Ontogeny of social skills: social complexity improves mating and competitive strategies in male brown-headed cowbirds

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Social individuals require a suite of skills to outcompete groupmates and gain reproductive advantage. Recently we showed that adult male cowbirds (*Molothrus ater*) exposed to enhanced social-learning opportunities (living in ‘dynamic’ social conditions) became more reproductively successful than males living in ‘stable’ conditions (White et al. 2010a, Animal Behaviour, 79, 385–390). The experiment left open important questions about how subjects turned the experiences they gained in the dynamic condition into a reproductive advantage. Here, 1 year later, we examined the within-individual plasticity of the effect by exposing some of the same subjects to opposite social conditions, followed by another opportunity to measure their relative reproductive success. Again, dynamic-condition birds outcompeted stable-condition birds, reversing individuals’ performances from the year before. We investigated the constituents of the dynamic-condition birds’ advantage, and found that they succeeded by using aggression to increase dominance rank, and by focusing courtship singing on forming consortships with particular females. Stable-condition birds adhered to no discernible strategy. This work affirms that adult experience can modify reproductive success, and suggests a mechanism for that modification: individuals that experience a wider array of social environments may improve their ‘behavioural control’, the ability to modulate behaviour to suit the competitive context. Natural selection may act on groups of traits that facilitate the development of behavioural control, including faculties for expressing or inhibiting behaviours and traits that regulate individuals’ exposure and attention to social experience.

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both elements, but in this investigation we attempted to distinguish between these two broad areas of possible effect: spending time in the dynamic condition could have elevated discrete traits of the DC males, or enhanced their behavioural control over those traits. We considered the concept of ‘behavioural control’ cautiously, to include the capacity to modulate trait expression without necessarily extending into the conscious orchestration of trait expression over time.

Within a Machiavellian intelligence framework, it makes sense for selection to favour such behavioural control as a means for navigating social environments. Animals that live in social groups face an unstable environment whose key features, other members of the group, can recombine (in mating partnerships or competitive alliances), shift their intentions (from neutrality to aggression, cooperation to competition), or simply alter their relevance (through emigration or immigration, movement within the dominance hierarchy, or a change in breeding condition). Succeeding in such a fluid social environment requires not only discrete cognitive skills (e.g. the ability to learn one’s place in a hierarchy), but also the ability to adapt one’s behaviour in response to changes in the social context: to turn some behaviours on (or up) and others off (or down) to suit the demands of a given social configuration. The ‘trigonal’ dilemma, which, by definition, involves three interacting males (Machamer & Mendl 1955; male A needs to court female B in the presence of rival C, is a classic example. Solving the dilemma requires not only mastery of courtship and competition-related behaviours, but the ability to modulate the expression of those behaviours in response to competing pressures from other social actors. A wide range of species have been observed to show flexibility in their behaviour or the amount of time spent on it (e.g. fiddler crabs, Uca mjoebergi; Reading & Backwell 2007; desert gobies, Chlamydogobius eremius; Wong & Svensson 2009: capuchin monkeys, Cebus spp.; Fragszy et al. 1990; chimpanzees, Pan troglodytes; and bonobos, Pan paniscus: Boesch et al. 2002). However, the difficulties associated with manipulating an entire social network make it challenging to build experiments that test whether social animals lose or gain reproductive fitness based on the degree to which they are able to control their behaviour to suit changes in the social environment.

The social behaviour of songbirds provides a powerful context in which to study behavioural control. Although the quality of a male’s courtship song may crystallize for adult birds, individuals can use their songs in a variety of distinct ways to regulate male—male competitive interactions and court females. By singing selectively to the most receptive females, choosing different songs from his repertoire in different contexts, or adjusting the rate or amplitude of singing in the presence or absence of dominant rivals, a male can tailor his use of courtship and competitive behaviours to succeed in different social situations. Byers et al. (2010) recently argued convincingly that females of many species rely on male display performance (as opposed to, or along with, ornamentation) to choose mates. Their argument focuses on physical performances (e.g. vocalizations, courtship displays and male—male combat) as indicators of physical quality. But their reasoning can easily apply to an environment wherein females make mate choice decisions based on displays of behaviour that evidence quality in terms of social skills. By the same token, males with greater social skills may get more opportunities to court females by doing a better job of navigating male—male competition.

