Sex differences in familiarity preferences within fission–fusion brown-headed cowbird, *Molothrus ater*, flocks

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Many vertebrates inhabit dynamic and loosely structured groups where group size and social composition continually fluctuates. The ability to sustain nonrandom interaction preferences across group changes is an important aspect in maintaining social organization. In two experiments, we explored the strength and persistence of social preferences for familiar conspecifics in brown-headed cowbirds. In the first experiment, we demonstrated that females preferentially associate with familiar females when introduced into a flock containing novel individuals. In the second experiment we investigated the consistency of familiarity preferences across a series of social introductions. Females maintained preferences to approach familiar conspecifics, and the individual strength of those preferences remained consistent across introductions. Male preferences changed across the introductions. In the first introduction, males showed a significant preference to approach familiar conspecifics, but increased their approaches towards novel conspecifics in subsequent introductions. Our findings suggest that female cowbirds are an important factor in maintaining social organization through their enduring associations with familiar individuals, whereas males facilitate social integration by extending connections towards novel individuals during periods of change.

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Many vertebrates inhabit loosely structured groups that exhibit fission–fusion processes where group size and composition change over short timescales. The social organization of these groups reflects the nonrandom interaction networks created through preferential associations with specific individuals (Hinde, 1976; Whitehead, 2008). If fission–fusion changes significantly alter social preferences, then individuals will 'rewire' their interaction networks, and the social organization will change over time (Flack, Girvan, de Waal, & Krakauer, 2006; Fushing, Jordà, Beisner, & McCowan, 2014). While social preferences are commonly seen as one of the core attributes of social organization (Whitehead, 2008), little is known about their strength and persistence across group fissioning and fusing.

In fission–fusion groups, individuals are often faced with a shifting composition of both familiar and novel conspecifics. Yet, consistent preferences for familiar individuals may give rise to stable subgroups that are sustained through multiple fission and fusion events (Ramos-Fernández & Morales, 2014; Zachary, 1977).

These subgroups can make interaction more predictable, lessen the chances of aggressive encounters and lower stress levels (Marler, 1976; Strodl & Schausberger, 2013; Takeda, Sato, & Sugawara, 2003). In turn, this can lead to more effective social learning, increased behavioural coordination and efficient foraging (Lachlan, Crooks, & Laland, 1998; Laland & Williams, 1997). Because of the potential benefits of interacting with familiar conspecifics, understanding the composition of stable subgroups can provide insights on the fitness consequences of social interactions within the group.

Across some social species, one sex plays an important role in constructing core groups while the other sex disperses from their natal group to avoid inbreeding and form new associations (Pusey, 1987). Such patterns suggest that one sex will benefit from forming stable relationships with familiar conspecifics (Silk et al., 2009), whereas the other will benefit from being able to interact with a diverse range of individuals. In yellow baboons, *Papio cynocephalus* (Silk, Alberts, & Altmann, 2003), and horses, *Equus ferus* (Cameron, Setsaas, & Linklater, 2009), females who form strong and enduring associations with other females show higher rates of offspring survival, suggesting that selection acts on the formation of consistent female–female networks. In adult greylag geese, *Anser anser*, females rest in close proximity to known females, while

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males rest closer to unrelated conspecifics (Frigerio, Weiss, & Kotrschal, 2001). Understanding how familiarity preferences and sex interact is likely to provide insights into the factors shaping the evolution of social organization.

In the current study, we investigated the strength and stability of familiarity preferences within brown-headed cowbirds, *Molothrus ater*. In particular, we tested whether males and females maintain consistent and preferential associations with familiar conspecifics when flock composition changed. For most birds little is known about the within-group association patterns outside of breeding periods (however see Shizuka et al., 2014). Nevertheless, within cowbirds, social interaction during these periods predicts later social development and reproductive performance (Kohn, King, Dohme, Meredith, & West, 2013a, 2013b). After breeding, cowbirds join mixed-sex and/or mixed-age flocks. These flocks often contain a mix of both resident and migratory birds from other populations. As they move southward from September to late November, these flocks will join with others to form larger migratory aggregations (Friedmann, 1929; Ortega, 1998).

During the autumn and spring, female cowbirds advertise, modify and share local mate preferences through close interaction with other females (West, King, White, Gros-Louis, & Freed-Brown, 2006; White, Gros-Louis, King, & West, 2006). Visual cues known as 'wing-strokes', which can only be assessed in close proximity (West & King, 1988), are used to communicate and evaluate one another's mate preferences. Females benefit from repeated associations with familiar individuals in order to effectively communicate local mate preferences. In male cowbirds, previous work has shown that males who experience more diverse social networks are more successful when courting and competing with others, and show higher reproductive success (Gersick, Snyder-Mackler, & White, 2012; White, Gersick, Freed-Brown, & Snyder-Mackler, 2010; White, King, & West, 2014). This suggests that males benefit from a diverse range of social interactions, and will seek out novel individuals. We hypothesized that females should show a significant and consistent preference to approach familiar conspecifics across fission–fusion changes, whereas males should show a preference to approach novel conspecifics when conditions change.

