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Social Traditions and the Maintenance and Loss of Geographic Variation in Mating Patterns of Brown-Headed Cowbirds

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Considerable geographic variation often exists in behaviors of different populations of a species. Of key interest are the mechanisms generating this variation, and the impact this variation may have on gene flow between two populations. Here, we review two sets of studies of brown-headed cowbirds, *Molothrus ater*, indicating that the social background of an individual can impact its ability to court, pair, and mate with individuals of one behavioral tradition/population relative to individuals of another behavioral tradition/population. The first studies involved two populations with extant differences in mating behaviors and found that young cowbirds of one population that interacted over ontogeny with members of a behaviorally-distinct population developed courtship behaviors and mating patterns similar to members of that 'foster' population. The second set of studies tested the possibility of generating distinct systems of mating behavior within one population and found that young cowbirds that interacted over ontogeny with different age-structured social groups developed effectively distinct mating patterns. Thus, social traditional processes in cowbirds can create, maintain, or dissolve population-level differences in courtship and communication. This work highlights the power of the social environment to act as a structuring ecology for behaviors fundamental to reproductive success.

There is often substantial behavioral variation among different populations across a species' range. Researchers in fields such as behavioral ecology, comparative psychology, evolutionary biology, and biological anthropology have been interested in intraspecific behavioral variation for many reasons. Behavioral variants are often hypothesized to be locally adaptive, may represent barriers to gene flow between different populations and, therefore, may facilitate increased divergence and possible speciation, and may be indicative of developmental plasticity specific to those populations (Dewsbury, 1990; Foster & Endler, 1999; Lott, 1991). Intraspecific variation has been particularly well studied in the case of vocal communication in the oscine songbirds (Kroodsma & Miller, 1996). Variation in vocal communication may be adaptive if it is associated with effective signal transmission in different habitats, if it serves a social function and ensures recognition and communication among members of distinct groups, or if it relates to strong preferences in mating partners for those particular vocal variants to facilitate mating between members of the same locally-adapted gene pool (Catchpole & Slater, 1995).

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In these species, social learning is often thought to play an important role in the development of these population-level differences in behavior (the vocal signals and, as is increasingly being discovered, the preferences for those signals). In this review, we point to a major implication of this social learning that has rarely been acknowledged. Namely, in some situations social transmission can facilitate the loss of population-level differences, and in other situations it can facilitate the generation of population-level differences—and furthermore, these changes in population-level variation in behavior can occur extremely rapidly, within a single generation. As the behaviors addressed in this review are related to courtship and reproduction, social transmission here can have a profound impact on the extent of gene flow between different groups.

Central to our argument in this review (and indeed the focus of this special issue) is that developmental processes at the level of the individual can potentially impact evolutionary processes at the level of the population. One way in which processes of phenotypic development in individuals may impact phenotypic evolution in populations is for there to exist a relationship between the developmental environments and selective environments of those individuals that persists across generations. This can occur if different developmental systems across individuals or populations result in differential survival and reproduction. Thus, research aimed towards understanding how processes of social transmission affect the development of behaviors related to courtship, mating preferences, and reproductive outcomes can potentially shed light on processes of evolutionary change at the population level.

Arguably the most important characteristic of a developmental system influenced by social learning is that the system is highly adaptable to changes in social environmental context (Avital & Jablonka, 2000; Bateson, 1988; Box & Gibson, 1999; Fragaszy & Perry, 2003; Gottlieb, 1992; Heyes & Galef, 1996; Johnston, 1982). When an individual learns behavioral traits characteristic of its species and/or population, this provides an effective mechanism to facilitate recognition of members of the same species and/or population. Work on song differences in various avian species has offered support for this notion that learning of these population-specific behavioral traits could play an important role in population divergence, both behaviorally and genetically (Baker & Mewaldt, 1978; Grant & Grant, 1996; Kroodsma, Baker, Baptista, & Petrinovich, 1985). Song in songbird species is tightly linked to reproduction. At the level of reproductive behavior, if the learning we describe in this review has fitness consequences (for example, in cases of sympatry between different populations), the social transmission of these characters will likely be adaptive. Alternatively, if there are few or no fitness costs to courting and mating with an individual of a behaviorally distinct population, the social learning of that population's courtship behaviors and preferences by individuals from a different population may lead to extensive gene flow between the two populations. Over time, social learning and increased gene flow in this case might be expected to result in behavioral convergence among formerly distinct groups. Thus, the individual adaptability brought about by this learning process could both limit and facilitate gene flow between behaviorally and perhaps genetically distinct populations, depending on the particular contexts of dispersal or mi-

gration of individuals and the fitness consequences of the learning. This point was raised by Wright over 70 years ago (Wright, 1931).