It makes sense to look for the role of behavioural control within mating systems where the relationships between traits and reproductive success are varied. Work on captive flocks of brown-headed cowbirds, which are obligate brood parasites that live in a wide variety of social structures across their range, has revealed many different relationships between song and reproductive success across social conditions. Under some conditions, song quality as measured by female’s preferences is related to mating success, but in other conditions, it is negatively related to mating success (White et al. 2002a). Male aggression has shown similarly variable patterns. The two most persistent correlates of reproductive success involve patterns of song use: female-directed singing and engaging in male—male singing bouts, but even these do not correlate with reproductive success in all groups (White et al. 2010b).

Furthermore, a long history of field research on brown-headed cowbirds details the extremely dynamic nature of the courtship process, which may demand both flexibility and behavioural control from individuals. The nature and sequence of cowbird migration and breeding patterns place a high value on a male’s ability to identify a primary target for his courtship efforts quickly, and to shuttle rapidly between behaviours designed to maintain a primary consortship, dominate potential rivals and pursue secondary mating opportunities. During the breeding season, while arriving females establish large breeding territories based on access to host species nest sites (Rothstein et al. 1984), males engage in a competitive scramble to establish consort relationships. A male will identify a receptive female and sing intensely to her (West et al. 1981) while guarding his consorts from interlopers (Friedmann 1929; Rothstein et al. 1986). The establishment of a consort relationship reliably predicts copulation and paternity (West et al. 1996; White et al. 2001). Although a male must quickly identify a receptive female, court and guard her, they may attempt to court and guard additional females if territories overlap (Davies 2010). These males must also deal with the continual introduction of new competitors (Darley 1982). Laskey (1950) observed that wild male gauders consorts by aggressively displacing interlopers. Furthermore, Darley (1982) proposed that apparent male ‘territoriality’ reported by some observers (Friedmann 1929; Rothstein 1972) might be an artefact of intrasexual competition incidentally observed at the boundaries of males’ breeding ranges. He proposed that males establish but do not defend breeding ranges that overlap with both the territories of female mates and male competitors. Instead, in areas of overlap the males aggress against one another to suppress rivals’ courtship efforts. Darley’s (1982) notion, that the crux of intrasexual aggression related not to territorial defence but to males’ efforts to reproducitively suppress other males, was supported by a small group of experiments with captive cowbirds which showed that dominant male birds aggressively suppressed the courting behaviours of others. Dufty (1986) experimentally established that captive male cowbirds form dominance hierarchies based on physical aggression (displacements) and song displays. In parallel experiments with captive birds, Darley (1978) and Rothstein et al. (1986) both reported that dominant members of captive dyads formed consortships while subordinates did not, and Rothstein et al. found that dominants suppressed the subordinates’ ability to sing (and consequently to court females) by persistently displacing them. He also showed that removing dominants from group cages caused an immediate increase in subordinates’ singing rates to particular (consort) females; subordinate males had already identified their target females (as indicated by low but directed levels of song) but did not court them actively until freed from suppression by the dominants. West et al. (1981) similarly found that dominance is linked to the ability to form the consortships that lead to mating. In summary, cowbird males routinely face the sorts of multidimensional social challenges posited by Chance & Mead (1953).
Behavioural control could be favoured by natural selection in a social context with as much inherent variability as the cowbird breeding system. Males that are able to respond to the social context and modulate their singing and fighting behaviour in a way that would lead to mating success would be at an advantage across different social contexts, whereas a male with one particularly effective trait, such as a high-quality song, or physical strength for fighting, might be successful in only a select set of contexts. The experimental design we used in White et al. (2010a), and again in the current experiment, is uniquely suited to assessing the strategies males use to reach reproductive success because the mating competency tournaments effectively provide numerous different social contexts in which males must compete with rivals and court females.