Our study proceeded in two stages. In the first experiment we explored whether cowbirds showed a significant preference for approaching novel or familiar conspecifics. During 2012, we conducted introduction experiments in two cowbird flocks, a control flock and a novel flock. Each flock was created through the fusion of two smaller subflocks. In the control flock, the subflocks had previously been housed together for an extensive period before the study, and were thus deemed familiar with all members of that group, while in the novel flock, both subflocks had never previously interacted. In the second experiment we investigated the persistence of familiarity preferences across multiple introductions. During 2013, four flocks were created through a series of introductions where they could either interact with familiar or unfamiliar conspecifics. We measured whether preferences to interact with familiar conspecifics persisted across the introductions at both the group and individual level.

METHODS

Subjects

All birds were originally captured in Philadelphia County, Pennsylvania or in Monroe County, Indiana, U.S.A. Each bird was provided with uniquely coloured leg bands for individual recognition. All birds were of the subspecies, *Molothrus ater ater*, with an average age of 6 years (range 1–12 years).

Aviaries

Each aviary (9.1 × 18.3 × 3.4 m) contained perches, vegetation (e.g. trees, shrubs and grass), an observation platform, a roofed feeding station and access to an indoor shelter. Both aviaries 1 and 2, and aviaries 3 and 4, can be connected forming two larger aviaries (aviaries 1–2 and 3–4) by removing a partition within the indoor shelters. Aviary 5 was visually and spatially (by 85 m) isolated from the rest of the aviaries (Fig. 1a). Birds were provided with ad libitum access to vitamin-treated water (Aquavite Nutritional Research, South Whitely, IN, U.S.A.) and a modified Bronx Zoo diet for omnivorous birds with canary seed and red and white millet. Birds were exposed to ambient climatic conditions and native insects and invertebrates.

Data Collection

Behavioural interactions were recorded using scan sampling (Altmann, 1974) using voice recognition technology (White, King, & Duncan, 2002). When used in combination with voice recognition technology, scan sampling can provide a more comprehensive data set than focal sampling (White & Smith, 2007). A single observation block lasted 7 min, and observers recorded social approaches between dyads. An approach was scored when one individual approached a conspecific within a radius of 30 cm around its body, and that individual remained in close proximity for at least 1 s. Thus, a successful approach demonstrates an individual's ability to maintain close proximity with another conspecific without eliciting an immediate withdrawal response. All observation blocks were conducted between 0700 and 1030 hours.

Reliability

Observer reliability between the two observers (G.M.K. and G.R.M.) was high during 2012, at 94% (ICC = 0.941, F = 33.2, P = 0.00843), and during 2013 (G.M.K. and F.R.M.), at 83% (ICC = 0.83, F = 10.9, P < 0.0001).

2012 Experiment

Baseline period

On 3 November 2012, new flocks were separated into the four aviary subsections of the large aviary complex. All birds separated between aviary 1 (9 females, 8 males) and aviary 2 (9 females, 9 males) were familiar with each other, as they had been housed together for 1 year and 4 months prior to separation. These flocks would be used for the control introduction (Fig. 1b). Birds in aviary 3 (9 females, 6 males) and aviary 4 (9 females, 5 males) were unfamiliar with each other, and had never previously interacted.

Previously, birds in aviary 3 had been housed together for 1 year and 4 months, while birds in aviary 4 had been housed together for 6 months in aviary 5. These flocks would be used for the novel introduction (Fig. 1b). All birds were allowed 3 days to adjust to their new conditions before data collection began. During the baseline period, from 6 November to 13 November 2012, two observers conducted daily counterbalanced 7 min block observations in which approaches were recorded. Two observers recorded a total of 91 blocks (aviary 1: 21 blocks; aviary 2: 20 blocks; aviary 3: 25 blocks; aviary 4: 25 blocks).

