



The ontogeny of social skills: experimental increases in social complexity enhance reproductive success in adult cowbirds

David J. White*, Andrew S. Gersick, Grace Freed-Brown, Noah Snyder-Mackler

Department of Psychology, University of Pennsylvania

ARTICLE INFO

Article history:

Received 22 June 2009

Initial acceptance 14 August 2009

Final acceptance 15 October 2009

Available online 2 December 2009

MS. number: A09-00414R

Keywords:

brown-headed cowbird

cowbird

development

mating success

Molothrus ater

social learning

The social environment can act as an important selective force on both morphological and behavioural traits by conferring a reproductive advantage on individuals that successfully navigate social interactions. The ontogeny of these social traits is poorly understood. We examined whether increasing exposure to more complex social environments could hone competitive skills and ultimately increase reproductive success in adult brown-headed cowbirds, *Molothrus ater*. We created two types of flocks ('Dynamic' and 'Stable') that differed in social complexity. In Dynamic flocks, birds were regularly exchanged across groups, whereas in 'Stable' flocks, the composition of birds remained static throughout a year. Social networking analyses revealed that males in the Dynamic flocks had larger and more variable singing networks during the manipulations than did the males in the Stable flocks. When we put males from the two conditions together into new environments with unfamiliar females, the Dynamic-condition males had greater mating success. Our results establish a link between social competence and reproductive success and suggest that social skills are extremely flexible characteristics, even in adulthood.

© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Social creatures require skills for successfully maintaining the balance between cooperation and conflict with groupmates, navigating dominance hierarchies and interpreting and responding appropriately to others' intentions. Most interest on social skills has focused predominantly on their relationship with fitness (Byrne & Whiten 1988, 1997). Research has largely explored the functional value of social and cognitive traits by making comparisons across species that vary in sociality. The last two decades have seen discoveries of skills and capacities in social species like sensitivity to dominance hierarchies (Bergman et al. 2003), flexible signalling in response to competition (Gros-Louis 2004), and even seemingly deceptive behaviour (Cyger & Marler 1988; Bugnyar & Heinrich 2006).

Substantially less is known about proximate causes and developmental influences on social skills. If interactions with others can modify social skills across an animal's lifetime, it would complicate comparisons of the skills of social and nonsocial animals. Moreover, without understanding how social traits are organized, how they are learned, or how malleable they are, it can be difficult to determine where and when selection may be acting (West et al. 2003). For example, differences in social skills may have derived from individuals' differences in their ability early in life to seek out and

engage with others. These early life propensities towards gregariousness or social learning could be where selection acts most directly.

One area where developmental influences on traits important for reproduction has been extensively explored is in the study of birdsong (Catchpole & Slater 1995). For example, in brown-headed cowbirds, *Molothrus ater*, social experience plays a key role in the development of effective song, which is necessary for achieving copulations (Rothstein & Fleischer 1987; Rothstein et al. 1988; West & King 1988). In addition, a long history of research on cowbirds has shown that a wide array of traits and skills beyond song quality also contributes to mating success (e.g. courtship persistence: King et al. 2003b; competitive behaviour: Dufty 1986; Rothstein et al. 1986; White et al. 2002c) and that these traits are all influenced by social learning during development.

While adult song quality in cowbirds as in many other species appears to be relatively fixed, recent work suggests that some of these other social skills may remain malleable and responsive to social experience even in adulthood. In a study of social influences on the reproductive behaviour of adult male cowbirds, White et al. (2002c) compared adult males housed in groups containing juvenile males with adult males housed only with other adults. Throughout the year there were very few differences among adult males in the two conditions as measured by amount and use of song, the quality of their songs, or the number of copulations they achieved. However, when the two groups of adult males were

* Correspondence: D. J. White, Department of Psychology, University of Pennsylvania, 3720 Walnut Street, Philadelphia, PA 19104, U.S.A.