In the current experiment we recreated the conditions and manipulations from White et al. (2010a), using the same birds; some were exposed to the same conditions (dynamic condition, DC, or stable condition, SC) they experienced 1 year prior in the White et al. experiment, and some were switched. In this iteration of the experiment we searched for the behavioural mechanisms that created the main effect in the mating competency tournament. We ran subjects through the same manipulations and mating competency tournament, adding new measures of male–male aggression and dominance. By using the same birds in reversed conditions, we examined whether the resultant effects were plastic enough to change across years and breeding seasons. We searched for sources of males’ success in our mating competency tournament by testing the roles of both discrete traits (song potency and aggression) and strategic behaviour (rate of singing to a consort female and dominance rank) in predicting males’ abilities to court females in the tournament environment. If DC males learned or adopted a more strategic approach to courtship and competition in the tournament, we would expect to see the application of behaviours, their degree of focus on singing to receptive females or their use of aggression to acquire dominance, playing an enhanced role in their success as compared to that of the SC birds.

METHODS

Except for the addition of data collection focused on male–male dominance interactions, our experimental methods replicated those of White et al. (2010a). Adult male cowbirds were assigned to two different social conditions designed to give one group greater access to social challenges. Past work has revealed that increased subgroup size relates to social complexity (Kudo & Dunbar 2001). We created conditions that allowed some birds to interact with many different males and females and other conditions where birds remained in static groups. Birds in two ‘stable-condition’ (SC) flocks remained together throughout the winter, spring and breeding season. Birds in two ‘dynamic-condition’ (DC) flocks were swapped in small subgroups at regular intervals during the spring prior to the breeding season. With each manipulation, males in the DC flocks had to reevaluate dominance relationships with new males. They also gained and lost opportunities to court females. At the start of the breeding season we stopped manipulations in the dynamic-condition flocks and returned birds to their home aviaries. We then began entering matched pairs of males (two from the SC condition, two from the DC condition) into a round-robin mating competency tournament designed to test individuals’ abilities to court females quickly and effectively in conditions that mimicked the competitive demands of wild breeding flocks (Friedmann 1929; Ortega 1998; Smith et al. 2002). Males from the two conditions were placed together into an unfamiliar avairy with unfamiliar females, and competed for opportunities to court those females.

Subjects and Housing: Winter and Summer

Twenty-two of the original males from White et al. (2010a) survived to enter the mating competency tournament and serve as subjects in the current experiment. All were wild-caught adult male cowbirds, ranging in age from 901 to 1757 days at the start of this experiment. During the winter and spring, male birds were evenly divided among four mixed-age, mixed-sex flocks of 17–21 birds each in four 18.3 × 6.1 × 4 m outdoor aviaries in Montgomery County, PA, U.S.A. Aviaries had trees, grass, shrubs, a feeding station, indoor shelters. Birds had ad libitum access to vitamin-treated water and a mixture of seed and a modified Bronx Zoo diet for omnivorous birds. All birds were coloured leg bands to permit individual identification. Experiments were conducted under the approval of the University of Pennsylvania’s Institutional Animal Care and Use Committee (IACUC Number 800439).

Data Collection

Data were collected in 15 min blocks by four observers. Behaviours were noted by subject’s colour band sequence, object’s colour band sequence (for directional behaviours), behavioural code and comments, all recorded using voice recognition technology (White et al. 2002c).

We collected data in three broad categories consistent with prior research: vocal, reproductive and aggressive behaviours (see e.g. Duffy 1986; King et al. 1986; Rothstein et al. 1986; White et al. 2002a, b, c). The first two categories were collected in all phases of the experiment. Data on direct aggression, which was our measure of interest for male–male competitive behaviour, was collected primarily during the tournament, when we added two new codes related to male–male aggression: ‘displacements’, defined as one male approaching another by air or on foot and usurping that male’s perch, with the displaced male ceding his position, and ‘beakups’, defined as one male approaching within 15 cm of another with beak pointed at a 90° angle to the ground. Data on fights, the final measure of aggression, was collected all year.

Observers occasion-sampled groups for vocal behaviours, noting each male that vocalized along with data on the social context surrounding every vocalization. Song could be scored as ‘undirected’ (if the singing male was not oriented towards a male or female receiver), ‘female-directed’ or ‘male-directed’ (if the singer was oriented at a 0–45° angle to a female or male, respectively, no farther than 61 cm away). Finally, we recorded all observed copulations and any fights that occurred.