Novel introduction

On 14 November, a partition separating aviaries 3 and 4 was opened and both flocks were allowed to interact. From 14 November to 18 November 2012, two observers conducted counterbalanced 7 min observations, during which all approaches were recorded. The two observers recorded a total of 70 blocks.
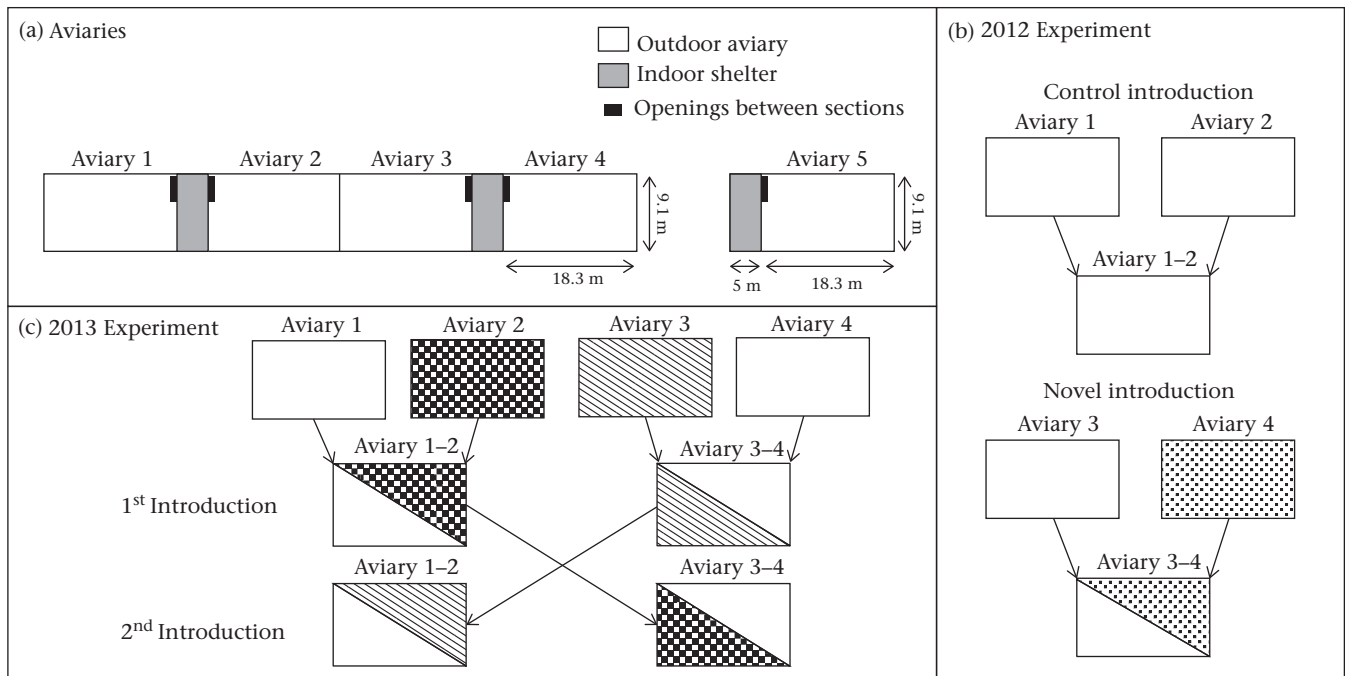
Figure 1. (a) Diagram of the large aviary complex consisting of aviaries 1–4 and the separate aviary 5. Aviaries 1 and 2, and aviaries 3 and 4 can be joined through opening up the sections between these aviaries. (b) Diagram of the experimental set-up for the control and novel introductions in the 2012 experiment. (c) Diagram showing the first and second introductions in the 2013 experiment. In both diagrams aviaries represented by the same pattern had previously interacted, while aviaries with two different patterns represent a novel introduction.

Control introduction

On 20 November, the partition separating aviaries 1 and 2 was opened and both flocks were allowed to interact. From 20 November to 27 November 2012, two observers conducted counterbalanced 7 min observations, during which all approaches were recorded. The two observers recorded a total of 73 blocks.

2013 Experiment

Baseline period

On 2 October 2013, birds were separated into the four aviaries within the large aviary complex. All birds separated into aviary 1 (10 females, 7 males) and aviary 2 (5 females, 8 males) and into aviary 3 (11 females, 7 males) and aviary 4 (6 females, 7 males) had never previously interacted. Prior to separation, birds from aviaries 1 and 3 were housed together for 4 months within the large aviary complex, whereas birds from aviaries 2 and 4 had been housed together for 2 months in aviary 5 (Fig. 1c). Individuals were randomly assigned to each new flock to assure the resulting flocks maintained equivalent levels of approach tendencies. All birds were allowed to acclimate to the new surroundings from 2 October to 19 October.

First introduction

On 20 October, the partitions separating aviaries 1 and 2 as well as those between aviaries 3 and 4 were opened, allowing the pairs of flocks to interact and to form aviaries 1–2 and 3–4, respectively (Fig. 1c). From 20 October to 28 October 2013, two observers conducted observations. The two observers recorded a total of 328 blocks (164 in aviary 1–2, 164 in aviary 3–4).

