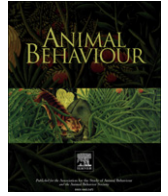




Contents lists available at ScienceDirect

Animal Behaviour

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

Social niches and sex assortment: uncovering the developmental ecology of brown-headed cowbirds, *Molothrus ater*

Gregory M. Kohn*, Andrew P. King, Leah L. Scherschel, Meredith J. West

Department of Psychological and Brain Sciences, Indiana University

ARTICLE INFO

Article history:

Received 1 March 2011
 Initial acceptance 26 April 2011
 Final acceptance 6 July 2011
 Available online xxx
 MS. number: A11-00172R

Keywords:

brown-headed cowbird
 development
 mate choice
Molothrus ater
 niche construction
 sex assortment
 sex segregation
 social ecology
 social niche

Variation in individual interaction patterns creates different social niches. Social niches afford differential exposure to social information that individuals utilize to develop species-typical behaviours. Brown-headed cowbirds depend on social interaction to develop competent reproductive behaviour. We used a fission–fusion paradigm to perturb two flocks of birds: one adult flock ($N = 38$) and one juvenile flock ($N = 24$). We split the two flocks, then recombined them while recording the frequency of individual approaches. Both adult and juvenile females maintained stable social niches, but males did not. Females maintained equivalent levels of gregariousness and attractiveness across perturbations. Juvenile females maintained the highest levels of sex assortment. The consistency of female niche construction may be explained by females' reliance on interaction with other females to assess males. Early sex assortment may also foster the development of social preferences and influence reproductive choices.

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Ecologists have traditionally used the concept of the niche to describe the places that organisms occupy within their ecological communities (Schoener & Cherrett 1989). A niche has been conceptualized as an address and occupation, or the spatial-temporal zone where organisms can be found interacting with their environment (Elton 1927; West & King 1987; Alberts & Cramer 1988; West et al. 1988). Niches are dynamic entities subject to reassembly and shaping as an organism engages and changes its proximal surroundings. The ability of organisms to assemble their own niches is known as niche construction. Through niche construction, individuals can open up new opportunities for learning that alter developmental outcomes (Lewontin 1983; West & King 1987; Odling-Smee et al. 2003). Traditionally, niche construction has focused on the organism's relationship with its physical environment. However, organisms also inhabit a rich social environment that affords different opportunities for interacting and learning. This study expands the niche concept to embrace social interaction patterns as the basis for defining a social

niche (Hinde 1976; Mason 1978; Chase et al. 2002). A social niche is defined by an individual's gregariousness and attractiveness. We define gregariousness as the frequency with which an individual initiates nonaggressive interactions with others, and we define attractiveness as the frequency with which an individual is the recipient of nonaggressive approaches from others. Individuals can construct their social niche through regulating their gregariousness and attractiveness. A major attribute of the social niche is its degree of stability, as individuals may maintain equivalent levels of both gregariousness and attractiveness over time and periods. Thus, the social niche captures individual variation in sociability and defines the availability of information from direct social interaction.

In many animal species, group composition continually fluctuates as individuals integrate or leave a group. In these fission–fusion situations, individuals can respond to changes in the social environment by constructing social niches that are either comparable to, or different from, previous conditions. Thus, social niche construction becomes a mechanism by which individuals can manage new social information. For example, individual graylag geese, *Anser anser*, maintain consistent patterns of sociability in different social contexts, and female capuchin monkeys, *Cebus capucinus*, form coalitions with other females in order to sustain their social ranks in a changing social environment (Silk 2007;

* 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@uemail.iu.edu (G. M. Kohn).

White 2010). Social niches can also be inherited, often through active social support of parents and siblings. Spotted hyaena, *Crocuta crocuta*, mothers intervene on behalf of their cubs, allowing their offspring to obtain social niches similar to their mothers (Lewis et al. 2007). Thus, by understanding social niches, we can uncover how variation in sociability shapes behavioural development and social organization (Snowdon & Hausberger 1997; Alberts 2007).

The brown-headed cowbird is an ideal species to study social niche construction because of its dependence on social interaction to develop the skills to successfully survive and reproduce. Cowbirds are obligate brood parasites, and thus have little contact with members of their own species during early life (Friedmann 1929). This has led many to assume that cowbirds exhibit a closed developmental system, and that much of their behaviour is a result of inborn tendencies (Mayr 1974). However, it has been shown that reproductive competence in male and female cowbirds is dependent on extensive social learning (Rothstein & Fleischer 1987; Freeberg et al. 1995, 2002; White et al. 2002b; King et al. 2003a). Male cowbirds receive feedback from females about the quality of their song, and female interaction guides the development of male courtship. Female interactions also shape the development of their mating preferences. For example, adult females, which do not sing, attend to other females' responses to song (Gros-Louis et al. 2003) and learn song preferences by attending to female rattle vocalizations (Freed-Brown & White 2009). Females must learn to discriminate male songs and reinforce male behaviour (West et al. 1996). Males must learn a range of skills for navigating the male social structure prior to interacting successfully with females (White et al. 2002b). Thus, access to close-range acoustical and social information is an essential component of development in cowbirds.