In the following review, we describe two series of studies that illustrate the possibility of extremely rapid loss or rapid generation of population-level differences in behaviors related to courtship and mating. These studies were conducted on brown-headed cowbirds, *Molothrus ater*, a common North American member of the family Embirizidae (subfamily Icterinae). Brown-headed cowbirds are obligate brood parasites – female cowbirds lay their eggs in the nests of other species, and the young cowbird therefore is always raised to independence by non-cowbird host parents (Friedmann, 1929; Ortega, 1998). This atypical (compared to other songbirds) natural history and early developmental environment of brown-headed cowbirds has led it to become an important test species for a number of core questions about developmental processes (e.g., Lehrman, 1970; Mayr, 1974; West, King, & Eastzer, 1981). In the next section, we describe studies of two behaviorally distinct populations of cowbirds that addressed whether young and naïve individuals of one population could develop courtship behaviors and mating preferences characteristic of adult members of the other population. These studies addressed a means by which social transmission can lead to the loss of population-level differences. In the third section of the paper, we describe studies focusing on one population of cowbirds that addressed whether young and naïve individuals could develop profoundly different patterns of courtship and mating if raised with different age classes of members of the same population. These studies addressed a means by which social transmission can lead to the generation of population-level differences in a single generation. In the concluding section of the paper, we point to some of the implications of this work and suggest some future directions we think might be fruitful for researchers interested in linking questions of individual development to questions of population evolution.

Losing Population-level Behavioral Differences in one Generation

The first set of studies we describe tested a fairly straightforward question: Can the courtship behaviors and mating patterns of young female and male cowbirds of one population be influenced by overwintering social experience with adult female and male cowbirds of a behaviorally distinct population to such an extent that the birds mate assortatively based on those behavioral differences? Stated differently, can birds of one population develop many of the fundamental features of the courtship behavioral system of a distinct population simply by interacting with members of that distinct population over the winter? The motivation for carrying out this work stemmed largely from a study by Eastzer, King, and West (1985) on two behaviorally distinct populations of cowbirds—one from the *M. a. ater* subspecies, and the other from the *M. a. obscurus* subspecies. Eastzer et al. (1985) found that the pairing and mating patterns of the birds in a common aviary exhibited positive assortment—female cowbirds paired and mated more frequently with males of their own population. Positive assortative mating is an important feature of reproductive behavior, because non-random mating is one of the forces that can drive evolutionary change in populations (Hartl & Clark, 1989). Based on the findings of Eastzer et al. (1985), Freeberg and colleagues conducted a

set of studies to test whether the behavioral differences that can result in positive assortative mating might be socially transmitted across generations of cowbirds.

The general methodology used for testing whether the social experiential background might influence courtship behaviors and mating preferences was based on a design for generating laboratory microcultures (Galef & Allen, 1995). A large set of juvenile female and male cowbirds from a Black Hills, South Dakota, population (*M. a. artemisiae*) was captured in late summer (they had already reached independence and were in large flocks of juvenile cowbirds) and was distributed roughly evenly across four large outdoor/indoor aviaries at the Laboratory of Avian Behavior in Bloomington, Indiana. In two of these aviaries, the young South Dakota birds were provided with adult female and male social models from the same South Dakota population (South Dakota culture). In the other two aviaries, the young South Dakota birds were provided with adult female and male social models from a behaviorally distinct Indiana population (*M. a. ater*, Indiana culture). The South Dakota and Indiana populations were known to be behaviorally distinct based upon findings from a pair of studies not described in detail here. In one study, Freeberg, King, and West (2001) found that the songs of Indiana males were quite different from those of South Dakota males in terms of their note cluster structure. In the other study, West, King, and Freeberg (1998) found that Indiana females and South Dakota females (captured in the wild as adults and brought into the lab) showed strong preferences for songs of males of their own population relative to songs of males of the other population, as assayed by the number of copulatory solicitation displays females produced to playbacks of the males' songs.