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 (Fig. 1c). From 4 November to 17 November 2013, two observers conducted observations, and a total of 306 blocks were recorded between them (138 in aviary 1–2, 138 in aviary 3–4).

Analysis

2012 experiment

For both the novel and control introductions, individuals housed within the same baseline flock were designated as 'familiar', whereas interactions with individuals from another baseline flock were designated as 'unfamiliar'. As the number of familiar and unfamiliar individuals was not equal, we calculated the approach rate per dyad for approaches directed towards both familiar and unfamiliar flock-mates for each individual. The approach rate was calculated by dividing the number of approaches that each individual initiated towards either familiar or unfamiliar flock-mates by the number of familiar or novel individuals present in the aviary, which was then divided by the number of sampling blocks.

We used generalized linear mixed models (GLMMs) using a Poisson distribution to assess the factors shaping approach rates. The dependent variable was the approach rates, and the explanatory factors included an individual's sex, familiarity (if the approach rates were directed towards familiar or unfamiliar flock mates) and the experimental condition (novel or control introductions), and all two-way interactions between these variables. In this model, the identity of the individual was included as a random factor.

Models were simplified through the selection of terms based on minimizing the Akaike's information criteria (AIC). If removal of a factor increased the AIC value, then that explanatory factor remained in the model. A minimal model was defined when the removal of any remaining nonsignificant explanatory factors increased the AIC value. Variable selection was done using both drop1 and stepAIC functions in R (R Development Core Team, 2012) with identical results. Post hoc analysis on approach rates was

conducted using Spearman's correlations on continuous explanatory factors, and Wilcoxon signed-ranks and Mann–Whitney U tests for categorical explanatory factors. Confidence intervals for Spearman's coefficients were calculated using resampling techniques. For the Wilcoxon signed-ranks test, zeros were handled using the Pratt's method (Pratt, 1959). Effect sizes (r) were obtained for the Wilcoxon signed-ranks test through calculating the Z score using permutation methods (wilcoxsign_test in the coin package) and dividing the Z score by the square-root of the sample size (Cohen, 1988).

2013 experiment

For the second experiment we conducted two GLMMs with a Poisson distribution to assess the factors shaping approach tendencies. We calculated the approach rate per dyad directed towards both familiar and unfamiliar male and female flock-mates for each individual. The dependent variable in the first model was the approach rate per dyad towards females, and the second model was the approach rate per dyad towards males. The explanatory factors in both models were the individual's sex, the introduction (first or second introduction), familiarity (if the approach rates was towards familiar or unfamiliar flock mates), and all two-way interactions between the variables. In each model, the identities of the individual and the aviaries were included as random factors. Model simplification and post hoc tests were the same as the 2012 model.

To assess the repeatability in the strength of individual familiarity preferences across contexts, we used intraclass correlation coefficients (ICC) and Spearman's correlations across the two introductions. Our measure of familiarity preference was the proportion of approaches an individual initiated towards familiar conspecifics divided by the number of total approaches. We conducted the analysis separately for both males and females. Significant differences in the consistency of preferences across males and females were assessed using 95% confidence intervals (CI) around the correlation coefficients. Nonoverlapping confidence intervals indicate a significant difference in the consistency of familiarity preferences across males and females.

RESULTS

Sex Differences in Approach Behaviour

2012 introductions

We observed a total of 6003 approaches during this study, including 1661 (range 1–96, $\bar{x} = 25.9$) approaches during the baseline period and 4342 (range 5–201, $\bar{x} = 67.8$) approaches during novel and control introductions. There was no significant difference in the overall rate of approaches per observation block between the novel and control introductions (Mann–Whitney U test: $U = 45$, $N_1 = 28$, $N_2 = 36$, $P = 0.65$), or between males and females across both introductions ($U = 55$, $N_1 = 28$, $N_2 = 36$, $P = 0.45$). In both the novel and control introductions, females showed a significant preference to approach other females (Wilcoxon signed-ranks test: control: $Z = 2.0474$, $N = 18$, $P = 0.0396$, $r = 0.48$, novel: $Z = 3.5933$, $N = 18$, $P < 0.0001$, $r = 0.84$), whereas males displayed no significant preference to interact with either sex in the control introduction ($Z = -1.1838$, $N = 17$, $P = 0.2532$, $r = 0.28$), but displayed a significant preference to approach females in the novel introduction ($Z = 2.228$, $N = 11$, $P = 0.02441$, $r = 0.67$).

