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Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird

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Many animals repeat standardized displays multiple times while attracting a mate or deterring a rival. In such contexts the ability to perform each display or signal type in a consistent fashion may be under direct selection. Studies on sexual selection on song learning in birds have focused on differences in repertoire size with less attention paid to the potential importance of being able to perform each song/syllable type with high consistency. We investigated whether syllable type consistency is related to age, social dominance and reproductive success in tropical mockingbirds, *Mimus gilvus*. The variation between renditions of each syllable type decreased as the birds grew older (i.e. they became more consistent). In addition, more consistent males tended to have higher dominance status and reproductive success. These findings stress the importance of consistency in the performance of sexual displays and suggest that this parameter may be very relevant even in species that are selected for high vocal diversity (i.e. large repertoires). We hypothesize that, in addition to signalling dominance status and age, syllable type consistency may also indicate the integrity of brain function in birds analogous to the tests used for neuropsychological assessment in humans.

Songbirds are among the few taxa that must learn their species-specific signals of communication from other individuals (Kroodsma 1988). Learning how to sing involves the development of appropriate neuromuscular structures, exposure to relevant social stimuli, and practice (reviewed in Beecher & Brenowitz 2005). Early stages of vocal learning include the production of soft, rambling sounds known as 'subsong', followed by more stereotypical vocalizations known as 'plastic songs' (Hultsch & Todt 2004). In most known bird species, song elements eventually 'crystallize' into standard types that are repeated thereafter with remarkably low variability (Tumer & Brainard 2007). Crystallized types are observed in both age-restricted and open-ended learning species (Read & Weary 1992).

Previous studies on the potential information content and selective advantages of song learning have focused on differences in repertoire size (reviewed in Gil & Gahr 2002) and have overlooked the importance of being able to sing each learned type in a consistent fashion (but see Byers 2007). This bias stems from the tacit assumption that the most important aspects of learning occur prior to crystallization. However, recent evidence suggests that learning continues after song crystallization. For example, adult birds can adaptively adjust their motor patterns to optimize performance and minimize variability among renditions of each type when exposed to disruptive stimuli (Tumer & Brainard 2007). Thus, we hypothesized that the amount of variability in syllable type performance could be a signal of individual quality, with higher quality individuals showing less variability (i.e. being more consistent). A similar relationship between performance variability and individual quality has been suggested for motor displays in other modalities (Zahavi 1980; Jordao et al. 2007).

We tested our hypothesis in the tropical mockingbird, *Mimus gilvus*, investigating whether within-type consistency is related to age, social dominance and reproductive success. Tropical mockingbirds live in cooperative breeding groups with multiple members of each sex that cooperate in the defence of a territory (Morton et al. 2004; Botero et al. 2007). Same-sex group members are organized in linear dominance hierarchies. In some groups, the two highest-ranking males (i.e. the alpha and beta males) compete

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with each other for mating with the highest-ranking female (Botero et al. 2007). Both alpha and beta males build nests and sing conspicuously prior to a breeding attempt, but alpha males tend to displace betas rather than be displaced by them, to perch higher when in the same tree, and to have higher song output (Botero et al. 2007). Tropical mockingbirds are multibrooded and their peaks in reproductive activity coincide with the rainy season (Paredes et al. 2001). Most male song occurs prior to a breeding attempt (Paredes et al. 2001). Each male learns over 100 different syllable types (Botero et al. 2008) and combines them in multiple ways to produce a much larger number of songs (Fig. 1). Songs are presented with eventual variety and syllable types are conserved from year to year.

METHODS

Study Population

From August to December 2004 and from August 2005 to May 2006, we monitored 23 social groups of individually colour-banded tropical mockingbirds in Villa de Leyva, Colombia as part of an ongoing study on song learning and song use (Botero et al. 2007). These social groups include a mean ± SE of 1.8 ± 0.20 males and 1.8 ± 0.16 females (data based on 19 groups for which molecular data are available). Adult birds were captured once using nylon mist nets (mesh = 38 mm) and received two coloured darvic bands on one leg and one coloured darvic band plus a numbered aluminium band on the other (www.avinet.com). Before releasing each subject, we collected a small genetic sample by extracting approximately 0.05 ml of blood from the brachial vein on the left wing. Samples were obtained by gently poking the vein with a sterile insulin needle and collecting a drop of blood with a heparinized capillary tube. Blood samples were stored in Queen's lysis buffer until the time of analysis (see below). Capture, banding and genetic sampling protocols were approved by Cornell University's Institutional Animal Care and Use Committee and, locally, by the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Cross-sectional Analysis

We recorded 23 reproductively active males, each from a different focal group, opportunistically during periods of sustained song output (11 alpha males and 12 beta males). Recordings were made at close proximity with a Marantz PMD690 digital recorder (16 bits per sample, 48 000 samples/s) and a Sennheiser ME67 directional microphone. Dominance ranks were determined through direct observation of agonistic interactions and comparison of song output.

