S = 0.66$, $N = 13$, $P = 0.01$, 95% CI = 0.22−0.89; female: $r_S = 0.62$, $N = 13$, $P = 0.01$, 95% CI = 0.16−0.89).

There was no significant relationship between the number of approaches initiated by individual females (all females: $r_S = -0.29$, $N = 24$, $P = 0.16$, 95% CI = −0.59−0.04; laying females: $r_S = -0.30$, $N = 13$, $P = 0.32$, 95% CI = −0.67−0.56) and the strength of females' same-sex preferences (all females: $r_S = 0.03$, $N = 24$, $P = 0.87$, 95% CI = −0.33−0.39; laying females: $r_S = 0.06$, $N = 13$, $P = 0.85$, 95% CI = −0.66−0.28) or female age (all females: $r_S = -0.13$, $N = 24$, $P = 0.55$, 95% CI = −0.52−0.50; laying females: $r_S = 0.01$, $N = 13$, $P = 0.79$, 95% CI = −0.60−0.49) on the number of eggs they produced.

DISCUSSION

To my knowledge, this is the first documentation that social familiarity preferences during nonbreeding periods reflect later reproductive output in birds. In cowbirds, the organization of familiar social networks remained predictable across introductions. During the breeding season, females with stronger familiarity

Table 1
Tests for predictability of social network structure across the first and second introductions

	Predictors			Full model		
MRQAP	Aviary	Estimate	*P*	*F*	*R*^{2}	*P*
	1	0.31	<0.0001[a]	22.22	0.13	0.001[a]
	2	0.52	<0.0001[a]	50.16	0.17	<0.0001[a]
	3	0.46	<0.0001[a]	234.1	0.46	<0.0001[a]
	4	0.57	<0.0001[a]	41.41	0.21	<0.0001[a]
Structural correlation	Aviary	*r*	*P*			
	1	0.48	0.25			
	2	0.60	<0.001[a]			
	3	0.61	<0.001[a]			
	4	0.51	0.005[a]			
Mantel test	Aviary	*Z*	*P*			
	1	6028	0.225			
	2	2086	0.035[a]			
	3	7958	0.017[a]			
	4	4145	0.007[a]			

MRQAP: multiple regression quadratic assignment procedure.
[a] Indicates significant effect.
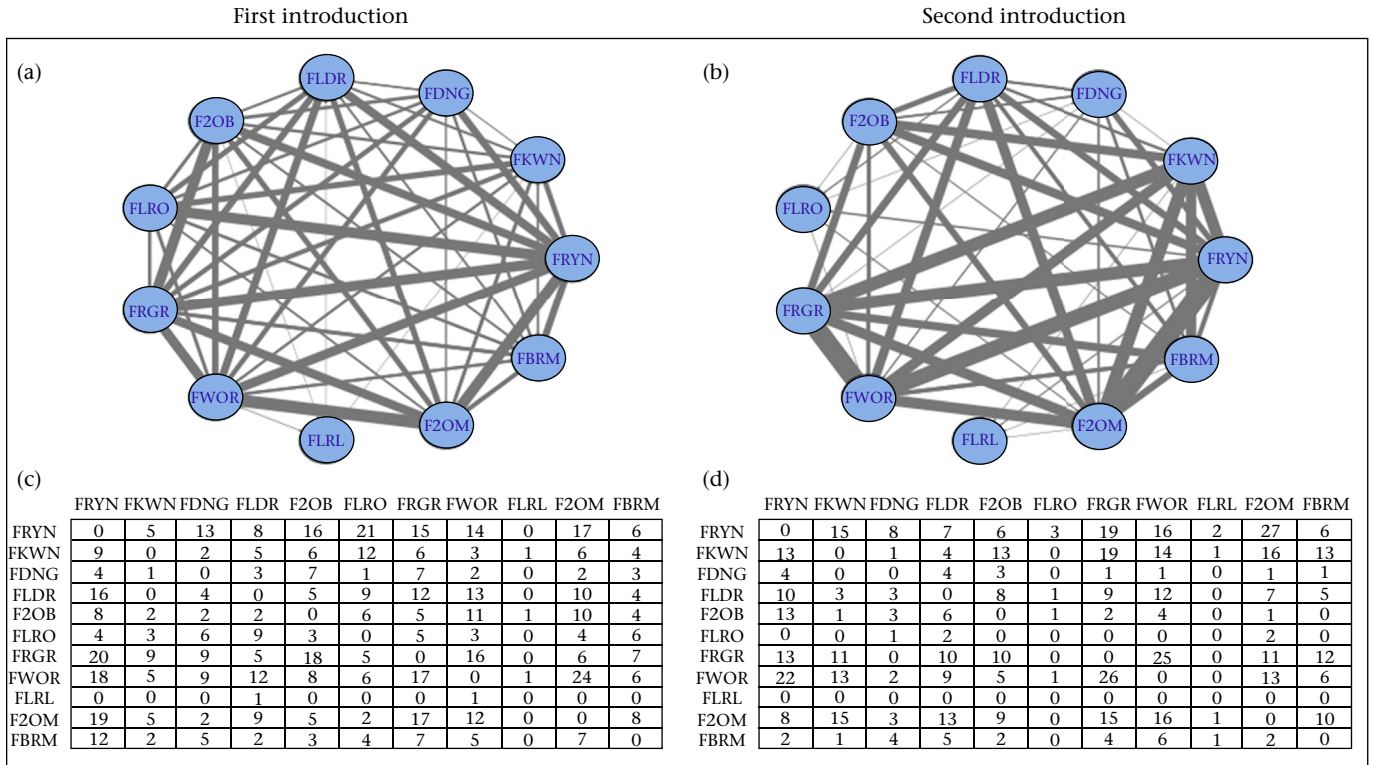
First introduction