Conditions and Manipulations

Conditions and manipulations replicated our experimental design from White et al. (2010a), with the addition of measures taken to change the home social condition for half of the subject birds. In spring (start date: 23 March 2008), flocks were divided into four subgroups within two social conditions: a stable condition (SC, N = 10) and a dynamic condition (DC, N = 11). The four subgroups were defined by whether member males remained in the social condition they had occupied in the first iteration of the experiment (White et al. 2010a) or were switched. Thus, the SC flock contained two subgroups, males that were SC birds both years (SC–SC, N = 4) and those that were DC birds during White et al. (DC–SC, N = 6); the DC flock was similarly composed of SC–DC (N = 5) and DC–DC (N = 6) males. Males were randomly chosen to retain or switch their social condition; females were assigned to flocks to ensure all males were housed with females with whom they had no prior reproductive history. All participants in the experiment were adult birds that had reached sexual maturity and...
all males had developed mature song at least one breeding season prior to the beginning of the experiment.

The two SC flocks, containing 19 and 21 individuals, respectively, retained the same membership throughout the winter, spring, and the first half of the breeding season. The two DC flocks, containing 17 and 19 individuals, were subject to frequent changes in membership during this same period. Specifically, we removed and reintroduced females from both DC flocks, and swapped small subgroups of male and female birds between the two DC flocks every 3–8 days.

When the breeding season began we stopped all manipulations and returned all DC birds to their home aviaries. All birds remained in their home aviaries for 27 days (11 May 2008–6 June 2008, approximately half of the active breeding season), during which time we collected baseline data on reproductive behaviour. We used patterns of copulations and egg production to create matched pairs of males (two from each condition, matched by comparable levels of reproductive activity in their home aviaries) for the tournament. At the end of this period we began our tournament.

**Mating Competency Tournament**

The mating competency tournament took place in two aviaries unfamiliar to the subjects. Males were held in single-sex holding cages before entry to the tournament and returned to those cages after competition.

Tourism groupings consisted of four males (two from an SC flock, two from a DC flock) and 11 unfamiliar females. The sex composition of these groups followed established protocol from prior research (Freeberg et al. 1995; White et al. 2002a, b); the female-biased sex ratio provided all competitors the opportunity to court multiple females and ensured that there would be reproductively active females in the pool of potential consorts that we presented to males.

As in White et al. (2010a), males exited the tournament based on copulation and singing measures that reliably predict reproductive success (Freeberg et al. 1995; White et al. 2002c, 2010a): either (1) copulation success, measured by copulating on 3 consecutive days or copulating more than three times on 1 day, or (2) singing persistently to females, measured as singing at least 15 songs to a particular female on 3 consecutive days (a singing rate that corresponds to consort formation in nontournament conditions (see, e.g. White et al. 2002b)). Males could exit the tournament successfully in as little as 1 day (by copulating three times). We considered a male unsuccessful and removed him from competition if he did not reach criterion for success in 7 days. Whenever a male exited the tournament, we replaced him with a new male from the same home condition. Thus, the basic configuration of two SC males, two DC males, and 11 females was constant in all tournament groupings.

**Methods for determining and validating dominance rankings by competitive group**

Dominance was measured by three directional aggressive behaviours: displacements, breakups and fights. Displacements accounted for the vast majority (84%) of behaviours recorded (501 of 597 total interactions), breakups were significantly less frequent (10%; 61 interactions), and fights were the least commonly observed behaviour (6%; 35 interactions). Dyadic dominance, as determined by displacements alone, reliably predicted the directionality of breakups (85% agreement) and fights (79% agreement), so we had the option of basing ranks and hierarchies on patterns of displacement alone. However, removing fights and breakups from the data set resulted in apparent ‘ties’ for a number of dyads where we observed only a few interactions. As such, we collapsed all interactions into a single pool of data on directional aggression.