Within-type consistency was measured as the average spectral cross-correlation (SPCC) for 20 randomly selected syllable types per individual ($N = 10$ exemplars per type, each exemplar was correlated against every other exemplar of its type). Syllables were defined as a sound, or group of sounds, that was separated from other sounds by more than 0.04 s of silence (see Fig. 1). The only exceptions to this rule were the rare occasions on which the same types of sounds happened to be separated, within a single recording, by less than 0.04 s of silence in at least eight exemplars and by more than this threshold in the remaining ones, or the other way around (e.g. compare syllable type 13 with types 17 and 18 in Fig. 1). In these situations, we considered all repetitions of these sounds as exemplars of one or two syllable types depending on the decision that applied to the majority of cases. Classification of syllables into types was done jointly by R.J.M. and C.A.B., based on overall similarity in sound, structure and duration. Types were only classified on a male-by-male basis and we made no attempt to determine which types were shared by different focal males or, in the longitudinal analysis described below, by the same male in different years. Exemplars were selected by R.J.M. without any knowledge of the social status or age of the focal males. Because of the low number of syllable types sampled per bird, the low number of exemplars per type, the large structural differences between types (see Fig. 1), and our strict time-based rules to define syllables, there was full concordance between observers in the classification of syllables into types.

SPCC coefficients were computed with Avisoft-SASLab Pro (www.avisoft.com). These coefficients reflect the similarity