Second introduction

Figure 1. Examples of the social networks observed between familiar females during the (a) first and (b) second introduction from one of the four original aviaries (Aviary 3), and the social interaction matrix with the frequencies that familiar females approached each other during the (c) first and (d) second introduction from Aviary 3. Rows represent individuals who initiated the approach, and columns represent individuals who received the approach.
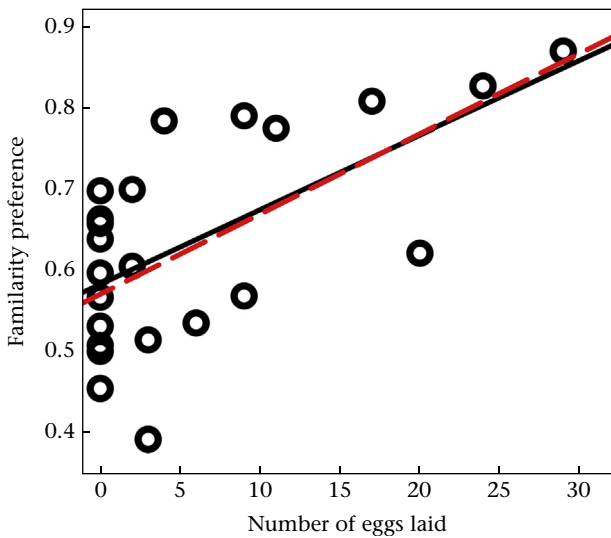
(c)

	FRYN	FKWN	FDNG	FLDR	F2OB	FLRO	FRGR	FWOR	FLRL	F2OM	FBRM
FRYN	0	5	13	8	16	21	15	14	0	17	6
FKWN	9	0	2	5	6	12	6	3	1	6	4
FDNG	4	1	0	3	7	1	7	2	0	2	3
FLDR	16	0	4	0	5	9	12	13	0	10	4
F2OB	8	2	2	2	0	6	5	11	1	10	4
FLRO	4	3	6	9	3	0	5	3	0	4	6
FRGR	20	9	9	5	18	5	0	16	0	6	7
FWOR	18	5	9	12	8	6	17	0	1	24	6
FLRL	0	0	0	1	0	0	0	1	0	0	0
F2OM	19	5	2	9	5	2	17	12	0	0	8
FBRM	12	2	5	2	3	4	7	5	0	7	0

(d)

	FRYN	FKWN	FDNG	FLDR	F2OB	FLRO	FRGR	FWOR	FLRL	F2OM	FBRM
FRYN	0	15	8	7	6	3	19	16	2	27	6
FKWN	13	0	1	4	13	0	19	14	1	16	13
FDNG	4	0	0	4	3	0	1	1	0	1	1
FLDR	10	3	3	0	8	1	9	12	0	7	5
F2OB	13	1	3	6	0	1	2	4	0	1	0
FLRO	0	0	1	2	0	0	0	0	0	2	0
FRGR	13	11	0	10	10	0	0	25	0	11	12
FWOR	22	13	2	9	5	1	26	0	0	13	6
FLRL	0	0	0	0	0	0	0	0	0	0	0
F2OM	8	15	3	13	9	0	15	16	1	0	10
FBRM	2	1	4	5	2	0	4	6	1	2	0

Figure 2. Correlation between autumn familiarity preferences. Solid line is the regression line from the permuted linear regression for all individuals, and the dashed line represents the permuted linear regression only for individuals that laid eggs.

preferences across the two autumn introductions laid more eggs than other females. These findings demonstrate that stronger preferences for a consistent and familiar social environment are predictive of later reproductive benefits in females.