To operationalize the concept of a social niche, we used a social network measure termed 'degree centrality'. Centrality measures are designed to capture how an individual relates to others in a group (Freeman 1979). When interactions are directed towards specific individuals, degree centrality uses the frequency of approaches directed towards others to calculate gregariousness and the frequency of approaches that are received from others to calculate attractiveness. Degree centrality is therefore a useful construct for measuring an individual's social niche by capturing both directions in how individuals relate to others (Faust & Skvoretz 2002; Flack et al. 2006). We expected to find stable variation in the characteristics of social niches, with some individuals being more gregarious or attractive than others. Degree centrality allows us to quantify these niche characteristics and see whether they are related. For instance, gregarious individuals may also be highly attractive. Thus, using degree centrality, we can uncover the characteristics and stability of an individual's niche.

We sought to investigate the stability of adult and juvenile social niches when the social environment is perturbed. One way to learn about stability of social niches is through perturbation studies where an existing group is changed by removing or adding individuals. Perturbation studies in primates have looked at the role of policing behaviour in maintaining group cohesion and found destabilization upon removing significant individuals (Flack et al. 2006). Studies in cowbirds used perturbation techniques to understand the role of assortment to alter developmental trajectories within a flock (King et al. 2003b; Gros-Louis et al. 2006; White et al. 2007). In the present study, we separated two flocks, one with familiar adults and one with naïve juveniles, into two smaller flocks and then recombined them. Because female interaction shapes the social organization of cowbird flocks (King et al. 2003b), we hypothesized that adult females would maintain stable social niches throughout the perturbations. Males must

reassess their relationship with other potentially more dominant males when conditions change, and, therefore, we hypothesized that perturbing the social environment would cause males to reshape their social niche. Naïve juveniles may show considerable variability in their social niches, as they do not yet possess competent social skills. Thus, we hypothesized that juveniles would not maintain stable social niches when the context changed.

METHODS

Subjects

All birds were originally captured either in Philadelphia County, Pennsylvania or Monroe County, Indiana, U.S.A., and housed in aviaries in Monroe County, Indiana. All subjects were *Molothrus ater*. Previous studies found no differences between these two populations in song or social structure (A. P. King, unpublished data). We used 33 female and 29 male cowbirds. The adult flocks contained 21 adult females and 17 adult males, and the juvenile flocks contained 12 juvenile females and 12 juvenile males. At the beginning of the study, adults ranged in age from 3 to 11 years, with an average age of 6, and juveniles ranged in age from 55 to 75 days old, with an average age of 73 days. Adult birds were housed together for 1 year, and juveniles were housed together for 1 month, prior to the present study. After capture, juveniles were housed separately from adults and had no further direct interactions with adults. Each bird was marked with uniquely coloured leg bands to allow for individual recognition. All birds were provided daily with a diet of vitamin-treated water (Aquavite Nutritional Research, Keighley, West Yorkshire, U.K.), red and white millet, canary seed and a modified Bronx Zoo diet for blackbirds.

Aviaries

We used three aviaries that were visually isolated and substantially acoustically attenuated or isolated from each other, each with identical dimensions (9.1 × 21.4 × 3.4 m). Environmental conditions were similar throughout all aviaries, with shrubs, trees, grass, covered feeding stations and access to indoor enclosures. All aviaries allowed birds to be exposed to ambient climatic conditions, wild cowbirds and occasional interaction with predators.

Data Collection

An approach was scored when one individual approached another individual with any part of its body within a radius of 30 cm. We recorded the identity of the individual that initiated the approach and the individual that was approached. Throughout the study, we used a scan-sampling procedure: behaviours were recorded as they were observed using voice recognition technology (White et al. 2002a). When used in combination with voice recognition technology, scan sampling can accurately acquire a more comprehensive data set than focal sampling (White & Smith 2007). Observations were conducted between 0700 and 1030 hours, when cowbirds are most active, and were counterbalanced so that each observer took the same number of scan-sampling blocks in each aviary at the same time of day. All work was conducted under ASAB/ABS guidelines and approved by the Institutional Care and Use Committee of Indiana University (08-018).

Experiment 1: Adults

Stage 1

Baseline period. On 2 September 2009, all individuals were moved into Aviary 1. During 3–18 September 2009, two observers

conducted daily, counterbalanced 7 min observations, during which all approaches were recorded ($N = 126$ observation blocks).

Stage 2

Fission period. On 18 September, we separated the birds into Aviaries 1 and 2 based on their frequency of approaches during the baseline period so that both flocks contained a similar range of approaches. Aviary 1 contained 11 females and 9 males, and Aviary 2 contained 10 females and 8 males. From 19 September to 21 November, two observers conducted daily, counterbalanced 7 min observations, during which all approaches were recorded ($N = 573$ observation blocks: 286 blocks in Aviary 1; 287 blocks in Aviary 2).

Stage 3

Fusion period. On 21 November, the partition separating the two aviaries was opened and both flocks were allowed to interact. From 21 November to 4 December, two observers recorded approaches during 7 min blocks in both Aviaries 1 and 2 ($N = 108$ observation blocks).