The young South Dakota birds and their adult social models were housed in these aviaries from late summer until early May of the following year, when the breeding season began. During the breeding season (May through early July), the courtship behaviors and pairing preferences of the young female cowbirds of the South Dakota culture and Indiana culture were tested in a fifth large outdoor/indoor aviary with young male cowbirds of the South Dakota culture and Indiana culture. At all times, females were tested with males with which they were unfamiliar – for example, South Dakota culture females and males from the same overwintering aviary were never tested together in the breeding season. Females and males were removed from the aviary once they had paired and were replaced with birds of the same sex and culture to try to maximize the number of unique female-male pairings over the course of the breeding season. After the first breeding season was complete for these young female and male birds of the South Dakota culture and the Indiana culture, they were returned to their original social housing aviaries, where they were kept with the same adult social models as they had experienced the previous overwintering period, until the following breeding season. During that second breeding season, the courtship behaviors and pairing patterns of the South Dakota culture and Indiana culture birds were again tested in a fifth aviary, using the same methodology as in the birds' first breeding season.

During their first two breeding seasons, females of the South Dakota culture and Indiana culture were found to pair more with males of their same culture than with males of the different culture (Freeberg, 1996). In the first breeding season, 21 unique pairings were documented, of which 15 (71%) were between females and males of the same culture. In the second breeding season, 32 unique

pairings were documented, of which 26 (81%) were between females and males of the same culture. The data on female pairings are presented in terms of females' overall preferences (some females paired more than once) in Table 1.

Table 1

Summary of Tests of the Social Transmission of Courtship and Mating Behavior in 'South Dakota Culture' (SDC) and 'Indiana Culture' (INC) Cowbirds.

Female	Female paired:		
	more with South Dakota culture male	more with Indiana culture male	with one male each of both cultures
<i>1st Set of South Dakota culture and Indiana culture birds – 1st breeding season^a</i>			
SDC	5	2	2
INC	1	6	1
<i>1st Set of South Dakota culture and Indiana culture birds – 2nd breeding season^b</i>			
SDC	9	1	1
INC	2	10	0
<i>1st Set of South Dakota culture and Indiana culture birds – female mate choice^c</i>			
SDC	4	0	5
INC	1	6	2
<i>2nd Set of South Dakota culture and Indiana culture birds – 1st breeding season^d</i>			
SDC	8	0	3
INC	3	5	3

Fisher Exact tests of whether SDC female pairing pattern is significantly different from that of INC female pairing pattern: ^a $p = 0.051$, ^b $p = 0.001$, ^c $p = 0.015$, ^d $p = 0.013$.

^{a, b} Freeberg, 1996; ^c Freeberg, Duncan, Kast, & Enstrom, 1999; ^d Freeberg, 1998.

A subsequent study with these same birds tested for the influence of social experiential background specifically on female mate choice, by controlling for any effect of male-male or female-female interactions in courtship and mating decisions. Nine females of the South Dakota culture and nine females of the Indiana culture were tested twice each in a sequential mate choice design with males of the two cultures, resulting in 36 tests of females with unique pairings of males. The sequential mate choice design involved testing each female individually first with a male of one culture and then with a male of the other culture, with presentation of Indiana culture and South Dakota males counterbalanced across females. Of those 36 tests, females showed mating preferences for males of their own culture 27 times (75%; Freeberg, Duncan, Kast, & Enstrom, 1999). The data on female preferences are presented in terms of females' overall preferences in Table 1 (each female chose twice – some chose a South Dakota culture male twice, some an Indiana culture male twice, and some chose a male of one culture in one test and a male of the other culture in the second test). Taken together, these findings indicate that social learning during the overwintering months can influence the courtship behaviors and pairing patterns that result in positive assortative mating.