Organisms shape the social environment they experience through their behavioural interaction choices (Flynn, Laland, Kendal, & Kendal, 2013; Laskowski & Pruitt, 2014; Saltz & Nuzhdin, 2014). Variation in the frequency and selectivity of

social interaction is a significant component of success in the group and will shape how individuals respond to changes in group size and composition (Cote, Dreiss, & Clobert, 2008; Farine & Sheldon, 2015). In cowbird flocks, some females are more likely to seek out interactions with novel conspecifics in response to group changes. When novel conspecifics integrate into an established group, they disrupt previously existing social networks and thus create some social instability. Other females will be more likely to maintain connections with familiar conspecifics, which strengthens the cohesion of the familiar network and buffers against the instability caused by novel conspecifics. By understanding the reproductive correlates of such variation we will gain insights into the factors shaping the evolution of social organization in unstable environments.

Social instability is associated with adverse effects across a range of vertebrates (Baranyi, Bakos, & Haller, 2005; Capitanio & Cole, 2015; Guibert et al., 2010; Herzog et al., 2009; Sapolsky, 1983; Wikelski, Hau, & Wingfield, 1999). In some social contexts increased social exploration allows individuals to assess potential competitors and cooperators, learn novel behaviours and select advantageous social environments (McDonald, 2007; Oh & Badyaev, 2010; White, Gersick, & Snyder-Mackler, 2012). In less stable contexts there are fewer benefits to seeking interactions with novel individuals, as high instability can induce chronic stress, depression and anxiety and result in lower overall sociability (Baranyi et al., 2005; Haller, Fuchs, Halász, & Makara, 1999; Herzog et al., 2009). Mice and rats that experience compositional changes in group housing show reduced fat distributions, higher rates of metabolic disease and lasting deficits in spatial memory (DeVries, Glasper, & Detillion, 2003). Female Japanese quail, *Coturnix japonica*, exposed to novel conspecifics deposited more testosterone in their eggs, and their offspring developed more slowly

than females housed in predictable social conditions (Guibert et al., 2010). When housed in a changing social group, macaques (*Macaca mulatta*) with simian immunodeficiency virus (SIV) were more likely to engage in aggressive interactions, had higher concentrations of the SIV virus and higher rates of mortality (Capitanio et al., 1998; Mendoza, Capitanio, & Mason, 2000).

To offset these challenges, individuals should seek to form enduring connections with familiar individuals when group compositions change. Strong and enduring bonds between familiar females have been shown to provide substantial advantages (Silk, 2007). In primates and horses, females that have stronger bonds with other familiar females have higher reproductive success, experience lower levels of aggression and stress and have longer life spans (Cameron et al., 2009; Capitanio et al., 2008; Silk, 2007). In savanna baboons, *Papio cynocephalus ursinus*, stronger bonds between familiar females are associated with higher levels of offspring survival (Silk et al., 2009).

While less is known about the benefits of familiar relationships in birds, the similarities between avian and mammalian social systems are increasingly being demonstrated (Emery et al., 2007; de Waal & Tyack, 2002). The association between egg production during the spring and familiarity preferences across changing autumn flocks suggests that social interactions can have long-term implications for cowbird fitness. In territorial great tits, *Parus major*, familiar neighbours are more likely to participate in joint nest defense, and pairs that retain more familiar neighbours across years have larger clutches and exhibit higher offspring survival (Grabowska-Zhang, Sheldon, & Hinde, 2012; Grabowska-Zhang, Wilkin, & Sheldon, 2011). In dark-eyed junco, *Junco hyemalis*, flocks, familiarity with the most dominant individual results in higher status in the social hierarchy after the fusion of two groups (Cristol, 1995). These finding demonstrate that the familiarity and predictability of social networks plays a role in shaping individual success in bird flocks and may shape the evolution of avian social organization.