2013 introductions

We observed a total of 17 198 approaches during this study, including 7939 (range 16–386, $\bar{x} = 130$) approaches during the first introduction, and 9259 (range 13–562, $\bar{x} = 156$) approaches during

the second introduction. We uncovered no significant differences in the overall rate of approaches per observation block initiated by either males or females (first intro: $U = 475$, $N_1 = 29$, $N_2 = 32$, $P = 0.87$; second intro: $U = 403$, $N_1 = 29$, $N_2 = 32$, $P = 0.38$). Within both introductions, females maintained strong preferences to interact with other females (first intro: $Z = 3.983$, $N = 32$, $P < 0.001$, $r = 0.70$; second intro: $Z = 4.2823$, $N = 32$, $P < 0.001$, $r = 0.76$), whereas males did not show any sex preferences (first intro: $Z = -0.8761$, $N = 29$, $P = 0.39$, $r = 0.16$; second intro: $Z = -1.674$, $N = 29$, $P = 0.095$, $r = 0.31$).

Familiarity Preferences

2012 introductions

Our minimal model contained only two factors, one was experimental condition (GLMM: coef $= -0.16$, $Z = -0.891$, $P = 0.37$) and a significant interaction effect between experimental condition and familiarity (coef $= 0.19$, $Z = 1.983$, $P = 0.047$). In the novel introduction, females showed an overall significant preference for interacting with familiar versus unfamiliar conspecifics ($Z = -2.919$, $N = 18$, $P = 0.002$, $r = 0.71$; Fig. 2). When we looked at the interactions by the sex of the recipient we discovered that females showed a significant preference to interact with familiar females ($Z = 3.027$, $N = 18$, $P = 0.001$, $r = 0.71$) but not familiar males ($Z = 1.20$, $P = 0.25$, $N = 18$, $r = 0.28$). Neither males nor females showed any significant preference to interact with familiar or unfamiliar individuals in the control introduction (females: $Z = -0.41$, $P = 0.70$, $r = 0.1$; males: $Z = -0.167$, $P = 0.89$, $r = 0.04$).

2013 introductions

Both male and female models showed a significant main effect of familiarity on an individual's approach behaviour (Table 1). Across all introductions, females were more likely to approach both familiar males and females over unfamiliar males and females (Table 2). Our male model also uncovered a significant interaction effect between familiarity preference and introduction. Males showed a strong and significant bias to approach both familiar males and females during the first introduction, but during the second introduction no significant preferences for familiar or unfamiliar conspecifics were observed (Table 2). From the first to second introduction, males increased their rate of approaches towards both unfamiliar males ($Z = 4.076$, $N = 29$, $P < 0.0001$, $r = 0.76$) and unfamiliar females ($Z = 2.687$, $N = 29$, $P = 0.006$, $r = 0.50$).

Repeatability of Individual Familiarity Preferences

2013 introductions

Across the first two introductions, females showed significant repeatability in their preference to approach familiar conspecifics (ICC $= 0.637$, $P < 0.0001$, 95% CI $= 0.365–0.81$), whereas males did not (ICC $= -0.05$, $P = 0.606$, 95% CI $= -0.41–0.32$; Fig. 3). As the confidence intervals were nonoverlapping, this also indicates that males were significantly less consistent when compared to females. Furthermore, females also showed rank-ordered consistency in their tendency to approach familiar conspecifics (Spearman rank correlation: $r_S = 0.60$, $N = 32$, $P = 0.0005$, 95% CI $= 0.36–0.76$), whereas males did not ($r_S = -0.20$, $N = 29$, $P = 0.304$, 95% CI $= -0.51–0.15$).