E-mail address: whitedj@psych.upenn.edu (D.J. White).

brought together in a mating competency tournament and allowed to compete with each other for mating opportunities with a new group of females, significant differences among males in the two conditions emerged. Adult males that had formerly been housed with juvenile males mated earlier and copulated more frequently than adults that had been housed only with peers. These results demonstrated that the mating skills of adult birds were malleable and could be influenced by prior social experience. The mechanism of that influence was less clear. What was it about the inclusion of juvenile males that increased the competitiveness of affiliated adults? We suggest that the increased variability in the social environment introduced by juveniles might be responsible; juvenile birds are more erratic in their behaviour than adults: they interact more frequently with a wider array of partners and they are more likely to court adult males' consort females. This lack of reliable social behaviour from groupmates may have given the affiliated adult males more experiences monitoring the social group and dealing with social challenges; experiences which may have produced their increased success in the mating tournament.

If this is true, it suggests an ontogenetic analogue to the social complexity hypothesis: environments that provide more opportunities for effective social learning should produce more skilled and reproductively competitive individuals. The present study was designed to test that hypothesis. We examined the malleability of social skills of adult male cowbirds living in two different social conditions. The manipulations that occurred during the year-long experiment were designed to give one group greater access to social challenges. In many species, increased subgroup size relates to social complexity (Kudo & Dunbar 2001). Thus we manipulated social complexity by creating conditions where some birds interacted with many different males and females in consistently changing groups ('Dynamic' flocks), while other birds remained in static groups ('Stable' flocks). Birds in the two 'Stable' flocks remained together throughout the autumn, winter, spring and breeding season. Birds in the two 'Dynamic' flocks were swapped in small subgroups in the winter and spring prior to the breeding season. Thus, while all groups were always maintained at the same size, the manipulations imposed more social demands on birds in the Dynamic flocks. With each manipulation, males had to reevaluate dominance relationships with new males. They also gained and lost opportunities to court females.

In late spring, we stopped manipulations and for the first month of the breeding season we measured courtship and singing for all the males in the four groups. In the second half of the breeding season we conducted a mating competency tournament where males from the two conditions competed directly against each other in a new environment for mating opportunities with new females. The tournament was designed to test individuals' abilities to compete with males and court females quickly and effectively in conditions that mimicked the competitive demands of wild breeding flocks (Friedmann 1929; Rothstein et al. 1986, 1988; Ortega 1998). We anticipated that access to a wider array of social experiences would differentially improve the courtship and competitive skills of the males in the Dynamic conditions, ultimately increasing their reproductive success in the tournament.

METHODS

Subjects for this experiment were 32 adult male cowbirds (15 wild-caught and 17 hand-reared). We trapped wild-caught birds in Montgomery County, Pennsylvania, U.S.A., in June of 2004, 2005 and 2006. We hand-reared birds in 2004 and housed them in mixed age-sex flocks until the experiment. Thus, all of the males participating in the experiment had reached sexual maturity and developed mature song at least one breeding season prior to the

inception of the experiment. Based on extensive observations across the years we have found that the behaviour of wild-caught and hand-reared birds is similar in every measured category (unpublished observations). Also present in the conditions were 48 females (28 wild-caught, 20 hand-reared). All birds wore individually distinct coloured leg bands to permit individual identification. Two males died over the course of the year (one from each Stable flock). We removed their data from all analyses.

Apparatus

We housed birds in four large 9.1 × 21.4 × 3.4 m outdoor aviaries during the experiment. All aviaries contained grass, trees, shrubs and shelter, and the physical layout of all of the aviaries was similar. The subject males had been housed in the laboratory prior to the study and each of them had spent some time in each of the aviaries prior to commencement of the experiment. Birds had ad libitum access to fresh water and a mix of millet and canary seed plus a modified Bronx Zoo diet for omnivorous birds.

Procedure

Starting on 10 October, we randomly assigned eight males and 12 females to each of the four aviaries. Wild-caught and hand-reared birds were equally represented in all groups. We randomly assigned two of the groups to the Dynamic condition and two of the groups to the Stable condition. These initial organizations were considered to be the birds' baseline conditions. Overall, the experiment was organized into three phases. First, there was a manipulation phase that occurred in the autumn, winter and spring where birds in the Dynamic condition were swapped in small subgroups. In the second phase, the birds were returned to their baseline flocks for the first half of the breeding season. Finally, in the third phase, pairs of males from the two conditions competed against each other in a 'mating competency tournament'.