The organization of familiar social networks in cowbirds is robust. Familiar conspecifics maintained similar relationships with each other across novel group mergers. Such consistency is not inevitable, as group changes can rewire the connections between familiar individuals (Flack, Girvan, de Waal, & Krakauer, 2006; Sih & Watters, 2005). This is especially true in animals with strong dominance hierarchies, where the addition of a single individual can shift all previously established dominance relationships (Kubitza, Suhonen, & Vuorisalo, 2015). Such predictable familiar networks have also been observed in other avian species. Golden-crowned sparrows, *Zonotrichia atricapilla*, exhibit cross-year stability in who they flock with on wintering grounds (Shizuka et al., 2014). Eurasian siskins, *Carduelis spinus*, maintain social bonds with familiar individuals across group changes (Senar, Camerino, & Metcalfe, 1990) and move across the landscape in familiar groups (Senar, Kew, & Kew, 2015). While the mechanisms underlying the maintenance of familiar networks are unknown, their consistency over time suggests that individuals in many avian species seek to sustain, rather than change, their relationships with other familiar individuals.

The present study uncovered a predictive relationship between consistent individual differences in autumn familiarity preferences and later reproductive output in females. Many potential mechanisms could mediate this relationship. For instance, females that are healthier could be better able to control whom they associate with during the breeding season, be more dominant and better able to outcompete others for access to mates and food. Thus, healthy and dominant females may be more selective in their interactions during autumn and produce more eggs during the breeding season.

Nevertheless, as females do form stable familiar subgroups over group changes (Kohn et al., 2015), it is likely that strong autumn familiar bonds provide benefits that have cascading influences on later reproductive output.

A common benefit of familiar relationships is the reduction of aggressive interactions (Marler, 1976). This is especially important for females where the cost of aggression or harassment by novel males can be substantial and reduce later reproductive output (Cameron et al., 2009; Dadda, Pilastro, & Bisazza, 2005; Gros-Louis et al., 2003; Persuad & Galef, 2003). Cowbirds show site fidelity on their breeding and wintering grounds and likely contact familiar cowbirds across years. During migratory periods, cowbirds join large flocks with both familiar and novel conspecifics (Ortega, 1998). While the risk of aggressive behaviours between familiar and unfamiliar cowbirds is unknown, studies have shown that females are more aggressive when the density of a flock is greater (Yokel, 1989), and that behavioural or acoustic cues from novel cowbirds elicit aggressive responses from females (Rothstein, Yokel, & Fleischer, 1988). While the design of this study did not assess the influence of familiarity on aggression, the findings suggest that strong familiarity preferences can provide a buffer against unnecessary aggressive interactions with novel individuals during unstable periods.

Cowbirds learn local mate preference through interacting with other females during autumn (Freeberg, 1997; Freeberg, Duncan, Kast, & Enstrom, 1999; West, King, & Freeberg, 1996; West, King, White, Gros-Louis, & Freed-Brown, 2006). Learning from familiar conspecifics would allow individuals to acquire relevant mate preferences and competent courtship behaviours, making them better prepared to navigate reproductive interactions during the breeding season (West et al., 2006). Preferences for familiar males might foster better mate complementarity, allowing earlier pairing and more coordinated courtship and mate guarding (Choudhury & Black, 1994). In the breeding season, female behavioural and vocal responses to male courtship displays stimulate eggs production (Maguire, Schmidt, & White, 2013), and females could be more likely to respond to familiar male courtship displays in contrast to novel male courtship displays. Across changing autumn flocks, familiar preferences may contribute to the emergence of local mate preferences by directing attention towards local males and the mate preferences of other local females. While it is currently unknown how variation in social preferences influence the strength and quality of a female's mate preferences, further investigations will explore how variation in familiarity preference affects the development of mate preferences in female cowbirds.

Interactions with conspecifics outside of breeding periods are common in most vertebrates, and uncovering how such interactions shape later fitness will further our understanding of the evolution of social organization. Social preferences are the basis for animal social organization (Hinde, 1976; Maier & Schneirla, 1964), and variation in preferences will directly shape the environment that individuals experience. This study is the first to provide evidence that a strong autumn preference for familiar conspecifics is linked to increased reproductive success in birds, findings previously restricted to social mammals (Capitanio et al., 1998; Mendoza et al., 2000; Silk, 2007). Coping with social instability is a major challenge in complex social systems, and the selection pressures arising from changing groups will have a significant influence on the evolution of animal social organization (Aureli et al., 2008; Marler, 1976; Silk et al., 2009). Exploring how individual variation in social preferences develops and shapes fitness will lead to a better understanding of the mechanisms governing the stability and evolution of social organization.