Experiment 2: Juveniles

Stage 1

Baseline period. From 7 September to 11 October 2010, three observers conducted daily, 7 min observations in Aviary 1, during which all approaches were recorded ($N = 165$ observation blocks).

Stage 2

Fission period. On 13 October, we separated birds into Aviary 1 and Aviary 2 based on their frequency of approaches during the baseline period so that both flocks contained individuals with a similar range of approaches. Both aviaries contained 12 males and 12 females. During 13–24 October, three observers conducted daily, 7 min counterbalanced observations, during which all approaches were recorded ($N = 195$ observation blocks: 98 blocks in Aviary 1; 97 blocks in Aviary 2).

Stage 3

Fusion period. On 27 October, all birds were moved into Aviary 1. From 27 October to 6 November, three observers conducted daily 7 min observations, during which all approaches were recorded ($N = 166$ observation blocks).

Analysis

We checked all data for normality using a Kolmogorov–Smirnov test. To uncover the influence of age, sex and period on the degree of sex assortment, we conducted a general linear mixed model. The proportion of approaches towards females was the dependent variable, with period (baseline, fission, fusion), age (adult, juvenile) and sex (male, female) as the fixed factors and individual included as a random factor. We conducted a further Bonferroni-adjusted post hoc pairwise comparison based on the estimated marginal means to uncover the degree and direction of difference between the variables. We determined significant values for the fixed factors and the post hoc comparisons using two-tailed P values with $\alpha = 0.05$, with confidence intervals reported for the estimated marginal means. Comparison of the approach proportions between aviaries during the fission period revealed no significant differences in adult or juvenile flocks (adults: Mann–Whitney U test: $U = 158$, $N_1 = 20$, $N_2 = 18$, $P = 0.52$; juveniles: $U = 75$, $N_1 = 12$, $N_2 = 12$, $P = 0.87$). Therefore, data from the fission period were combined for our model.

Using the approach data, we calculated the degree centrality for each individual during each period. Because interactions in this

study were directed, degree centrality was parsed into indegree and outdegree centrality. Individuals that approach more individuals more frequently have a higher outdegree centrality, and individuals that attract more approaches from more individuals have a higher indegree centrality (Faust & Skvoretz 2002). Outdegree centrality corresponds to an individual's gregariousness, and indegree centrality corresponds to their attractiveness (Wasserman & Faust 1994). For the fission period, we calculated indegree and outdegree centrality for each of the two separated flocks, and for the baseline and fusion periods, we calculated indegree and outdegree centrality for the entire (adult or juvenile) flock. We used Spearman correlations to investigate whether there was a relationship between an individual's outdegree and indegree in each period, and whether an individual's indegree/outdegree centrality showed repeatability across periods.

To test whether individuals approached the same individuals at similar frequencies across periods, we used a K_r row-wise matrix correlation with 4000 permutations. The K_r correlation was developed to compare directed interaction matrices and can be used to demonstrate whether stable interaction preferences among pairs of individuals are sustained across contexts (Hemelrijk 1990). Significant K_r correlations approaching 1.0 would indicate that most individuals interacted with the same individuals between the different periods. We compared male–male, female–female, male–female and female–male interaction matrices from the baseline and fusion periods for both the adult and juvenile flocks to determine whether individuals approached the same males or females when the flocks were recombined.

Observer bias was tested using Kruskal–Wallis tests (juvenile flocks: baseline: $H_2 = 0.339$, $P = 0.56$; fission: $H_2 = 1.280$, $P = 0.26$; fusion: $H_2 = 0.083$, $P = 0.77$), revealing no significant differences between observers in the number of approaches observed in each period (Ottoni et al. 2005). We used interclass correlation components (ICC) to test observer reliability. All observers ranked birds similarly based on the number of approaches in each period (ICC: adults = 0.85, $P < 0.0001$; juveniles = 0.73, $P = 0.002$).

All statistical analysis was conducted using the R statistical computing platform version 2.11.0 (the R project website, <http://www.r-project.org/>) and SPSS (2005, SPSS, Chicago, IL, U.S.A.), and degree centrality measures were calculated using UCInet (Borgatti et al. 2002).

RESULTS

We observed significant age–sex differences in how individuals approached others. Females of both age classes sustained significant levels of sex assortment by preferentially approaching other females (Fig. 1, Table 1), but juvenile females showed a greater propensity to interact with other females than did adult females. Adult and juvenile females also showed high repeatability in attractiveness and gregariousness, demonstrating that females maintained comparable social niches across social contexts.