Manipulation phase

The Stable birds remained in their baseline conditions throughout the autumn, winter and spring into the breeding season, during which time we swapped small subgroups of Dynamic birds between the two Dynamic aviaries. The schedule for manipulations is provided in Table 1. To control for handling, we caught subgroups of Stable birds on the same schedule but then released them back into their home condition.

Throughout the experiment we measured the singing and social behaviour of the birds based on published procedures (West et al. 2002; White et al. 2002b, c, 2007). Briefly, four observers collected measures of song use of the individual males in each aviary using ad libitum sampling (Altmann 1974) in 15 min censuses. We collected

Table 1
Outline of manipulations of Dynamic group

Date	After swap		
	Individuals swapped	Original birds	Other birds
2 Dec	4 females	8 males, 8 females	4 females
19 Mar	4 females	8 males, 4 females	8 females
11 Apr	4 females	8 males	12 females
25 Apr	3 males	5 males	3 males, 12 females
30 Apr	3 males	2 males	6 males, 12 females
5 May	2 males		8 males, 12 females
15 May	All birds returned to baseline conditions		

Date and number of individuals exchanged between the two Dynamic flocks. The two flocks were always maintained at eight males and 12 females. 'Original' refers to birds that were in the flock in baseline conditions. 'Other' refers to birds that had been introduced from the other Dynamic flock during manipulations.

at least two censuses per day in each aviary every day (weather permitting) and increased censuses to six per day during the breeding season. We conducted censuses in the morning: at 0800 hours (before the breeding season) and at 0600 hours (during the breeding season). We used voice recognition software and programmable databases that automatically recorded spoken data-collection code, then transcribed, error-checked and summarized the data (White et al. 2002a). Within each census, we noted the individual identity of any male that sang or whistled, whether the song was directed to another bird (sung within 60 cm and oriented towards another individual), or was undirected. If directed, we noted whether the song was directed to a male or a female. These behavioural measures provided information about dominance and courtship persistence: males direct songs to other males in order to establish dominance hierarchies, and sing to females to court them. For the months prior to the breeding season, we collected 1369 censuses of the song and social behaviour of the males. We thus had large data sets of the singing behaviour of each of the males in all of the groups.

Breeding season baseline phase

The birds remained in their baseline conditions for the first month of the breeding season. We collected 304 censuses during this time. In these censuses we collected the same song measures and followed the same procedures as we did prior to the breeding season, but in addition we also recorded all observed copulations (copulations do not occur outside of the breeding season).

Mating competition tournament phase

In the second half of the breeding season, we tested males' abilities to court and compete in a new context. We placed pairs of males together from the two conditions into a new aviary with females and measured their ability to mate. Tournament groupings consisted of four males (two from a Stable flock, two from a Dynamic flock) and 11 females. We randomly selected one Dynamic group to be paired with one Stable group for the competition and paired the remaining Dynamic group and Stable group for a second competition. Within each competition, we selected the males that would compete directly against each other based on their performance in the first half of the breeding season. We took pairs of males from the two conditions that had similar levels of copulation success in the baseline conditions.

The tournament aviary and females were unfamiliar to the males. Criteria for a successful exit from the tournament were based on copulation and singing measures used in past experiments (West et al. 1996; White et al. 2002b, c) that predict male reproductive success: (1) copulation success, measured by copulating on 3 consecutive days, or copulating more than three times on 1 day, or (2) establishing a consortship with a female, as measured by singing persistently (more than 15 songs per day) to a single female on 3 consecutive days. Consortships reliably predict that the pair will copulate (West et al. 1996). We considered males unsuccessful if they did not meet the criteria for success in 7 days. As males exited the tournament by meeting criteria either for success or failure, we added new males to the tournament from the same home flock as the exiting males so that the basic configuration of four males and 11 females was retained throughout. We collected 384 censuses (12 per day) in the tournament.