To further investigate the change in male preferences, we conducted an additional analysis to see whether the strength of a male's familiarity preference during the first introduction reflected a significant increase in their tendency to approach unfamiliar individuals in the second introduction. The approach rate towards unfamiliar individuals during the second introduction minus the
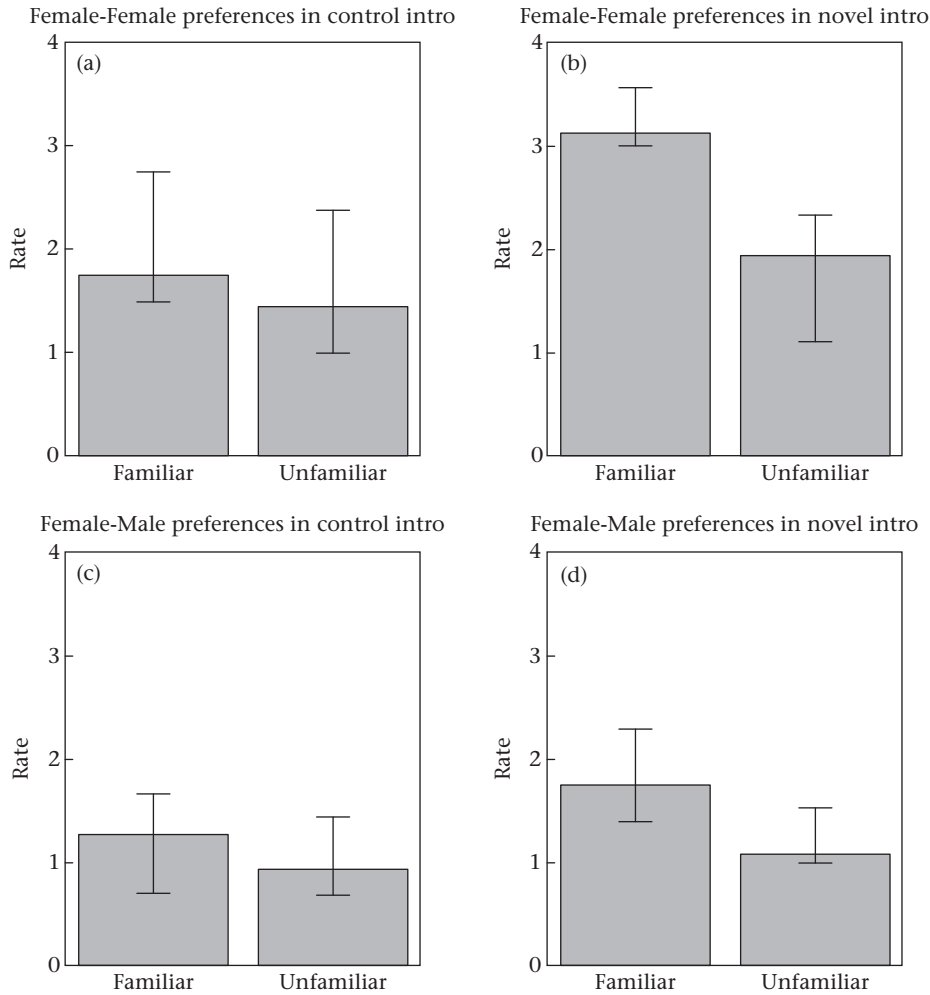
Figure 2. Differences in the female to female (a, b) and female to male (c, d) preferences across the control (a, c) and novel (b, d) introductions. Bars represent the median rate of approaches per individual towards familiar or unfamiliar individuals within the control and novel introductions. Error bars represent the 95% confidence interval around the median.

Table 1
Model results for the minimal models in the second experiment

Model	Factor	Coef	SE	Z	P
Females	Sex	−0.339	0.179	1.88	0.059
	Familiarity	−0.517	0.084	6.138	<0.0001
	Familiarity * introduction	0.308	0.088	3.493	0.0004
Males	Sex	0.48	0.24	1.958	0.05
	Introduction	0.31	0.075	4.068	<0.0001
	Familiarity	0.85	0.10	8.169	<0.0001
	Familiarity * introduction	0.67	0.12	5.424	<0.0001

Contains all factors that remained in both the model of approaches towards females and males after simplification.

Table 2
Wilcoxon singed-ranks tests examining the rate-per-dyad approaches to familiar or novel individuals for female to female (F-F), female to male (F-M), male to male (M-M) and male to female (M-F) approaches

Dyad	First introduction			Second introduction		
	Z	P	r	Z	P	r
F-F	2.4403	0.01	0.43	3.0278	0.007	0.54
F-M	3.9838	<0.0001	0.70	2.19	0.03	0.39
M-M	4.1314	<0.0001	0.76	0.2391	0.818	0.05
M-F	4.3033	<0.0001	0.70	0.353	0.736	0.07

approach rate to unfamiliar individuals in the first introduction was used as the rate of change across introductions. We found a significant positive correlation between the strength of an individual male's familiarity preference during the first introduction and an increase in approaches to unfamiliar males ($r_S = 0.43$, $N = 29$, $P = 0.025$) and females ($r_S = 0.46$, $N = 29$, $P = 0.015$).