Acknowledgments

References

Arnberg, N. N., Shizuka, D., Chaine, A. S., & Lyon, B. E. (2015). Social network structure in wintering golden-crowned sparrows is not correlated with kinship. *Molecular Ecology, 24*(19), 5034–5044.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., et al. (2008). Fission–fusion dynamics. *Current Anthropology, 49*, 627–654.

Baranyi, J., Bakos, N., & Haller, J. (2005). Social instability in female rats: The relationship between stress-related and anxiety-like consequences. *Physiology & Behavior, 84*(4), 511–518.

Butts, C., & Carley, K. (2001). *Multivariate methods for inter-structural analysis* [CASOS working paper]. Pittsburgh, PA: Center for the Computational Analysis of Social and Organization Systems, Carnegie Mellon University www.casos.cs.cmu.edu/publications/papers/multiv001a.pdf.

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the United States of America, 106*(33), 13850–13853.

Capitanio, J. P., Abel, K., Mendoza, S. P., Blozis, S. A., McChesney, M. B., Cole, S. W., et al. (2008). Personality and serotonin transporter genotype interact with social context to affect immunity and viral set-point in simian immunodeficiency virus disease. *Brain, Behavior and Immunity, 22*, 676–689.

Capitanio, J. P., & Cole, S. W. (2015). Social instability and immunity in rhesus monkeys: The role of the sympathetic nervous system. *Philosophical Transactions of the Royal Society B: Biological Sciences, 370*(1669), 20140104.

Capitanio, J. P., Mendoza, S. P., Lerche, N. W., & Mason, W. A. (1998). Social stress results in altered glucocorticoid regulation and shorter survival in simian acquired immune deficiency syndrome. *Proceedings of the National Academy of Sciences of the United States of America, 95*(8), 4714–4719.

Choudhury, S., & Black, J. M. (1994). Barnacle geese preferentially pair with familiar associates from early life. *Animal Behaviour, 48*, 81–88.

Cote, J., Dreiss, A., & Clobert, J. (2008). Social personality trait and fitness. *Proceedings of the Royal Society B: Biological Sciences, 275*, 2851–2858.

Couzin, I. D. (2006). Behavioral ecology: Social organization in fission–fusion societies. *Current Biology, 16*, R169–R171.

Cristol, D. A. (1995). The coat-tail effect in merged flocks of dark-eyed juncos: Social status depends on familiarity. *Animal Behaviour, 50*, 151–159.

Dadda, M., Pilastro, A., & Bisazza, A. (2005). Male sexual harassment and female schooling behaviour in the eastern mosquitofish. *Animal Behaviour, 70*, 463–471.

Darley, J. A. (1982). Territoriality and mating behavior of the male brown-headed cowbird. *Condor, 84*, 15–21.

Dekker, D., Krackhardt, D., & Snijders, T. A. (2007). Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika, 72*(4), 563–581.

DeVries, A. C., Glasper, E. R., & Detillion, C. E. (2003). Social modulation of stress responses. *Physiology & Behavior, 79*(3), 399–407.

Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive adaptations for social bonding in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*(1480), 489–505. http://dx.doi.org/10.1098/rstb.2006.1991.

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods in Ecology and Evolution, 4*(12), 1187–1194.

Farine, D. R., & Sheldon, B. (2015). Selection for territory acquisition is modulated by social network structure in a wild songbird. *Journal of Evolutionary Biology, 28*(3), 547–556.

Firth, J. A., & Sheldon, B. C. (2016). Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. *Ecology Letters, 19*(11), 1324–1332.

Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439*, 426–429.

Flynn, E. G., Laland, K. N., Kendal, R. L., & Kendal, J. R. (2013). Developmental niche construction. *Developmental Science, 16*, 296–313.

Freeberg, T. M. (1997). *Cultural transmission of behaviors facilitating assortative courtship and mating in cowbirds (*Molothrus ater*)* (Ph.D. thesis). Bloomington, IN: Indiana University.

Freeberg, T. M., Duncan, S. D., Kast, T. L., & Enstrom, D. A. (1999). Cultural influences on female mate choice: An experimental test in cowbirds, *Molothrus ater. Animal Behaviour, 57*, 421–426.