Subsequent studies found that the courtship and mating preferences detected in this first set of young South Dakota subjects could be successfully trans-

mitted on to a second set of young South Dakota subjects, in the absence of the original adult South Dakota and adult Indiana social models. Here, the South Dakota culture and Indiana culture subjects of the first study (described above) served as the adult social models for the second set of young South Dakota birds. Thus, in this study, all of the birds were genetically South Dakota; the only differences in the four aviaries had to do with the social experiential backgrounds of the adult social models—whether the young birds’ adult social models were from the South Dakota culture or were from the Indiana culture. The young female and male birds of this second set were housed with their respective adult social models over the winter until the following breeding season, when their courtship behaviors and pairing preferences were assessed as described above. 31 unique pairings were documented for the birds of the second set, of which 22 (71%) were between females and males of the 2nd South Dakota culture or between females and males of the 2nd Indiana culture (Freeberg, 1998). The data on female pairings are presented in terms of females’ overall preferences (some females paired more than once) in Table 1. These findings indicate that the courtship behaviors and pairing patterns that result in positive assortative mating can be socially transmitted across generations in cowbirds, even in the absence of the original sources of the behavioral differences, the adult South Dakota and adult Indiana social models. Unfortunately, the study could not be continued to test for the courtship patterns of the same 2nd South Dakota culture and 2nd Indiana culture in their second breeding season, after an additional overwintering period of social interaction with their 1st South Dakota culture and 1st Indiana culture (respectively) adult social models. Thus, we cannot answer whether the seemingly more equivocal pairing preferences of the 2nd Indiana culture females (Table 1) were due to a loss of the ‘cultural effect’ in the absence of the original adult social models or were due to an apparently lower motivation to court and pair in their first breeding season for South Dakota cowbirds, relative to later breeding seasons (Freeberg, 1996, 1998).

Analyses of songs produced by the two sets of South Dakota culture males and the two sets of Indiana culture males found that the initial song differences detected between the original South Dakota and Indiana adult social models were transmitted with high fidelity across generations (Freeberg et al., 2001). Songs of male brown-headed cowbirds typically comprise two or three clusters of individual notes at relatively low frequency, followed by a concluding high frequency whistle that is often frequency modulated. Over 19,000 songs, from the nearly 100 males in the studies described above, were assessed for the number of individual notes composing the note clusters that make up the songs. South Dakota males had significantly fewer notes in their first note cluster, and significantly more notes in their third note cluster, than did Indiana males. These differences in the first and third note cluster were transmitted across both sets of South Dakota culture and Indiana culture males. Furthermore, the extent to which a male’s songs were more South Dakota-like or more Indiana-like in terms of the number of notes in his note clusters was highly predictive of the male’s courtship effectiveness with South Dakota culture females or Indiana culture females, respectively. These findings suggest a behavioral mechanism, at least from the standpoint of male cowbirds, for the patterns of assortative pairing seen in the studies reviewed above—females appear

to have based their socially-learned pairing preferences, at least in part, on socially-learned differences in male songs.

Putting these results together, we find that the courtship behaviors and pairing preferences that produce assortative mating by population can be socially transmitted across generations of cowbirds. Furthermore, in that the songs of the young South Dakota males housed with adult social models from Indiana appeared to be very similar to the songs of those Indiana adults, the findings suggest that the behavioral differences seen in South Dakota and Indiana birds can be substantially diminished (at least in the case of the South Dakota birds that were tested) in a single generation. In other words, individual adaptability appears strong enough and flexible enough in at least the cowbirds of the South Dakota population, that behaviorally they can become very similar to Indiana birds. In nature, this conceivably could occur if young South Dakota birds overwintered with Indiana birds and if, instead of migrating back to their natal grounds, those South Dakota birds remained with their 'foster' population into the breeding season. Provided there was no selection against hybrids of the two populations, this sort of developmental mechanism would likely result in increased gene flow between the two populations, perhaps ultimately resulting in ever-diminishing differences between the two. We return to this point in the concluding section of the review.

The studies reviewed above indicated that the social experiential background of young cowbirds could effectively diminish population-level differences in behaviors fundamental to reproductive success. The work was able to uncover little in the way of potential mechanisms driving the social learning, however. One study with the same birds in their overwintering aviaries indicated that young male cowbirds associated more with adult males than they did with females, and that young female cowbirds associated more with adult females than they did with males (Freeberg, 1999; see also Smith, King, & West, 2002). These patterns of spatial association suggested that young cowbirds learning fundamental aspects of their social behaviors might interact primarily with same-sex conspecifics. More recent work, described in the next section, has addressed this question in far greater detail, and has gotten much closer to the answer of social mechanisms of learning in this species. Furthermore, this more recent work has suggested that individual adaptability can lead to increased behavioral differences among groups within the same population—in some cases, differences of the same magnitude as seen across subspecies.