DISCUSSION

In our experimental flocks, female cowbirds showed significant preferences to associate with known conspecifics, and these preferences remained consistent across changes in social composition. This suggests that female cowbirds construct reliable familiar subgroups within the shifting composition of fission–fusion flocks. Unlike females, males did not show consistent familiarity preferences. The individual variation in the strength of a male's familiarity preference was not significantly repeatable, and during the second introduction of our second experiment males increased their approaches towards unfamiliar individuals. Males therefore changed how they interacted with novel individuals in response to either prior experience with unfamiliar conspecifics, or changes in the social dynamics of the group. If the differences in association preferences we observed in these experiments reflect broader behavioural patterns, then males and
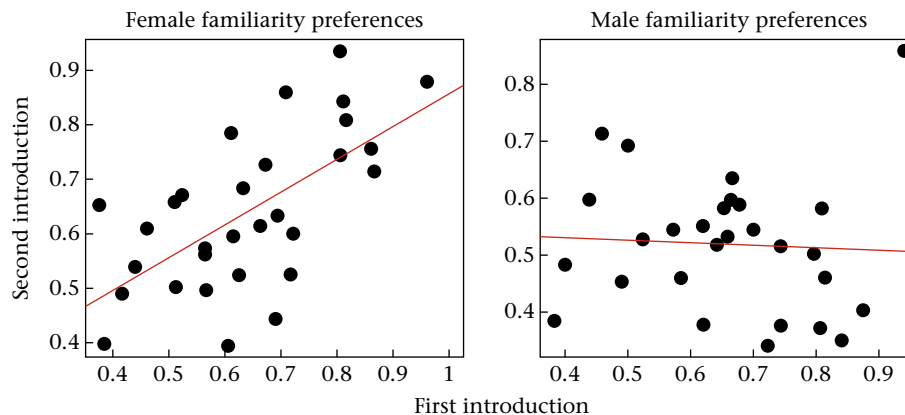
Figure 3. Consistency of familiar approach preferences across the first and second introductions for both males and females. The line represents a linear regression fitted to the data in order to illustrate the direction of the effects across introductions.

females may have distinct roles in the social organization of autumn cowbird flocks.

Recurrent associations will facilitate information exchange, especially when signals can only be assessed through close social interaction (McGregor, 2005). In autumn, females use visual signals, known as wing-strokes, to communicate mate preferences with both males and females (Dohme, King, Meredith, & West, 2014; Gros-Louis, White, King, & West, 2003; West & King, 1988). In spring, female cowbirds assess and adopt the mate choices of other females by attending to their 'chatter' vocalizations (Freed-Brown & White, 2009). Enduring associations with familiar conspecifics will shape the mate preferences a female is exposed to in autumn, and may cause familiar females to adopt similar mate choices during spring. Therefore, if familiarity preferences are maintained across seasons, it will shape how information is shared within cowbird flocks, and potentially lead to the emergence of local mate preferences.

Unlike females, males did not show consistent familiarity preferences. In 2013, significant familiarity preferences were observed during the first introduction, but disappeared as males increased their approaches towards novel individuals in the second introduction. Some studies have demonstrated that males can benefit from interacting with a wide diversity of conspecifics. White et al. (2010) and Gersick et al. (2012) found that male cowbirds housed in a flock with a changing social composition had higher mating success, were better able to compete with other males and were more likely to be paired than males housed in an unchanging flock. Oh and Badyaev (2010) found that male house finches, *Haemorhous mexicanus*, with less elaborate plumage were able to increase their pair bond success by frequently changing the groups they associated with. Our results, along with these studies, suggest that there are either few benefits to maintaining strong bonds in males, or that males face competing demands to investigate novel conspecifics and sustain familiar associations. Further studies will investigate the benefits and costs of novel versus familiar associations in males, and how contextual changes in group size, composition and singing behaviour mediate these effects.

The strength of an individual female's familiarity preference remained consistent across introductions, while males did not. While previous studies have shown that females maintain repeatable rates of autumn social approaches (Kohn et al., 2013b) and head-down displays (Kohn et al., 2013a), this is the first study to show that females also sustain repeatable preferences for familiar conspecifics. As social behaviour during the autumn can predict courtship and reproductive behaviour during the breeding season

(Kohn et al., 2013b), further studies will investigate how the between-individual variation in autumn familiarity preferences predicts a female's reproductive behaviour and social preferences during the breeding season.

Female bonds play an important role in maintaining social organization (Archie, Moss, & Alberts, 2011; Couzin, 2006; Griffiths & Magurran, 1998; Henzi & Barrett, 2007). In the wild, bird flocks are complex and dynamic systems, which makes it challenging to identify the variables underlying their social organization (Silk, Croft, Tregenza, & Bearhop, 2014). Our findings demonstrate that female cowbirds create stable social networks through their enduring associations with familiar individuals across flock changes. To our knowledge, this is the first such finding in birds. The weaker tendency to approach familiar conspecifics in males will facilitate social integration by extending connections towards novel individuals when two flocks meet. Therefore, as in other social species, the different interaction networks constructed between the sexes play different roles in the stability and flexibility of social organization.

Acknowledgments

References

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*, 227–267.