Freed-Brown, S. G., King, A. P., Miller, J. L., & West, M. J. (2006). Uncovering sources of variation in female sociality: Implications for the development of social preferences in female cowbirds (*Molothrus ater*). *Behaviour, 143*, 1293–1315.

Friedmann, H. (1929). *The cowbirds: A study in the biology of social parasitism.* Springfield, IL: C. C. Thomas.

Grabowska-Zhang, A., Sheldon, B., & Hinde, C. (2012). Long-term familiarity promotes joining in neighbour nest defence. *Biology Letters, 8*(4), 544–546.

Grabowska-Zhang, A. M., Wilkin, T. A., & Sheldon, B. C. (2011). Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*). *Behavioral Ecology, 23*(2), 322–333. http://dx.doi.org/10.1093/beheco/arr189.

Gros-Louis, J., White, D. J., King, A. P., & West, M. J. (2003). Female brown-headed cowbirds' (*Molothrus ater*) social assortment changes in response to male song: A potential source of public information. *Behavioral Ecology and Sociobiology, 53*, 163–173.

Guibert, F., Richard-Yris, M.-A., Lumineau, S., Kotrschal, K., Guémené, D., Bertin, A., et al. (2010). Social instability in laying quail: Consequences on yolk steroids and offspring's phenotype. *PLoS One, 5*(11), e14069.

Haller, J., Fuchs, E., Halász, J., & Makara, G. B. (1999). Defeat is a major stressor in males while social instability is stressful mainly in females: Towards the development of a social stress model in female rats. *Brain Research Bulletin, 50*(1), 33–39.

Handcock, M. S., Hunter, D. R., Butts, C. T., Goodreau, S. M., & Morris, M. (2008). statnet: Software tools for the representation, visualization, analysis and simulation of network data. *Journal of Statistical Software, 24*(1), 1–11. http://dx.doi.org/10.18637/jss.v024.i01.

Herzog, C., Czéh, B., Corbach, S., Wuttke, W., Schulte-Herbrüggen, O., Hellweg, R., et al. (2009). Chronic social instability stress in female rats: A potential animal model for female depression. *Neuroscience, 159*(3), 982–992.

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man, 11*, 1–17.

Kohn, G. M., Gwendẃr, M. R., Magdaleno, F. R., King, A. P., & West, M. J. (2015). Sex differences in familiarity preferences within fission–fusion brown-headed cowbird (*Molothrus ater*) flocks. *Animal Behaviour, 106*, 137–143.

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R., & West, M. J. (2013a). In the company of cowbirds, *Molothrus ater ater*: Robust patterns of sociability predict reproductive performance. *Journal of Comparative Psychology, 127*(1), 40–48. http://dx.doi.org/10.1037/a0029681.

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R., & West, M. J. (2013b). Robust autumn social attributes predict spring courtship skills in juvenile female brown-headed cowbirds, *Molothrus ater. Animal Behaviour, 85*, 727–732. http://dx.doi.org/10.1016/j.anbehav.2013.01.009.

Kohn, G. M., King, A. P., Scherschel, L. L., & West, M. J. (2011). Social niches and sex assortment: Uncovering the developmental ecology of brown-headed cowbirds, *Molothrus ater. Animal Behaviour, 82*, 1015–1022.

Kubitza, R. J., Suhonen, J., & Vuorisalo, T. (2015). Effects of experimental perturbation of group structure on hierarchy formation and behaviour in house sparrows. *Ornis Fennica, 92*(4), 157–171.

Laskowski, K. L., & Pruitt, J. N. (2014). Evidence of social niche construction: Persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society B: Biological Sciences, 281*(1783), 20133166. http://dx.doi.org/10.1098/rspb.2013.3166.

Maguire, S. E., Schmidt, M. F., & White, D. J. (2013). Social brains in context: Lesions targeted to the song control system in female cowbirds affect their social network. *PLoS One, 8*(5), e63239. http://dx.doi.org/10.1371/journal.pone.0063239.

Maier, N. R. F., & Schneirla, T. C. (1964). *Principles of animal psychology.* New York, NY: Dover.

Marler, P. (1976). On animal aggression: The roles of strangeness and familiarity. *American Psychologist, 31*, 239–246.

McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences of the United States of America, 104*(26), 10910–10914. http://dx.doi.org/10.1073/pnas.0701159104.