Song quality

We assessed the 'potency' of the males' songs by playing recordings of their courtship songs to a group of females in sound-attenuation chambers and measuring each song's effectiveness at eliciting the females' copulation solicitation displays (King & West 1977; King et al. 2003a; White et al. 2006). We made recordings of

songs from each of the males in the experiment during the first week of the breeding season using Sennheiser RF condenser microphones and a Marantz PMD-670 solid-state recorder. We recorded approximately 30–90 songs from each male and selected from this set one song from each male based on recording quality. We obtained recordings from 22 of the males (11 from each condition) for the playback test. The other males did not vocalize enough to get a recording of comparable quality. On 5 May 2007 we placed eight pairs of females into 1 m³ sound-attenuation chambers. These females were not familiar with the males in the experiment. We housed females in pairs because social housing drastically reduces stress associated with being confined in the small chambers. Past analyses have shown that social housing has no effect on copulatory responding in playback tests (West et al. 1996; V. A. Smith et al. 2000). We played songs beginning at 0600 hours each morning. We broadcast songs from a Compaq Deskpro computer through an LG XDSS amplifier to Bose 161 speakers located in each chamber. Mean \pm SE sound pressure level of songs was 85 ± 2 dB (a weighted impulse reading at 0.8 m from the speaker). We played six songs per day to females with no less than 90 min elapsing between song presentations. We played each of the 22 songs six times across the entire playback session. Songs from males in the two social conditions were counterbalanced each day, and song order was counterbalanced across days such that each song was played equally often early in the day, in the middle of the day and late in the day. No song was played twice in one day or on successive days. Closed-circuit video cameras located in each chamber displayed females' responses on a monitor in another room of the laboratory. Three observers, blind to the condition in which the males were assigned, recorded whether or not each song elicited a female's copulatory solicitation display. To measure each song's potency, we measured for each song how often females responded with a posture during the six broadcasts of that song (averaged across females).

Data Analysis

We compared the patterns of singing of the males in the two conditions across the manipulations (Table 1). We focused only on the manipulations that involved switching males (manipulations beginning 4/25) because the female manipulations occurred at a time in the year when many males vocalized so infrequently that the data sets had many missing values. We also compared the structural properties of the groups for these manipulations using social network analyses. Using UCINET 6.207 (Borgatti et al. 2002), we compared measures of centrality of the two conditions during and after each manipulation. Centrality measures assess the relationships between individuals in a group and have been used effectively in studies of cowbird social behaviour (Miller 2008). We assessed degree centrality for the males, which measures how many directed singing interactions males had with other birds. We also assessed closeness centrality, which measures how interconnected each male was in terms of directed singing with the other birds in the group. High levels of closeness indicate that males spread out their singing interactions with many individuals, whereas low levels would indicate that they only interact with some individuals and thus the connections to other individuals are indirect. While these measures are typically used to assess routes of information flow, we used them to characterize the social structure of the groups and to assess whether males use their directed song in different ways in different groups.

The two mating competency tournaments each assessed the relative courtship abilities of males from one of the Dynamic flocks compared to males from one of the Stable flocks. Males in the competition were paired based on reproductive performance from

the first half of the breeding season. Thus we used matched-pairs *t* tests to compare each pair of males' performance in the tournament.

RESULTS

Manipulation Phase

There was only one measure that significantly differentiated the conditions across manipulations, which remained significant after correcting for multiple comparisons; Dynamic males had significantly higher levels of closeness ($t_{24.2} = 8.2$, $P < 0.0001$), indicating that within each manipulation, Dynamic males had a larger network of singing partners than did the Stable birds. There were also significant differences in the variability of the social network measures across manipulations, with higher variance for Dynamic males (degree: $t_{27} = 2.074$, $P < 0.05$; closeness: $t_{22} = 2.92$, $P < 0.01$), indicating that the social structure of the Dynamic groups changed more than that of the Stable groups across the manipulations. Other than this difference, the two groups were remarkably similar. Even without corrections for multiple comparisons, Dynamic and Stable group males did not differ significantly in their patterns of total song ($t_{22.1} = 1.1$, $P > 0.30$), female-directed song ($t_{27.7} = -0.50$, $P > 0.62$) or male-directed song ($t_{26.3} = -1.91$, $P = 0.07$) produced.