Generating Population-level-like Behavioral Differences in one Generation

The work to this point indicated that studying social effects in large, complex social environments revealed aspects of behavior that likely could not be seen in more confined conditions (King, West, & White, 2002). Freeberg had shown that the ontogeny of courtship behavior could be influenced by social factors. But how did these distinct population level differences come to exist? Could social experience like that studied by Freeberg and colleagues play a role in forming these extant differences seen across subspecies? The next series of experiments was designed to determine whether different social compositions of cowbirds within

flocks could drive distinct differences in groups to the level Freeberg had found across subspecies.

As Freeberg's work did, this work stemmed from reports of cowbird social behavior in the wild. Across their range, cowbirds experience a striking amount of variation in their social ecology. Variation has been reported in population density (Johnsgard, 1997), sex ratio (Rothstein, Yokel, & Fleischer, 1986; Woolfenden, Gibbs, & Sealy, 2001), and migration (Ortega, 1998). In some populations, throughout their first year juveniles may never interact with adults, while in other locations juveniles join flocks of other cowbirds while adults are still in the final days of breeding and remain with them for the entire year (Friedmann, 1929; O'Loughlen & Rothstein, 1993; Rothstein, Verner, & Stevens, 1980). Flocks composed of all females, all juveniles, and mixed sex and age classes have been reported in the field (Friedmann, 1929). If such variation in social demographics creates different developmental ecologies where different types of information may be present, then different opportunities for social learning might exist.

Within the aviaries, it became clear that not all social groups were the same. An earlier large aviary experiment revealed that members of a large flock of cowbirds did not interact randomly; they self-assorted into subgroups based on age and sex (Smith et al., 2002). Also, the number of near neighbor affiliations (defined as one individual perching within 0.3 m of another individual) that juvenile males had with adult males during the year correlated with the juveniles' mating competence in the breeding season. This suggested that juveniles might be learning from adults how to engage in effective courtship behavior. It also suggested that not all learning environments are equally effective at providing social information.

Although the patterns from the Smith et al. (2002) study indicated that the composition of the social groups was important for influencing information flow, learning, and development, the data were correlational; birds were able to self-select their subgroups as well as interact with non-subgroup members. The next step was to create subgroups experimentally. White, King, and West (2002b) created two distinct groups of juvenile males in separate aviaries. Both groups contained adult and juvenile females, but only one group contained adult males. All birds remained in their flocks for a year into the juveniles' first breeding season. As early as a month after creation of the groups, there were significant differences in the social behavior of the juvenile males in the two conditions (Table 2; see also White, King, Cole, & West, 2002). Juvenile males housed with adult males (JA juveniles) engaged in significantly more near neighbor associations with other juveniles and with females than did the juveniles housed without adult males (J juveniles). Being near others more often led to more opportunities to interact through song. JA juveniles directed significantly more song to other males and to females than did the J juveniles. The J juveniles sang predominately in undirected soliloquies.

The differences cascaded such that the two conditions continued to diverge into the breeding season (see Table 2 for a summary of differences). As the spring approached, the JA juveniles began countersinging, a behavior that progresses from male directed singing. When countersinging, two or more juvenile males sing

Table 2
Patterns of Behavior for White et al. (2002b) and White et al. (in press).

Behavior	White et al. (2002b)		White et al. (sub) Experiment 1		White et al. (sub) Experiment 2	
	JA juvs	J juvs	JA juvs	J juvs	S juvs	O juvs
Prior to Breeding:						
	+	-	+	-	+	-
NN males	+	-	+	-	+	-
Leaves	-	+	-	+	-	+
Breeding season:						
Countersinging	+	-	+	-	+	-
NN males	+	-	+	-	+	-
Leaves	-	+	-	+	-	+
Fights	+	-	+	-	+	-
Cops	=	=	=	=	=	=
Pot	-	+	-	+	-	+
Mating	monog	promis	monog	promis	monog	monog

Note. Summary of general behavior patterns of juveniles from White et al. (2002b) and White et al. (in press). Table illustrates which group had significantly more (+) or less (-) of the measures listed for the breeding season. NN males = near neighbour associations with males, Cops = copulations, Pot = song potency, Mating = mating patterns (monogamous or promiscuous).