Proportion of Approaches in Adult and Juvenile Flocks

Our model demonstrated that the fixed effects of period ($F_{2,116} = 6.038$, $P = 0.003$) and sex ($F_{1,58} = 91.285$, $P < 0.0001$) significantly influenced the proportion of approaches towards females, whereas age had a marginally significant effect ($F_{1,58} = 3.917$, $P = 0.053$). Post hoc analysis revealed that females directed a significantly higher proportion of approaches towards females (mean \pm SE = 0.66 ± 0.015 , 95% confidence interval, CI = 0.63, 0.69) than males did (0.45 ± 0.016 , 95% CI = 0.42, 0.48; mean \pm SE difference = 0.21 ± 0.022 , $P < 0.0001$). Juveniles tended to direct a higher proportion of approaches towards females

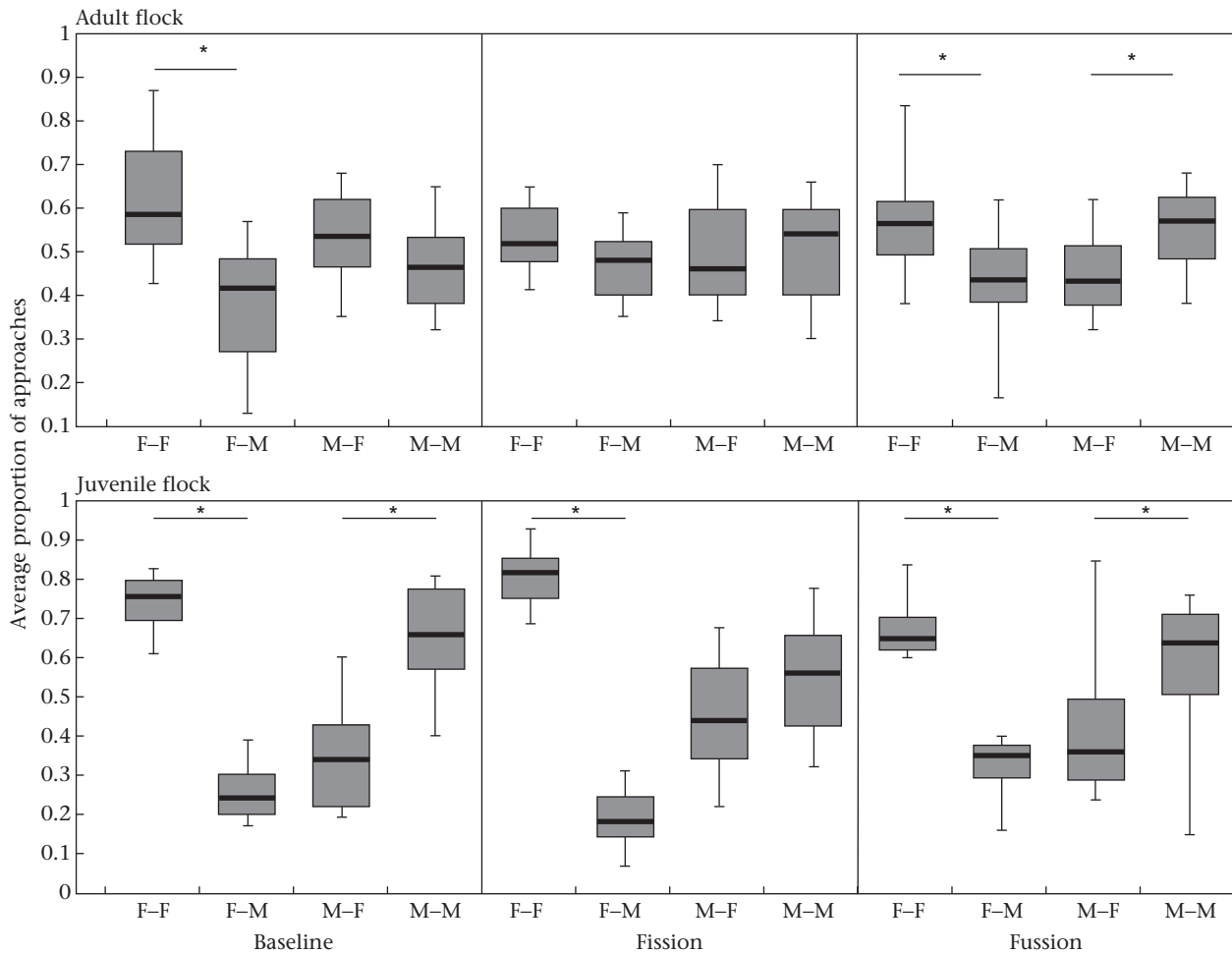


Figure 1. Proportion of male- and female-directed approaches in adult and juvenile flocks of cowbirds during baseline, fission and fusion periods. Box plots show the 25th and 75th percentiles (box), the median (line within the box) and the 5th and 95th percentiles (whiskers). Significant differences ($*P < 0.05$) were calculated using a nonoverlapping 95% confidence interval (CI) of estimated marginal means. Adult flock: baseline: FF = 0.61 (95% CI = 0.57, 0.67) versus FM = 0.38 (95% CI = 0.34, 0.43); fusion: FF = 0.57 (95% CI = 0.52, 0.67) versus FM = 0.44 (95% CI = 0.39, 0.48); MF = 0.47 (95% CI = 0.39, 0.49) versus MM = 0.55 (95% CI = 0.50, 0.61). Juvenile flock: baseline: FF = 0.75 (95% CI = 0.69, 0.81) versus FM = 0.25 (95% CI = 0.19, 0.31); MF = 0.35 (95% CI = 0.29, 0.41) versus MM = 0.65 (95% CI = 0.59, 0.71); fission: FF = 0.80 (95% CI = 0.75, 0.87) versus FM = 0.19 (95% CI = 0.13, 0.25); fusion: FF = 0.67 (95% CI = 0.61, 0.73) versus FM = 0.33 (95% CI = 0.27, 0.39); MF = 0.41 (95% CI = 0.35, 0.47) versus MM = 0.59 (95% CI = 0.53, 0.65).