Breeding Season Baseline Conditions

During the first half of the breeding season, when the birds were held in their baseline aviaries, we saw few distinct differences between conditions, even after collapsing across groups to maximize power (though increasing the risk of false positive errors). There was no significant difference in mean copulation success between conditions (mean \pm SE: Dynamic birds: 1.94 ± 0.57 copulations; Stable birds: 1.5 ± 0.63 copulations; $t_{28} = 0.52$, $P > 0.61$; Fig. 1). Also, there were very few differences in measures of song use between conditions. No differences existed in production of total song, male-directed song or female-directed song (all $t_{28} \leq 1.8$, all $P > 0.10$). One significant difference between conditions was that the proportion of male-directed

songs to female-directed songs was higher for Stable males (0.61 ± 0.03) than it was for Dynamic males (0.47 ± 0.03 ; $t_{28} = 3.53$, $P < 0.001$). Thus, when examining the birds in their baseline conditions, the manipulation phase produced no noticeable effects on the males' courtship or singing abilities.

Mating Tournament Phase

Whereas breeding behaviour appeared comparable when males were in their home aviaries, the mating competency tournament revealed dramatic differences between the two conditions. We tested 15 Dynamic birds and 10 Stable birds before the end of the breeding season. This provided us with 10 matched pairs for direct comparison. The males from the Dynamic flocks outcompeted males from the Stable flocks, both in number of copulations (mean observed copulations per day: Dynamic males: 0.96 ± 0.13 , Stable birds: 0.46 ± 0.13 ; paired *t* test: $t_9 = 2.34$, $P < 0.05$; Fig. 2) and in the speed with which they reached success criteria and exited the tournament. Dynamic birds spent a mean \pm SE of 3.30 ± 0.23 days in the tournament, with all birds exiting after reaching criteria for success. In contrast, Stable birds remained in the tournament for a mean \pm SE of 5.30 ± 0.54 days ($t_9 = 4.98$, $P < 0.001$), with significantly fewer males (64%) reaching criteria for success by the seventh day (Fisher's exact test: $P = 0.022$).

We examined singing patterns and social interactions during the tournament to see whether there were behavioural differences among males in the two conditions that might explain this difference in performance. There were no differences in the total amount of song produced by males in the two conditions ($t_9 = 0.12$, $P > 0.91$), but there were differences in how males directed their song. Dynamic males directed a higher proportion of song to females than to males (Dynamic males: 0.68 ± 0.04 ; Stable males: 0.46 ± 0.04 ; $t_9 = 3.71$, $P < 0.005$). In addition, Dynamic males were better able to focus on singing to individual females as opposed to singing infrequently to a variety of females (proportion of female-directed song sung to consort females: Dynamic males: 0.86 ± 0.02 ; Stable males: 0.68 ± 0.08 ; $t_9 = 2.22$, $P < 0.05$). Males also differed in male-directed singing. Stable males sang substantially more songs to males from their home condition than did the

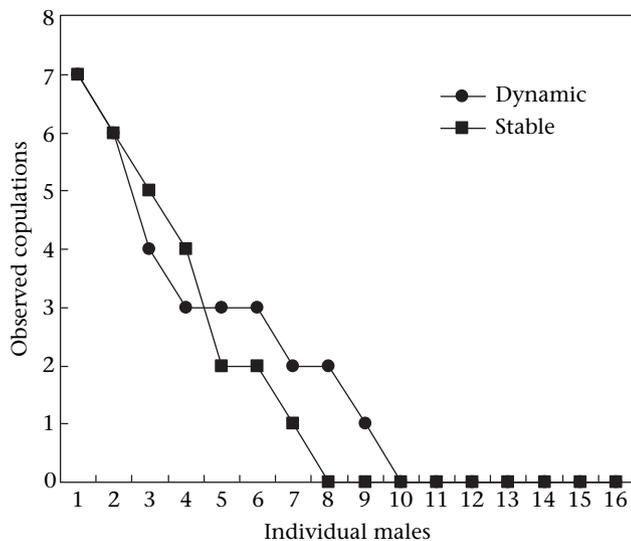


Figure 1. Total number of observed copulations for all male cowbirds in the Stable and Dynamic conditions (collapsed across flocks and organized from highest to lowest) in their home conditions during the first half of the breeding season.