in turns to one another at close proximity (usually less than 0.2 m apart). Anywhere from two to over twenty songs can be exchanged in these bouts. JA juveniles engaged in countersinging with other juveniles as well as with the adult males. J juveniles, however, engaged in significantly less countersinging. These males seemed to have learned that the most appropriate response to a directed song was to fly away (or “leave”). J juveniles had significantly more leaves than did the JA juveniles. In the breeding season, both groups of juveniles managed to copulate, but they went about getting copulations in very different ways. JA juveniles engaged in mating patterns common to Indiana cowbirds. They countersang, often escalating these singing bouts into fights. They courted individual females, singing consistently to one female, and guarding the females from the singing advances of other males. Finally, the males copulated with their consort females monogamously. However, J juveniles showed no aggression toward one another. Since they did not countersing, singing interactions rarely escalated into fights. These males instead sang to several different females, showed no aggression when other males sang to the females, and they copulated promiscuously. Females in the J condition had significantly more partners than did females in the JA condition.

Finally, J juveniles developed songs that were structurally different than those of the JA juveniles. J males’ songs had more notes and more note clusters than the JA songs. In addition, based on song playback experiments to females in sound attenuating chambers, J males’ songs were significantly more “potent”—

they were more effective at eliciting females' copulatory responses than were the songs of the JA juveniles, a finding seen in earlier studies with both the Indiana population and the South Dakota population (Freeberg, King, & West, 1995; West, King, & Freeberg, 1996).

This experiment revealed a dramatic degree of plasticity in cowbird social behavior. There was individual adaptability in traits that are commonly considered characteristics of a species, such as aggression, male-male competition, mate guarding, promiscuity and song structure. In one generation 'cultural' differences in social behavior were created just by changing the age class composition of the flocks. The presence of adult males had a stimulative effect on juveniles' competitive abilities, but a suppressive effect on their song quality. Not only did the juvenile males develop differently, but the females in the two conditions displayed different social behaviors (West, White, & King, 2002), and subsequent studies have revealed that adult male behavior can be influenced by the presence or absence of juvenile males (White, King, & West, 2002a).

Are these differences in behavior persistent? Can they be transmitted to a new generation? And can they be maintained when social conditions are not experimentally imposed? All of these questions needed to be answered in order to understand how such individual adaptability can function to maintain group-level differences and potentially to restrict gene flow. The next experiment set out to answer these questions. White et al. (in press) undertook a social transmission experiment wherein the juveniles from the original White et al. (2002b) study (plus individuals from replicate flocks) as adults served as social models for a new generation of juveniles. In the first experiment, two groups of juvenile males were given two months of exposure to the adult males of either the J or JA developmental histories (females were also present in the conditions). Juveniles interacted with the adults in the spring immediately prior to the breeding season, a time in nature when juveniles would be returning from migration and interacting with adults on their breeding grounds. Before the adult male exposure, all juveniles were housed together in an aviary without adults. Notably, the two conditions were housed in adjacent aviaries where juveniles could see and hear everything that occurred in the other condition. For the breeding season, adults were removed and juveniles then courted and mated with the resident females. The young male subjects replicated the first year mating patterns of the adult males with whom they were housed. They showed similar differences across groups in countersinging, aggression, song potency, and promiscuity. Even though the adults were removed from the study before the breeding season and thus the juveniles never had the opportunity to observe directly their mating patterns, social transmission of the mating patterns was observed.

For the second half of the breeding season, the barrier separating the two conditions was removed and the two groups of juveniles were allowed to interact. They rarely did so, however. Singing, near neighbor associations, and courting were organized by initial condition. Females mated assortatively with males from their initial condition. Females even showed near neighbor preferences for females from their own initial condition.