(mean \pm SE = 0.57 ± 0.017 , 95% CI = 0.54, 0.61) than adults did (0.53 ± 0.014 , 95% CI = 0.50, 0.56; mean \pm SE difference = 0.044 ± 0.022 , $P = 0.053$). The proportion of approaches towards females was significantly lower during the fusion period than during all other periods (baseline: 0.56 ± 0.014 , 95% CI = 0.54, 0.59; fission: 0.57 ± 0.014 , 95% CI = 0.54, 0.60; fusion: 0.52 ± 0.014 , 95% CI = 0.49, 0.55; mean \pm SE difference: baseline–fusion = 0.042 ± 0.015 , $P = 0.02$; fission–fusion = 0.048 ± 0.015 ,

$P = 0.005$). Thus, our model demonstrates that although the overall proportion of approaches towards females changed with the social perturbations, females preferentially approached other females.

We also discovered a significant interaction between sex and age ($F_{1,58} = 33.946$, $P < 0.0001$; Fig. 1) on the proportion of approaches towards females. Juvenile females maintained the highest proportion of approaches towards females (mean \pm SE = 0.74 ± 0.024 , 95% CI = 0.69, 0.79), whereas juvenile males maintained the lowest (0.40 ± 0.024 , 95% CI = 0.36, 0.45). Post hoc analysis revealed that juvenile females maintained a significantly higher proportion of approaches towards females than did adult females (0.57 ± 0.018 , 95% CI = 0.53, 0.61; mean \pm SE difference = 0.172 ± 0.030 ,

Table 1

Total number of female–female (F–F), male–female (M–F), female–male (F–M) and male–male (M–M) approaches for the baseline, fission and fusion periods for the adult and juvenile flocks of cowbirds

| | F–F | M–F | F–M | M–M | Total |
|------------------|------|------|------|------|--------|
| Adults | | | | | |
| Baseline | 877 | 801 | 513 | 541 | 2732 |
| Fission | 5023 | 5412 | 4378 | 4226 | 19 039 |
| Fusion | 966 | 892 | 696 | 851 | 3405 |
| Total | 6866 | 7105 | 5587 | 5618 | 25 176 |
| Juveniles | | | | | |
| Baseline | 742 | 331 | 265 | 667 | 2005 |
| Fission | 1178 | 580 | 339 | 694 | 2791 |
| Fusion | 972 | 650 | 546 | 1087 | 3255 |
| Total | 2892 | 1561 | 1150 | 2448 | 8051 |

Table 2

Spearman rank correlations in indegree and outdegree centrality for adult male and female cowbirds over the three periods

| | | Baseline–Fission | Fission–Fusion | Fusion–Baseline |
|---------------|-----------|------------------|----------------|-----------------|
| Adult males | Indegree | 0.32 | 0.35 | 0.02 |
| | Outdegree | 0.64* | 0.67** | 0.75*** |
| Adult females | Indegree | 0.63** | 0.80*** | 0.68** |
| | Outdegree | 0.71*** | 0.81*** | 0.73*** |

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$.

Table 3

Spearman rank correlations in indegree and outdegree centrality for juvenile male and female cowbirds over the three periods

| | | Baseline–Fission | Fission–Fusion | Fusion–Baseline |
|------------------|-----------|------------------|----------------|-----------------|
| Juvenile males | Indegree | 0.62* | –0.06 | –0.38 |
| | Outdegree | 0.82** | 0.72* | 0.55 |
| Juvenile females | Indegree | 0.80* | 0.77** | 0.65* |
| | Outdegree | 0.85** | 0.79** | 0.75* |

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$.

$P < 0.0001$), whereas adult males sustained a significantly higher proportion of approaches towards females (0.49 ± 0.02 , 95% CI = 0.45, 0.53) than did juvenile males (mean \pm SE difference = 0.085 ± 0.032 , $P = 0.01$). In both the adult and juvenile flocks, females maintained a significantly higher proportion of approaches towards other females than they did towards males (mean \pm SE difference: adults: 0.082 ± 0.027 , $P = 0.004$; juveniles: 0.338 ± 0.034 , $P < 0.0001$). These findings demonstrate that an individual's age and sex influenced how they allocated their approaches, and that juvenile females biased their approaches towards other juvenile females over juvenile males (Fig. 1).

Degree Centrality

Adult females maintained equivalent patterns of interaction throughout the study. Across all three periods, we observed significant correlations in adult female indegree and outdegree centrality ($N = 21$; Table 2), and within all periods, adult female outdegree centrality was significantly correlated with indegree centrality (Spearman rank correlation: baseline: $r_s = 0.61$, $N = 21$, $P = 0.004$; fission: $r_s = 0.75$, $N = 21$, $P < 0.0001$; fusion: $r_s = 0.76$, $N = 21$,

$P < 0.0001$). Consequently, adult females constructed stable social niches, as gregariousness was correlated with attractiveness in all periods.