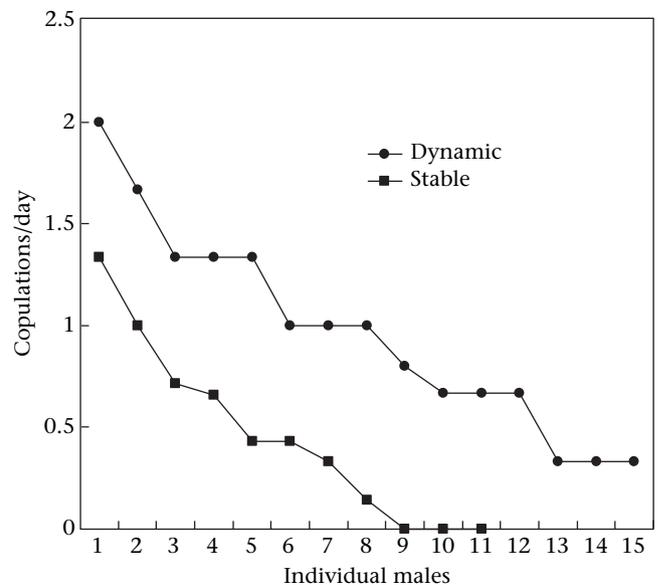


Figure 2. Number of observed copulations per day in the mating competency tournament for male cowbirds that were initially in Stable and Dynamic conditions.

Dynamic males. Stable males sang a mean \pm SE of $59 \pm 3\%$ of their male-directed song to males from their home condition, whereas Dynamic males sang $42 \pm 6\%$ of male-directed song to males from their home condition ($t_9 = 2.66$, $P < 0.03$).

Song Potency

We found no differences between the two conditions in any measures of song, including note and whistle structure, repertoire size, song sharing, or, importantly, song potency as measured by the playback tests (all $t_{20} \leq 1.7$, all $P_s > 0.10$). The lack of difference between conditions rules out the possibility that the social manipulation modified males' song structure or potency.

DISCUSSION

Dynamic males outcompeted Stable males in the tournament. The males from the two conditions did not differ in what would commonly be considered characteristics important for mating success: song quality, size, age, or any other trait that becomes fixed in adulthood. The only explanation for the difference found between conditions therefore is that the courtship and competitive competence of the Dynamic males was enhanced as a result of the social manipulations that occurred earlier in the year.

The critical finding, that birds from the Dynamic flocks outperformed birds from the Stable flocks in the tournament, cannot be explained by Stable males' inability to adjust to tournament conditions: Stable males engaged in as much courtship and competition in the tournament as did the Dynamic birds, they were just less effective in reaching criteria for success. Also, past work has shown that when Stable males compete against less competitive males (juveniles), they have the ability to achieve high levels of reproductive success in these tournaments (White et al. 2002c). Thus the tournaments provide a means to compare relative courtship and competitive abilities of the males within the tournament.

The goal of this experiment, to increase the social complexity to which some individuals were exposed, provides challenges for analysis and interpretation. The mechanism underlying the effect found here is unknown at this point. While we modified reproductive success of the Dynamic-condition males, we cannot be sure what part of the manipulation phase was critical. Nor can we be sure at this point how the manipulations changed the males' skills. Possibly, the behaviours of the males can be thought of as representing alternative mating strategies. Males may have developed strategies appropriate to their home conditions, and the Stable birds were outcompeted because the tournament created social circumstances that were more comparable to dynamic environments, thus giving Dynamic birds the advantage. The problem with this interpretation is that the Stable birds showed no advantage in overall mating success in the first half of the breeding season, when all birds were held in stable conditions, a context that should have favoured the stable strategy, if such a strategy existed. If the Stable males were doing something that provided them a benefit in stable groups, we did not find it.