In a second experiment (White et al., in press), a new generation of juvenile males was again provided with social experience with adult males. In this

case, one group of juveniles was given access to adults in a large flock of 60 birds (socially exposed, “S” juveniles), while a second group of juveniles was housed adjacent to the large flock and thus could see and hear the activity in the large flock, but could not interact socially within it (observe only, “O” juveniles). In this experiment, the social exposure occurred for one month in the fall, a time at which adult males are engaging in very little singing behavior, very little competitive behavior, and no courtship. For example, over October and November, 23 adult males were observed to sing a total of only 54 countersinging songs. In the spring and breeding season, it would be possible for a single male to countersing this number of songs in one morning. Juvenile males thus had precious little in the way of courtship-like behavior to observe from these males. After the exposure to the large flock, the socially exposed juveniles were removed from the large flock and were maintained adjacent to the juveniles that were only visually and acoustically exposed to the flock (again both conditions also contained females). The birds remained in their conditions over the winter and into the breeding season. Once again the juveniles replicated the patterns from the past generations. Juveniles that were socially exposed to the large flock had significantly more near neighbor associations, developed countersinging, aggression, and mate guarding. Juveniles that were not socially exposed to the large flock sang more directed song, engaged in little aggression, countersinging, or guarding and they developed higher quality songs.

Similar to Experiment 1, the two conditions were allowed to merge for the second half of the breeding season and again birds rarely interacted with birds from the other condition. Singing, near neighbor, and courtship patterns were organized by initial condition. Again females mated assortatively with males from their initial condition. This experiment showed even more dramatically that behavior patterns can be socially transmitted even when the behaviors themselves are not copied, or even observed, by the new generation.

The focus of these studies has been on how modest differences in social experience within a flock can cause cascading effects in social behavior within the group and influence the developmental trajectories of the individuals living within the group. Admittedly at this stage the mechanisms of effect are only speculative. Adults seemed to serve to set the initial conditions for the groups by stimulating social interactions. The first difference seen between the two groups of juveniles was in near neighbor associations and in leaves. JA Juveniles seemed to learn from the adults not to leave in response to another’s song. This began a cascade of effects. Staying to song produced longer social interactions and more opportunities for countersinging contests, increased the chance for aggression to escalate, and allowed a social order among males to emerge. J juveniles never interacted with song in the same manner. Leaving to song never permitted males the opportunity to compete with each other or to evaluate each other. Small differences in early social behavior compounded into creating different learning environments, different opportunities to interact socially, and finally led to different breeding season behavior patterns.

More work needs to be done to understand the specific social learning mechanisms at work that lead to such developmental effects. Past work by West and King (1988; see also King, West, & Goldstein, 2005) has revealed that a num-

ber of subtle visual signals produced by females in the presence of singing males have the potential to shape male song development. These cues, such as the female's wingstroke response, are low frequency, extremely rapid signals that can only be seen by the human observer with the help of frame-by-frame video replay. In the aviaries, with so many potential sources of learning across a year, the opportunities for social interactions to influence development are pronounced, as are the opportunities for research.

Conclusions

Social effects on development can be difficult to detect. They require an experimental preparation where social factors can be manipulated while controlling for other potential confounds. In the field it is nearly impossible to compare distinct populations that differ only in social ecology and not also in some other aspect of physical ecology. In the lab it is often impossible to simulate ecologically realistic settings. The cowbird preparation provides a means to manipulate social groups in the lab, while maintaining functional courtship and communicative behavior. The preparation has revealed that the developmental social ecology experienced by juveniles in their first year of life can dramatically influence their behavioral phenotypes (West, King, & White, 2003). Juvenile cowbirds conformed to their social group, whether it was a result of exposure to a behaviorally distinct subspecies, or to different behavioral phenotypes from within a local population.

Most group-, population-, or species-level differences in behavior are generally considered to be a result of ecological, genetic, or phylogenetic differences across the populations (e.g., Lott, 1991; Mayr, 1963; Tinbergen, 1951). Without the ability to investigate the developmental ecology underlying these behavioral differences, however, it is impossible to detect the roles individual adaptability and social transmission might play in creating and maintaining these differences.

Cowbirds experience a wide variety of habitats, densities, and sex ratios. In some flocks, juveniles and adults do not interact over the juveniles' first year, whereas in other populations they live in mixed age flocks throughout their lifetimes. In sum, across their range, cowbirds can experience dramatic variation in social ecology. It is possible that this natural history has favored high levels of individual adaptability. Given that a young cowbird would have no a priori information about the type of social group it will enter, it may benefit by being a social conformist, allowing it to produce a locally adaptive repertoire of social behavior. The degree of individual adaptability that might be expected in populations of other species may depend greatly on other aspects of the species' natural history—dispersal and migration patterns (and their timing in relation to key periods of social learning) and the role age and sex structure might play in those patterns, and the extent to which mating decisions are based on more labile characters such as behavior or on less plastic characters such as plumage variation.