Mendoza, S., Capitanio, J., & Mason, W. (2000). Chronic social stress: Studies in non-human primates. In G. P. Moberg, & J. A. Mench (Eds.), *The biology of animal stress: Basic principles and implications for animal welfare* (pp. 227–247). New York, NY: CABI.

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*(3), E80–E89.

Ortega, C. P. (1998). *Cowbirds and other brood parasites.* Tucson, AZ: The University of Arizona Press.

Persuad, K. N., & Galef, B. G., Jr. (2003). Female Japanese quail aggregate to avoid sexual harassment by conspecific males: A possible cause of conspecific cueing. *Animal Behaviour, 65*, 89–94.

Riedstra, B., & Groothuis, T. G. G. (2002). Early feather pecking as a form of social exploration: The effect of group stability on feather pecking and tonic immobility in domestic chicks. *Applied Animal Behaviour Science, 77*(2), 127–138.

Rothstein, S. I., Yokel, D. A., & Fleischer, R. C. (1988). The agonistic and sexual functions of vocalizations of male brown-headed cowbirds (*Molothrus ater*). *Animal Behaviour, 36*, 73–86.

Saltz, J. B., & Nuzhdin, S. V. (2014). Genetic variation in niche construction: Implications for development and evolutionary genetics. *Trends in Ecology & Evolution, 29*(1), 8–14.

Sapolsky, R. M. (1983). Endocrine aspects of social instability in the olive baboon (*Papio anubis*). *American Journal of Primatology, 5*(4), 365–379.

Senar, J., Camerino, M., & Metcalfe, N. (1990). Familiarity breeds tolerance: The development of social stability in flocking siskins. *Ethology, 85*, 13–24.

Senar, J. C., Kew, J., & Kew, A. (2015). Do siskins have friends? An analysis of movements of siskins in groups based on EURING recoveries. *Bird Study, 62*(4), 566–568.

Shizuka, D., Chaine, A. S., Anderson, J., Johnson, O., Laursen, I. M., & Lyon, B. E. (2014). Across-year social stability shapes network structure in wintering migrant sparrows. *Ecology Letters, 17*(8), 998–1007.

Sih, A., & Watters, J. V. (2005). The mix matters: Behavioural types and group dynamics in water striders. *Behaviour, 142*, 1417–1431.

Silk, J. B. (2007). Social components of fitness in primate groups. *Science, 317*(5843), 1347–1351. http://dx.doi.org/10.1126/science.1140734.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences, 276*, 3099–3104.

de Waal, F. B. M., & Tyack, P. L. (2002). *Animal social complexity: Intelligence, culture and individualized societies*. Cambridge, MA: Harvard Press.

West, M. J., King, A. P., & Freeberg, T. M. (1996). Social malleability in cowbirds: New measures reveal new evidence of plasticity in the eastern subspecies (*Molothrus ater ater*). *Journal of Comparative Psychology, 110*, 15–26.

West, M. J., King, A. P., White, D. J., Gros-Louis, J., & Freed-Brown, G. (2006). The development of local song preferences in female cowbirds (*Molothrus ater*): Flock living stimulates learning. *Ethology, 112*, 1095–1107.

Wheeler, B. (2010). *lmPerm: Permutation tests for linear models* (R package version 1.1-2) http://CRANR-projectorg/package=lmPerm. (Accessed 25 August 2013).

White, D. J., Gersick, A. S., & Snyder-Mackler, N. (2012). Social networks and the development of social skills in cowbirds. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*, 1892–1900.

White, D. J., King, A. P., & Duncan, S. D. (2002). Voice recognition technology as a tool for behavioral research. *Behavioral Research Methods, Instrumentation, and Computers, 34*, 1–5.

White, D. J., & Smith, V. A. (2007). Testing measures of animal social association by computer simulation. *Behaviour, 144*, 1447–1468.

Wikelski, M., Hau, M., & Wingfield, J. C. (1999). Social instability increases plasma testosterone in a year-round territorial neotropical bird. *Proceedings of the Royal Society B: Biological Sciences, 266*(1419), 551–556.

Yokel, D. A. (1989). Intrasexual aggression and the mating behavior of brown-headed cowbirds: Their relation to population densities and sex ratios. *Condor, 91*, 43–51.

Zayan, R. (1991). The specificity of social stress. *Behavioural Processes, 25*(2–3), 81–93.