Alternatively it is possible that the suite of skills involved in achieving reproductive success is organized by social experience. The more effective social experiences an individual attains, the more skilled he becomes in courting and competing with others. While males in both conditions received social experience, the Dynamic condition represented a high 'social nutrition' condition, where males experienced more individuals and were continually challenged by novel social configurations. The Stable birds in contrast received only a limited number of social experiences; only one exposure to a novel social configuration, and once the

relationships had formed within that configuration, the patterns of the males' interactions did not vary.

We believe the combination of experiencing both a larger number of individuals and a greater degree of social novelty drove the variability in the Dynamic males' behaviour. In addition to this greater variability in singing, the higher closeness scores earned by Dynamic males prior to the breeding season derived from their tendencies to sing more frequently to a larger number of other males. In other words, Dynamic males distributed more singing to more of their competitors. Research across a wide range of species has shown that male competitive displays increase both in frequency and intensity when males are faced with rank uncertainty or closely ranked competitors (Enquist & Leimar 1983; Haley 1994; Kitchen et al. 2003). Whatever the mechanism may be, the manipulation did affect reproductive success. It thus provides the impetus to conduct more refined and controlled future examinations of the relationship between social experiences and mating competency.

In the wild, there most likely exists a continuum of social experiences cowbirds gain across their range. Cowbirds can be found in diverse social conditions where the demographic structure and stability of groups varies greatly (Friedmann 1929; Ortega 1998; J. N. M. Smith et al. 2000). Flock density, sex ratios, age-class composition and migration patterns all vary considerably across populations. Thus, depending on the structure of the flocks they join when they fledge, wild cowbirds can experience widely varying social conditions. The type and amount of social experience an individual gains may be primarily determined by the ecology and density of local cowbird populations. For example, migratory populations are exposed to many thousands of individuals, whereas birds in nonmigratory populations may remain in stable conditions and be exposed to far fewer individuals. It is also possible, however, that the social experiences males gain could be influenced by the traits of individuals that lead them to seek out effective social environments.

Prior work has focused on the expectation that natural selection would produce adaptations that help individuals successfully navigate social challenges. Our findings provide support for the contention that the challenges associated with complex social environments can affect individuals' reproductive fitness. Furthermore, our results add a new dimension: living in a complex social world provides opportunities within the life span of an individual to hone social skills and increase reproductive success. The traits that permit individuals to take advantage of these experiences therefore become sites for natural selection to act. If individuals have the capacity to improve social skills through experience, natural selection will favour those individuals that maximize their learning opportunities.

Acknowledgments

Dorothy Cheney and Robert Seyfarth provided thoughtful comments during the development of this work. Dave Stephens and two anonymous referees provided valuable feedback on the manuscript. All experiments were conducted under the approval of the University of Pennsylvania's animal use and care committee (no. 800439).

References

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.
- Bergman, T. J., Beehner, J. C., Cheney, D. L. & Seyfarth, R. M. 2003. Hierarchical classification by rank and kinship in baboons. *Science*, **302**, 1234–1236.
- Borgatti, S. P., Everett, M. G. & Freeman, L. C. 2002. *Ucinet for Windows: Software for Social Network Analysis*. Lexington, Kentucky: Analytic Technologies.