For each interaction, we scored a dominance point to the male that initiated the interaction (i.e. the male that displaced the other, approached the other in a ‘beakup’ position, or initiated a fight). For every male—male dyad, we considered the dominant male to be the one that initiated the majority of these interactions between the two (Hausfater et al. 1982; Dufty 1986; Martin & Bateson 1993).

We assigned dominance ranks to males based on the percentage of their dyadic relationships in which they dominated. In our sample, gross aggressive output (as measured by average number of aggressive acts per day) correlated strongly with the percentage of relationships that an individual dominated (Pearson correlation: \( r_{20} = 0.635, P < 0.001 \)) but the two did not perfectly overlap. Our rank score allowed for comparison across individual males’ competitive groups (the set of competitors a given male met in the tournament, which varied in sized depending on the number of days that male spent in competition) and allowed us to examine the relationship between males’ within-group dominance ranks and their ability to quickly court females and exit the tournament.

Once we had assigned hierarchical rankings to all members of each competitive group, we tested the validity and linearity of those rankings by calculating the percentage of the total dominance interactions in the group that were directionally consistent with individuals’ rank scores. That is, we asked what percentage of total directional aggression bore out the prediction implied by the rankings, that the top-ranked bird would dominate the second-ranked bird, the second-ranked bird would dominate the third-ranked bird, and so forth (see, e.g. Hausfater et al. 1982, for discussion of...
this method for validating rankings). Average by-group consistency of dominance interactions with rankings was greater than 90%.

RESULTS

Results from the First Half of the Breeding Season

As was the case in White et al. (2010a), social and reproductive activity across the two conditions was similar during the first half of the breeding season, when we stopped manipulations and housed DC and SC males in their home conditions. In terms of all major indicators of reproductive activity (number of consort pairs formed, rate of females’ egg production and mean copulation rate) as well as behavioural indicators of courtship and competitive activity (total song production, rates and proportions of undirected singing, male- and female directed singing and singing–male–male fights), the two flocks were the same (all $P > 0.1$). Most interestingly, in contrast with their singing behaviour during the tournament (discussed below), males in the two conditions were nearly identical in terms of the proportion of their female-directed song that they directed to a single consort female (mean $\pm$ SE proportion of female-directed songs to consorts: DC: $0.93 \pm 0.02$; SC: $0.93 \pm 0.02$; $P > 0.9$). When grouped with familiar males and females, in other words, males from both conditions focused their singing on establishing and maintaining a consort relationship; the two groups would diverge significantly in this respect once males from each condition were paired with one another and new females.

Tournament Results: Reversing, and Replicating, the Main Effect

Although breeding and competitive behaviours were comparable while males remained in their home conditions, results in the mating competency tournament replicated our results from the previous year, wherein condition had a profound effect on reproductive success (White et al. 2010a). DC birds successfully exited the mating competency tournament faster than SC birds (mean $\pm$ SE number of days in tournament: DC: $3.1 \pm 0.46$; SC: $6.1 \pm 0.43$; log-rank survival analysis: $\chi^2 = 14.2, P < 0.0005$; Fig. 1). Furthermore, the groups differed significantly in the overall success rates of participants: all but one DC bird exited the tournament by reaching criterion (92%), while only 50% of SC birds reached criterion by day 7 (Fisher’s exact test: $P = 0.005$). DC males also achieved significantly more copulations per day (mean $\pm$ SE: $0.91 \pm 0.26$) than SC males ($0.16 \pm 0.10$) (permutation test: $P < 0.02$).

When we examined the effect of change (or lack of change) in condition across the 2 years of manipulations, we found that this effect was plastic: birds that experienced the same condition both years (i.e. dynamic conditions in both year 1 and year 2, or stable conditions in both years) did not significantly change in their tournament success (Wilcoxon signed-ranks test: $T = 10, P = 0.499$; Fig. 2), while birds that did change conditions were significantly more successful in the competency tournament immediately following their dynamic-condition experience ($T = 0, P = 0.005$; Fig. 2).

Having replicated our prior results, we tried to understand the mechanism by which social experience had given DC males a reproductive edge in the tournament.

At the Level of Individual Traits, DC and SC Groups Are the same

We first investigated the possibility that the difference in the performances of the DC and SC groups could be explained by a group-level difference, expressed in the tournament, in traits critical to reproductive success, either song potency or rate of aggression.