Archie, E. A., Moss, C. J., & Alberts, S. C. (2011). Friends and relations: kinship and the nature of female elephant social relationships. In C. J. Moss, H. Croze, & P. E. Lee (Eds.), *The Amboseli elephants: A long-term perspective on a long-lived mammal* (pp. 238–245). Chicago, IL: University of Chicago Press.

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*, 13850–13853.

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale, NJ: L. Erlbaum.

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

Dohme, R., King, A. P., Meredith, G. R., & West, M. J. (2014). Is female visual signaling to male song socially regulated in brown-headed cowbirds? *Ethology, 121*, 327–334. http://dx.doi.org/10.1111/eth.12341.

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.

Freed-Brown, G., & White, D. J. (2009). Acoustic mate copying: female cowbirds attend to other females' vocalizations to modify their song preferences. *Proceedings of the Royal Society B: Biological Sciences, 276*, 3319–3325.

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

Frigerio, D., Weiss, B., & Kotrschal, K. (2001). Spatial proximity among adult siblings in greylag geese (*Anser anser*): evidence for female bonding? *Acta Ethologica, 3*, 121–125.

Fushing, H., Jordà, Ò., Beisner, B., & McCowan, B. (2014). Computing systemic risk using multiple behavioral and keystone networks: the emergence of a crisis in primate societies and banks. *International Journal of Forecasting, 30*, 797–806.

Gersick, A. S., Snyder-Mackler, N., & White, D. J. (2012). Ontogeny of social skills: social complexity improves mating and competitive strategies in male brown-headed cowbirds. *Animal Behaviour, 83*, 1171–1177.

Griffiths, S. W., & Magurran, A. E. (1998). Sex and schooling behaviour in the Trinidadian guppy. *Animal Behaviour, 56*, 689–693.

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.

Henzi, S. P., & Barrett, L. (2007). Coexistence in female-bonded primate groups. *Advances in the Study of Behavior, 37*, 43–82.

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

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R., & West, M. J. (2013a). Robust autumn social attributes predict spring courtship skills in juvenile female brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour, 85*, 727–732.

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R., & West, M. J. (2013b). In the company of cowbirds, *Molothrus ater ater*: robust patterns of sociability predict reproductive performance. *Journal of Comparative Psychology, 171*, 40–48.

Lachlan, R. F., Crooks, L., & Laland, K. (1998). Who follow whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour, 56*, 181–190.

Laland, K. N., & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal Behaviour, 53*, 1161–1169.

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

McGregor, P. K. (Ed.). (2005). *Animal communication networks*. Cambridge, U.K.: Cambridge University Press.

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.

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

Pratt, J. W. (1959). Remarks on zeros and ties in the Wilcoxon signed rank procedures. *American Statistical Association, 54*, 655–667.

Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution, 2*, 295–299.

R Development Core Team. (2012). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ramos-Fernández, G., & Morales, J. M. (2014). Unraveling fission–fusion dynamics: how subgroup properties and dyadic interactions influence individual decisions. *Behavioral Ecology and Sociobiology, 68*, 1–11.

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*, 998–1007.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science, 302*, 1231–1234.

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.

Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission–fusion social group dynamics in birds. *Ibis, 156*, 701–715.

Strodl, M. A., & Schausberger, P. (2013). Social familiarity relaxes the constraints of limited attention and enhances reproduction of group-living predatory mites. *Oikos, 122*, 1217–1226.

Takeda, K. I., Sato, S., & Sugawara, K. (2003). Familiarity and group size affect emotional stress in Japanese Black heifers. *Applied Animal Behaviour Science, 52*, 1–11.

West, M. J., & King, A. P. (1988). Female visual displays affect the development of male song in the cowbird. *Nature, 334*, 244–246.

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.

White, D. J., Gersick, A. S., Freed-Brown, G., & Snyder-Mackler, N. (2010). The ontogeny of social skills: experimental increases in social complexity enhance reproductive success in adult cowbirds. *Animal Behaviour, 79*, 385–390.

White, D. J., Gros-Louis, J., King, A. P., & West, M. J. (2006). A method to measure the development of song preferences in female cowbirds. *Animal Behaviour, 72*, 181–188.

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., King, A. P., & West, M. J. (2014). The individual in context: a social network approach to the study of behavior. In K. Yasukawa, & Z. Tang-Martinez (Eds.), *How and why animals do the things they do* (pp. 325–350). Santa Barbara, CA: Praeger.

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

Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. Chicago, IL: University of Chicago Press.

Zachary, W. W. (1977). An information flow model for conflict and fission in small groups. *Journal of Anthropological Research, 33*, 452–473.