- Bugnyar, T. & Heinrich, B.** 2006. Pilfering ravens, *Corvus corax*, adjust their behaviour to social context and identity of competitors. *Animal Cognition*, **9**, 369–376.
- Byrne, R. & Whiten, A.** 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. New York: Oxford University Press.
- Byrne, R. & Whiten, A.** 1997. *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge: Cambridge University Press.
- Catchpole, C. K. & Slater, P. J. B.** 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Duffy, A. M. Jr.** 1986. Singing and the establishment and maintenance of dominance hierarchies in captive brown-headed cowbirds. *Behavioral Ecology and Sociobiology*, **19**, 49–55.
- Enquist, M. & Leimar, O.** 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Friedmann, H.** 1929. *The Cowbirds: a Study in the Biology of Social Parasitism*. Springfield, Illinois: C.C. Thomas.
- Gros-Louis, J.** 2004. The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour*, **67**, 431–440.
- Gyger, M. & Marler, P.** 1988. Food calling in the domestic fowl, *Gallus gallus*: the role of external referents and deception. *Animal Behaviour*, **36**, 358–365.
- Haley, M. P.** 1994. Resource-holding power asymmetries, the prior residence effect, and reproductive payoffs in male northern elephant seal fights. *Behavioral Ecology and Sociobiology*, **53**, 374–384.
- King, A. P. & West, M. J.** 1977. Species identification in the North American cowbird: appropriate responses to abnormal song. *Science*, **195**, 1002–1004.
- King, A. P., West, M. J. & White, D. J.** 2003a. Female cowbird song perception: evidence for plasticity of preference. *Ethology*, **109**, 1–13.
- King, A. P., White, D. J. & West, M. J.** 2003b. Female proximity stimulates development of male competition in juvenile brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour*, **66**, 817–828.
- Kitchen, D. M., Seyfarth, R. M., Fischer, J. & Cheney, D. L.** 2003. Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology*, **53**, 374–384.
- Kudo, H. & Dunbar, R. I. M.** 2001. Neocortex size and social network size in primates. *Animal Behaviour*, **62**, 711–722.
- Miller, J. L.** 2008. Female social networks influence male vocal development in brown-headed cowbirds (*Molothrus ater*). *Animal Behaviour*, **76**, 931–941.
- Ortega, C. P.** 1998. *Cowbirds and Their Hosts*. Tucson: University of Arizona Press.
- Rothstein, S. I. & Fleischer, R. C.** 1987. Brown-headed cowbirds learn flight whistles after the juvenile period. *Auk*, **140**, 513–516.
- Rothstein, S. I., Yokel, D. A. & Fleischer, R. C.** 1986. Social dominance, mating, and spacing systems, female fecundity and vocal dialects in captive and free-ranging brown-headed cowbirds. *Current Ornithology*, **3**, 127–185.
- 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.
- Smith, J. N. M., Cook, T. L., Rothstein, S. I., Robinson, S. F. & Sealy, S. G.** 2000. *Ecology and Management of Cowbirds and Their Hosts*. Austin: University of Texas Press.
- Smith, V. A., King, A. P. & West, M. J.** 2000. A role of her own: female cowbird influences on vocal development. *Animal Behaviour*, **60**, 599–609.
- 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. & Freeberg, T. M.** 1996. Social malleability in cowbirds: new measures reveal new evidence of plasticity in the eastern subspecies (*Molothrus ater*). *Journal of Comparative Psychology*, **110**, 15–26.
- West, M. J., White, D. J. & King, A. P.** 2002. Female brown-headed cowbirds' (*Molothrus ater*) organization and behaviour reflects male social dynamics. *Animal Behaviour*, **64**, 377–385.
- West, M. J., King, A. P. & White, D. J.** 2003. The case for developmental ecology. *Animal Behaviour*, **66**, 617–622.
- White, D. J., King, A. P. & Duncan, S. D.** 2002a. Voice recognition technology as a tool for behaviour research. *Behavior Research Methods, Instruments and Computers*, **34**, 1–5.
- White, D. J., King, A. P. & West, M. J.** 2002b. Facultative development of courtship and communication in juvenile male cowbirds (*Molothrus ater*). *Behavioral Ecology*, **13**, 487–496.
- White, D. J., King, A. P. & West, M. J.** 2002c. Plasticity in adult development: experience with young males enhances mating competence in adult male cowbirds, *Molothrus ater*. *Behaviour*, **139**, 713–728.
- 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, *Molothrus ater*. *Animal Behaviour*, **72**, 181–188.
- White, D. J., King, A. P., Gros-Louis, J. & West, M. J.** 2007. Constructing culture in cowbirds (*Molothrus ater*). *Journal of Comparative Psychology*, **121**, 113–122.