Adult males were less able to construct equivalent patterns of interaction when the social context changed. While adult male outdegree centrality was significantly correlated over the three periods, there was no significant relationship with a male's indegree centrality across periods (Table 2). Male outdegree centrality was significantly correlated with indegree centrality only during the fission period ($r_s = 0.73$, $N = 17$, $P = 0.001$). Thus, adult males did not maintain stable niches, and their gregariousness was not correlated with their attractiveness in all periods.

Juvenile females maintained equivalent social niches throughout the study. Across all periods, we observed significant correlations in juvenile females' indegree and outdegree centrality ($N = 12$; Table 3). However, the characteristics of juvenile female niches differed from those of adult females. Juvenile female outdegree centrality was significantly correlated with indegree centrality only during the baseline period ($r_s = 0.6$, $N = 12$, $P = 0.04$; Fig. 2). Therefore, while juvenile females maintained stable social niches, their gregariousness was not correlated with their attractiveness throughout the study.

Juvenile males did not maintain equivalent social niches. Outdegree centrality was correlated over the baseline–fission and fission–fusion periods, and their indegree centrality was correlated only over the baseline–fusion periods (Table 3). The characteristics of juvenile male social niches changed over time. Juvenile males' outdegree centrality was significantly correlated with their indegree centrality during the baseline ($r_s = 0.65$, $N = 12$, $P = 0.01$) and fusion ($r_s = 0.59$, $N = 12$, $P = 0.045$; Fig. 3) periods. Thus, like adult males, a juvenile male's gregariousness was not correlated with his attractiveness throughout the study.

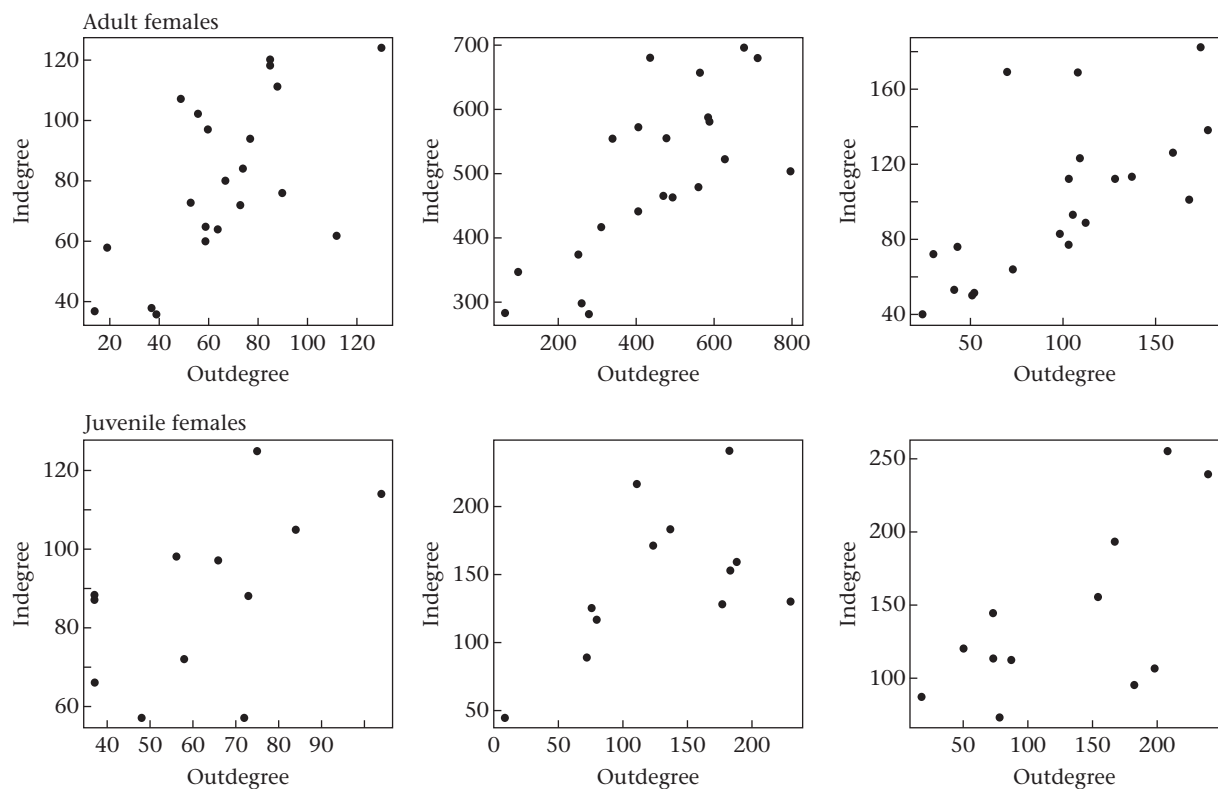


Figure 2. Scatter plots of individual indegree and outdegree centrality for adult and juvenile female cowbirds over all three periods (Spearman rank correlations: adult females: baseline: $r_s = 0.61$, $P = 0.004$; fission: $r_s = 0.75$, $P < 0.0001$; fusion: $r_s = 0.76$, $P < 0.0001$; juvenile females: baseline: $r_s = 0.60$, $P = 0.04$; fission: $r_s = 0.55$, $P = 0.06$; fusion: $r_s = 0.47$, $P = 0.12$).