We examined the results of the song potency tests we had conducted using courtship songs recorded from each male (see White et al. 2010a for a complete description of the potency test and scoring). Comparing the mean song potencies of DC and SC males, we found no significant difference between the groups DC mean song potency score (mean $\pm$ SE: DC: $0.44 \pm 0.07$; SC: $0.50 \pm 0.06$; permutation test: $P = 0.49$).

Similarly, we found no significant difference in the rate of aggression between the two groups (mean $\pm$ SE aggressive interactions that a male initiated per tournament day: DC males $4.95 \pm 2.18$; SC males: $4.45 \pm 1.9$; permutation test: $P = 0.89$).

Finally, we added an examination of males’ total output of directed song; again, we found no statistically significant difference between groups (mean $\pm$ SE number of directed songs: DC: $147 \pm 25$; SC: $116 \pm 22$; permutation test: $P = 0.35$).

Testing a Model for Mating Tournament Success

Having found that rates of courtship-related and competition-related behaviours did not differentiate DC and SC birds, we next turned to a multiple regression to explain reproductive success in the tournament, using key traits associated with reproductive

Figure 1. Survival analysis of male brown-headed cowbirds in the dynamic condition (DC) and the stable condition (SC) during their time in the tournament.

Figure 2. Effects of changes in experimental condition (dynamic condition (DC) versus stable condition (SC)) of male brown-headed cowbirds across 2 years of manipulations, showing the plasticity of males’ responses to the dynamic condition.
success, as well as behavioural measures that incorporate strategic application of multiple behavioural elements. The key traits we chose were, again, song potency and rate of aggression. The measures of controlled behaviour were (1) dominance rank and (2) proportion of female-directed song that was directed to a single consort female. When we queried our tournament data to see whether there was, in fact, a significant relationship between dominance and effective courtship, we found there was a significant correlation between dominance and days to criterion (Pearson correlation: $r_{122} = -0.55, P < 0.005$).

For static-condition birds, we found no significant link between reproductive success in the tournament and any of our measures ($r_{131} = 0.31, P > 0.2$). A male’s song potency and his overall aggressiveness did not predict his ability to form a consortship and exit the mating competency tournament; neither did the proportion of his directed song that he aimed at a consort female or the dominance rank he attained.

For the dynamic-condition birds, behavioural measures significantly predicted reproductive success ($r_{adj} = 0.62, P < 0.05$). Aggressive acts per day and potency failed to predict success for dynamic-condition birds; however, the model did show a significant relationship between days to criterion and our two measures of strategic, controlled behaviour: proportion of directed song directed to a consort female and dominance rank (Table 1).

**DISCUSSION**

Across 2 years of experiments, the results of our mating competency tournaments showed a categorical distinction between groups of dynamic-condition and static-condition birds; while these males behaved similarly in their home conditions, the DC birds consistently outcompeted SC birds in the tournaments by forming consortships and copulating with females. We had begun this analysis looking for the traits or strategies that would allow us to characterize the two groups and thus define the mechanism of this main effect of our manipulation. We found that only one of the groups used anything that could be described as a strategy. The majority of SC birds that did achieve success appeared to do so by idiosyncratic means; no trait or set of traits emerged that could describe how some of these birds managed to compete successfully. Perhaps one male had by far the best song in his tournament grouping, and another was by far the most aggressive, et cetera. DC birds, in contrast, succeeded in a patterned way: they applied their song and their aggression effectively, focusing their directed song on particular females and dominating other males.

We see an important distinction between two possible interpretations of this effect. In one reading, cowbirds may simply have a plastic ability to switch between two modes: (1) more efficiently aggressive and consort-focused 'DC-like' behaviour when it is called for; or (2) more 'SC-like' adherence to established hierarchies and less choosiness in courtship efforts, when that is called for. In this formulation, the DC birds would have done better because conditions in the tournament were closer to their home condition environment; having already flexed in the direction of the 'DC-like' mode, they would have been primed to outperform SC birds in the tournament. Alternatively, cowbirds may be plastic with an additional capacity to improve their behavioural control: broadly responsive to social conditions, but also better able to focus aggression and courtship the more they learn, from experience, to associate such behaviour with better outcomes. We favour a behavioural control interpretation because we think it appropriately describes the nature of the flexion we saw in DC subjects, which was a move towards, specifically, more targeted application of the same behavioural repertoire used by birds in both groups.

