



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

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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.

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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

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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.

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