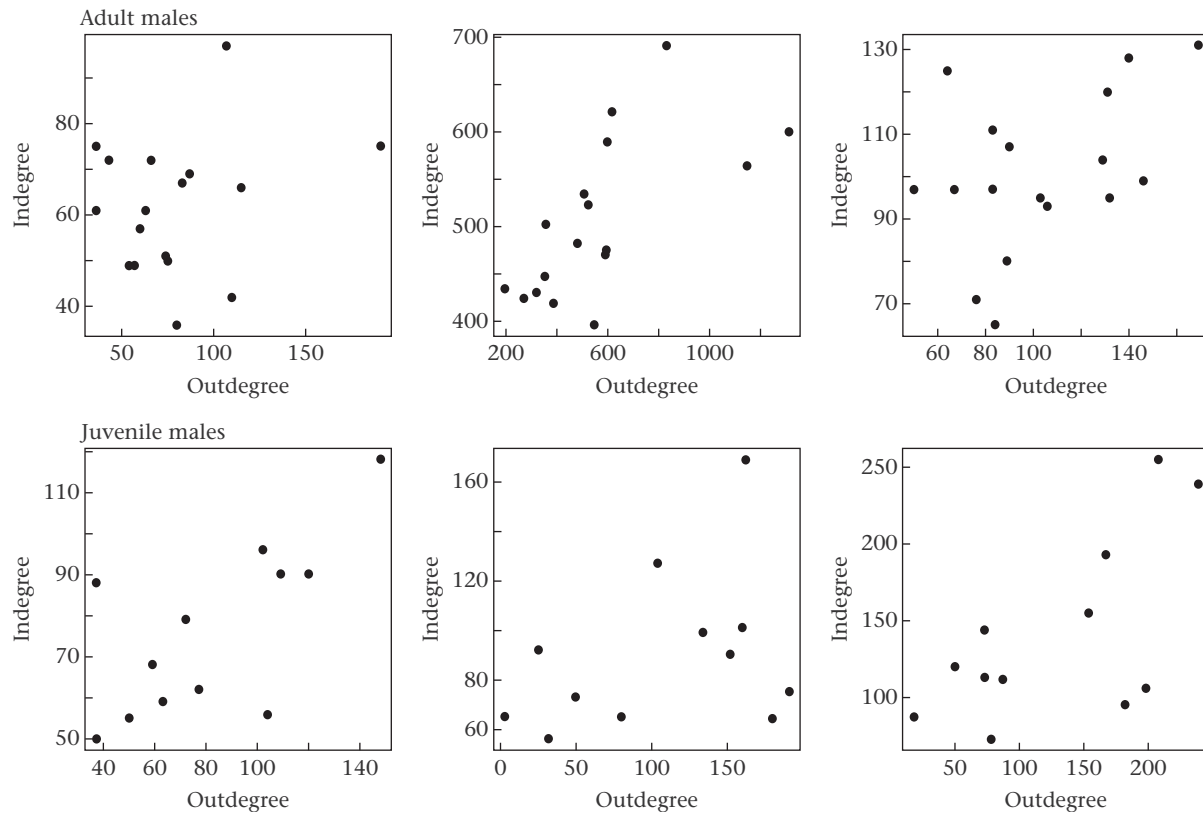


Figure 3. Scatter plots of individual indegree and outdegree centrality for adult and juvenile male cowbirds over all three periods (Spearman rank correlations: adult males: baseline: $r_s = 0.07$, $P = 0.74$; fission: $r_s = 0.73$, $P = 0.001$; fusion: $r_s = 0.31$, $P = 0.22$; juvenile males: baseline: $r_s = 0.65$, $P = 0.02$; fission: $r_s = 0.29$, $P = 0.35$; fusion: $r_s = 0.58$, $P = 0.05$).

Individual Association Patterns

Adult females showed a low but significant tendency to approach the same adult females between baseline and fusion periods ($\tau_{kr} = 0.172$, $P < 0.001$), but showed no tendency to approach the same adult males ($\tau_{kr} = 0.06$, $P = 0.1237$). Adult males also showed a low but significant tendency to approach the same adult females ($\tau_{kr} = 0.207$, $P < 0.001$), but showed no tendency to approach the same adult males ($\tau_{kr} = 0.001$, $P < 0.494$). There was no tendency for juvenile females to approach the same juvenile males ($\tau_{kr} = 0.02$, $P = 0.389$) or females ($\tau_{kr} = -0.037$, $P = 0.685$), and there was no tendency for juvenile males to approach the same males ($\tau_{kr} = -0.011$, $P = 0.55$) or females ($\tau_{kr} = 0.033$, $P = 0.35$) across the baseline and fusion periods. Thus, most individuals did not approach the same individuals when the flocks were recombined.