Although attaining a high dominance ranking involves behaving aggressively, simply raising one’s rate of aggression does not guarantee a corresponding increase in rank. Individuals may disproportionately aggress against particular rivals, especially rivals of close rank, without ascending a hierarchy through that aggression (Clutton-Brock et al. 1979; Kitchen et al. 2003). So, dominance actually reflects a controlled application of aggression by an individual that has distributed his aggression to dominate multiple rivals in a group. This, in turn, increases his ability to court females without interference from other males. A high rate of directed song allotted to a single consort female similarly involves a high rate of female-directed singing, but also reflects the extent to which a male has focused his female-directed singing on a single receptive target, which increases his chances of forming a consortship and gaining copulations. We do not think that DC males’ behaviour in the tournament required them to have engaged in strategic (in the sense of planful) cognition; however, the composite effect of their modulated responses to competitors and potential mates resembled a ‘strategy’ that was clearly superior to the various competitive approaches used by SC birds. Our ability to reverse and replicate our results shows that males’ facility with this ‘strategic’ approach to courtship is a dynamic product of social experiences.

Machiavellian intelligence theory proposes that individuals that can best take advantage of social situations will be most fit. By implication, social skills provide new ways to thread the needle of a complex social configuration: controlled applications of behaviours allow individuals to transcend the advantages conferred by particular traits like body size or song quality. The further implication is that social skills are subject to the same sort of evolutionary arms race that pushes the evolution of other sexually selected traits. In this light, we can view male—male competitive behaviour (dominance, suppression of rivals and mate guarding) as a set of adaptive social strategies that allow males with less potent songs to outcompete rivals for mates. Highly consort-directed singing may be a similarly adaptive alternative strategy, providing males without the size or aggressiveness to attain dominance with a pathway to mating. Being able to apply these strategies appropriately in a given social context is yet another layer of adaptive social skill, and DC birds appear to have attained greater mastery of this ability.

Our results across 2 years point to the plasticity with which adult birds can respond to social input. Males entered our dynamic condition without any group-level advantage, but exited as more socially competent competitors than stable-condition birds. This very plasticity raises questions about the nature of the behavioural changes we observed. Group sizes in the current experiment did not allow us to examine whether SC birds that had prior DC

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<thead>
<tr>
<th>Table 1</th>
<th>Multiple linear regression of the relationship between male brown-headed cowbirds that experienced the dynamic condition (DC) and their reproductive success in the tournament (as measured by days to criterion; see Methods)</th>
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<td>Intercept</td>
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<td>Aggressive acts per day</td>
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<td>Proportion of directed song that was directed to a consort female</td>
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<td>Song potency</td>
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<td>Dominance rank</td>
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The model significantly predicted reproductive success ($r_{adj} = 0.62, P = 0.038$), and the two measures of controlled behaviour (proportion of directed song directed to a consort female and dominance rank) were significantly related to days to criterion, as measured using a Markov chain Monte Carlo simulation (pMCMC). When we tested the overall model for males in the stable condition (SC), using the same parameters, it was not significant.
experience (in year 1) were able to outcompete birds housed in SC conditions during both years. Work that investigates the persistence of our effects is needed if we are to begin to understand the learning that supports the behaviour. The role of females in shaping reproductive outcomes like those seen in our mating tournaments is also an important topic for future investigation. Female procreative behaviour is critical to the development of male song (West & King 1988; Smith et al. 2000) and doubtless helps to direct the ongoing development of male social behaviour as well.

Finally, while much of the research on Machiavellian intelligence has focused on the cognitive traits that arise from social pressures, our results suggest that attention should be paid to traits that modulate individuals’ exposure to social interaction. If reproductive skills are reactive to social learning, that reactivity may influence where and when sexual selection may be acting on individuals (see White et al., in press).

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