The degree to which individual adaptability can influence gene flow does depend to some extent on the segregation in space of the different groups. In cowbirds, each new generation starts off in a host nest. If there is no means by which the young of one generation will necessarily come to join a group similar to the parents, then there will be no limitation to gene flow, as the young cowbird will

develop behaviors appropriate to its group. In this case, group differences can be maintained by social transmission, but different groups would never diverge genetically, as the genetic background would be reset every generation. If, however, there is some means by which different generations experience common developmental social ecologies, then these social effects may foster genetic divergence, as the characteristics that may be selected for in one social environment may not be the same in another (aggression, for example). One key feature of social ecologies that needs to be addressed involves the behavioral mechanisms by which smaller groups of individuals structure and associate themselves in space and time over the overwintering months when fundamental social and vocal behavioral transitions are occurring. For migratory populations on their overwintering grounds, young birds of a given species are likely coming into contact with conspecifics from potentially quite behaviorally distinct populations. To what cues or signals are young birds attending in deciding whether to interact with and associate more with birds of group A relative to birds of group B? Recent work by Warren (2002, 2003) on bronzed cowbirds, *Molothrus aeneus*, indicates that individuals may attend to differences in song dialects on the overwintering grounds, and this could play a role in the maintenance of distinct groupings over the winter. Are the smaller social groups that birds may reside in over the overwintering months 'set' on the natal grounds prior to migration, or is there considerable plasticity as to which social group(s) a young bird might join (and potentially follow back to that group's breeding grounds)? For an individual in the process of integrating into a social group, how important are social cues from adults relative to social cues from other young birds? How important are these social cues relative to its own cues, such as its own plumage and behavioral characteristics (e.g., Hauber, 2002; Hauber & Sherman, 2001)? Little is known about dispersal patterns and distances of juvenile birds in migratory populations of cowbirds (as well as for many other species), so this is not an easy question to answer. A laboratory preparation that could mimic this time period would involve testing the behavioral interactions and social associations of young birds exposed over the winter to groups of adults that differ substantially in their behavioral patterns, in effect asking the young to choose the groups with which they will associate. Breeding season tests of courtship and mating preferences would be able to determine the functional implications of such social grouping choices.

To conclude, we have presented evidence from two sets of studies that tested the role social transmission can play in geographic variation in behavior within a species. In the first set of studies we described, it was found that young cowbirds of one population housed over the winter with adult cowbirds from a behaviorally distinct population developed courtship signals that were similar to the adults of that population. Birds with a genotype characteristic of the South Dakota population exhibited courtship behaviors and mating patterns more characteristic of the Indiana population. Thus, this set of studies illustrated a process by which population-level variation in behavior (in this case, behaviors typical of the South Dakota population of cowbirds) can effectively be lost in a single generation. The second set of studies we described found that young males from an Indiana population housed in social groups with other young males and with females developed extremely different patterns of courtship and mating—indeed, essentially distinct

mating systems—depending upon whether they were exposed to adult males over the winter. Collectively these studies point to the fundamental role social ecologies play in the development of population-level differences in behavior – social ecologies may be a driving force in the geographic variation seen across the brown-headed cowbird’s range.

We believe these social transmission processes are likely important factors in population-level differences in behavior in species other than cowbirds (see Avital & Jablonka, 2000, Boyd & Richerson, 1985, Heyes & Galef, 1996). We hope that our review will stimulate research into these questions with other species of songbirds. Social transmission may impact population-level variation in behavior in other taxonomic groups as well, perhaps especially in species that have been found to learn communicative behaviors at least in part through interactions with members of their social groups (e.g., greater spear-nosed bats, *Phyllostomus hastatus*—Boughman, 1998; pygmy marmosets, *Cebuella pygmaea*—Snowdon & Elowson, 1999; bottlenose dolphins, *Tursiops truncatus*—Watwood, Tyack, & Wells, 2004). Finally, we argue that simply demonstrating an effect of social transmission on these systems of courtship behavior is not enough. We need to focus our work on measuring and manipulating the important features of the social ecologies of young animals developing their communicative systems if we wish to understand the processes by which social transmission can impact geographic variation in behavior.

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