DISCUSSION

Both adult and juvenile females maintained equivalent indegree/outdegree centrality levels over all periods. Females occupied stable niches when the social environment was perturbed, and thus experienced consistent access to social information despite a changing social composition. Perturbing the social environment changed the relative attractiveness of individual males and caused males to occupy different social niches. Adult and juvenile males did not maintain equivalent levels of indegree or outdegree centrality across periods. Complex social organization requires the persistence of stable interaction patterns over time and contexts to canalize developmental pathways and transfer information (Hinde 1976; West-Eberhard 2003). A social niche shapes the opportunities to learn from others by affording qualitatively different social

experiences (Alberts & Cramer 1988). The consistency of female social niches suggests that females play an important role in shaping social structure and information transfer within cowbird flocks.

Female proximity may be one of the more salient features involved in shaping the development of song, behaviour and social organization within cowbird flocks (Smith et al. 2000). Male–female social interactions are performed within inches of other individuals. For example, females respond to preferred male song variants with very rapid wing flicks called ‘wing-strokes’ (West & King 1988). Males that attend to female wing-strokes receive feedback about the quality of their song, and produce higher-quality song variants. Thus, female proximity affords access to communicative signals that shape the development of female song preference. In large flock settings, females (1) adopt the mate preferences of other females (Freed-Brown et al. 2006; West et al. 2006), (2) prefer male song when it is coupled with another female’s vocalizations (Freed-Brown & White 2009) and (3) respond to other females’ wing-strokes (Gros-Louis et al. 2003). The predictability of female social interactions provides the economy of perception that may guide the development of female song and mate preferences (Gibson 1966).

Age differences in social niches reflect developmental changes in how individuals interact with each other. Here we discovered that gregariousness in adult females was correlated with their attractiveness, as indegree centrality was correlated with outdegree centrality in all periods. In contrast, juvenile females’ gregariousness did not reflect their attractiveness. An important milestone in female cowbird social development is learning to manage proximity with others (King et al. 2003b). Although juvenile females maintained higher levels of sex assortment, they were more indiscriminate in the specific individuals with whom they

chose to interact. Thus, juveniles must learn to differentiate individual females and become more discriminative in females that they approach. A female's social niche therefore reflects the relative levels of social competence within the flock.

Although metrics of indegree/outdegree centrality showed consistency for the adult females, and less so for the males, stability of social structure was affected in the three periods: adult and juvenile males and females did not tend to approach the same individuals when the flocks were recombined. Therefore, the stability of a female's niche is not dependent on the presence of particular individuals but on individual variation in general gregariousness. Thus, during the autumn, females are able to construct a stable social niche within a de-individualized social structure. During the breeding season, cowbirds maintain socially monogamous pairings (White et al. 2002a). Further studies will show whether females maintain stable niches into the breeding season when individual interaction preferences emerge.

Cowbird flocks are characterized by sex- and age-biased assortment patterns (Smith et al. 2002; Gros-Louis et al. 2003). Many species, including humans, show sex-biased social structures (La Freniere et al. 1984; Bon & Campan 1996; Ruckstuhl 2007). By preferentially assorting with their own sex, the proximal social ecologies surrounding males and females differ. Our findings replicate those of Smith et al. (2002), by documenting pronounced sex assortment, and further extend Smith et al.'s study by investigating the stability and variation of individual interaction patterns. Juvenile flocks had higher levels of sex assortment over more periods than adults, and therefore sex-biased interaction preferences emerged without adult influence. Juvenile cowbirds may preferentially approach individuals of their own sex because they engage in similar kinds of behaviours. Jacklin & Maccoby (1978) documented that sex segregation in preschool play groups resulted from differences in behavioural compatibility, and Hassett et al. (2010) showed that variation in behavioural compatibility constructs male-only peer groups in rhesus macaques, *Macaca mulatta*. The presence of early sex-biased interaction preferences warrants further investigation, as they may structure the developmental trajectories and social niches of the sexes.

Juvenile females displayed higher levels of sex-biased assortment in more periods than did adult females. This may have occurred because juvenile females were avoiding the intrusive behaviour of juvenile males and therefore preferentially associating with other juvenile females by default. When in the presence of males, female Japanese quail, *Coturnix japonica*, preferentially form associations with other females, whereas when males are not present, females tend to avoid each other (Persuad & Galef 2003). In small-spotted catsharks, *Scyliorhinus canicula*, well-connected female networks remained stable despite introductions of new males into the group (Jacoby et al. 2010). Upon entering adult cowbird flocks, juvenile females can potentially access information about males from experienced females. The persistence of sex assortment into adulthood suggests that females may continually communicate their song/mate preferences with other females before initiating interactions with males. Thus, by avoiding the intrusive behaviour of males, females create a self-organized forum where they may exchange information on male quality.

This study demonstrates stability in female niche construction across perturbations. This was the case regardless of age, experience, familiarity or interaction preferences, suggesting that reliable female interaction patterns are a common denominator for cowbird social organization. As cowbirds are heavily dependent on culturally transmitted behaviour to become reproductively competent, it appears that evolution has selected for a nonhierarchical, highly distributed and stable social mechanism to be responsible for the development of species-typical behaviour.

Acknowledgments

We thank the Indiana University Foundation for providing funds for this research. We thank Lisa Byrge, Chris Harshaw and Jennifer Miller for comments on the manuscript and Uwe Pott for help with the research. We also thank Dr Peter Dunn and two anonymous referees for their useful comments.

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