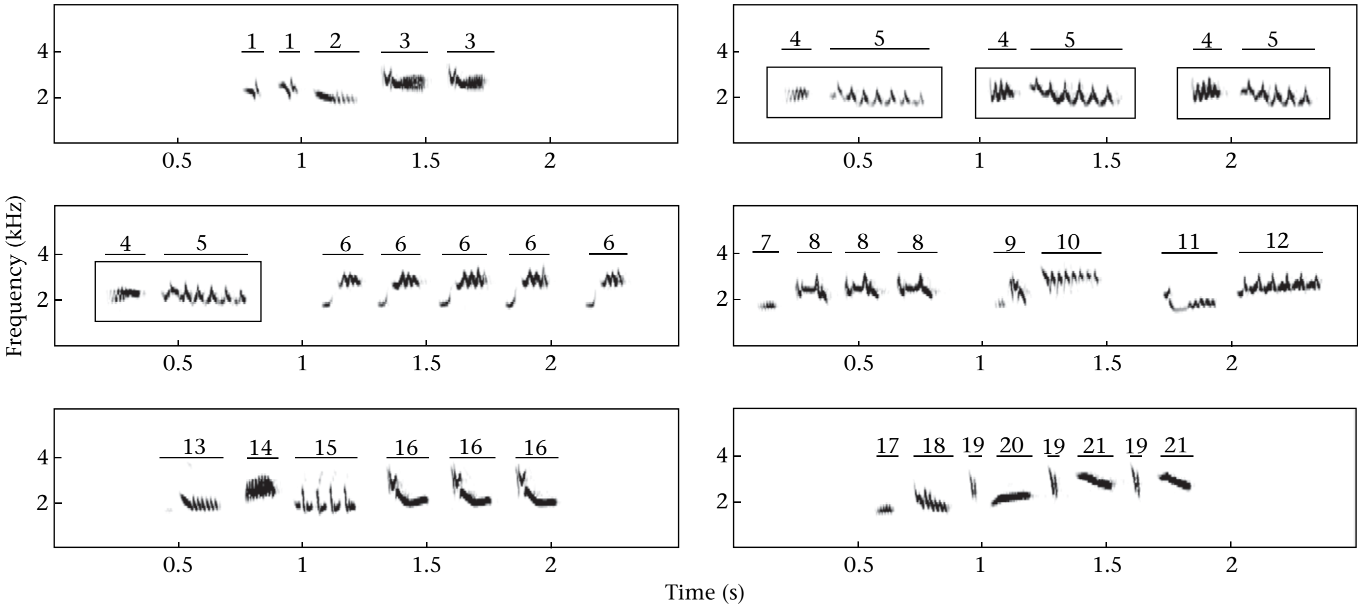

Figure 1. Selected songs of one of our focal male tropical mockingbirds in Villa de Leyva, Colombia. Lines above the spectrogram indicate syllables and numbers are used to identify syllable types. Grey boxes show how syllable types (in this case, types 4 and 5) are combined in different ways to produce a virtually unlimited number of song types. The songs with the grey boxes were recorded in different years, suggesting that at least part of the syllable type repertoire is conserved throughout an individual's life. The examples shown were chosen to illustrate the vocal diversity of male tropical mockingbirds and do not reflect the actual types included in our analysis.

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between two sounds and range from zero, when there is no similarity, to one, when the sounds are identical (Clark et al. 1987; Coleman et al. 2007). The effects of background noise on our results were minimized by computing the SPCC coefficients using only the frequency bands covered by each syllable type. Exemplars for a given syllable type were obtained from multiple songs recorded on a single day and were chosen based on a good signal-to-noise ratio and an absence of masking sounds. Given the repetitive singing style of the tropical mockingbird, all exemplars for a given type were usually collected within a short period. Different syllable types for a given individual were sampled within 5 days of each other ($\overline{X} \pm \text{SE} = 3.41 \pm 1.68$ days).

We used binary logistic regression to determine whether mean within-type consistency is a good predictor of social dominance status. The regression model corrected for mean syllable duration and mean frequency bandwidth (also measured with Avisoft-SASLab Pro) because these parameters might have an important effect on the outcome of SPCC. SPCC is a technique that compares images and the larger the area of these images, the larger the number of pixels that need to be compared. Sounds that last longer or cover a larger frequency range will produce spectrograms with larger area and, thus, may show lower similarity values.

Within-group Reproductive Success

Eleven focal groups used in the cross-sectional analysis produced young after we sampled the songs of their constituent alpha and/or beta males ($\overline{X} \pm \text{SE} = 2.3 \pm 0.6$ months from acoustic sample to fledging date). We collected genetic samples from the nestlings produced in these reproductive events ($N = 23$) at day 13 posthatching using the same method described for the adults. In a few cases we collected blood from the tarsal rather than the brachial vein. Mockingbird nestlings are almost fully grown by day 13 and leave the nest a few days later. We determined the most likely candidate father for each of these nestlings using genetic markers and the program CERVUS 3.0 (Marshall et al. 1998). Of 26 microsatellite loci known to amplify in the genus *Mimus* (see Hughes & DeLoach 1997; Rubenstein 2005), only five showed sufficient polymorphism in our study population (Table 1). A multiplex reaction containing 0.1–0.24 μM of each of these primers (primer concentrations were varied to obtain similar fluorescent peaks) was optimized to 0.25 U Taq polymerase and 3.25 mM $MgCl_2$. Forward primers were tagged with 5′-fluorescent labels (NED, PET, 6-FAM or VIC; Applied Biosystems Inc., Foster City, CA, U.S.A.). Polymerase chain reactions consisted of one cycle at 95 °C for 2 min, 35 cycles at 95 °C for 50 s, 56 °C for 1 min, 72 °C for 1 min, followed by a final extension cycle of 30 min at 72 °C. Fluorescent PCR products were diluted 1:14 in water and mixed with a size standard (Genescan LIZ-500) and formamide before electrophoresis on a 3100 Genetic Analyzer (Applied Biosystems). Allele sizes were analysed using GeneMapper version 3.7 (Applied Biosystems).

Table 1
Microsatellite loci in *Mimus gilvus* and the number of alleles observed in a sample of 16 adults from our study population

Loci	Alleles
SS2-53, SS2-106, SS2-29, SS2-80, SS2-83, SS2-130, SS2-49, SS2-52, SS2-82, SS2-114, SS2-40	1
SS2-32, SS2-119, SS2-16	2
SS2-56, SS1-11	3
MpATT 24	3
MpATT 86*	4
MpAAT 18*, MpATT 83*	7
MpATT 84*	8
MpAAT 26*	9

Asterisks identify the loci used to genotype all individuals in this study.

Longitudinal Analysis

To explore how within-type consistency varies over time, we sampled 11 alpha males and one beta male an additional time in a subsequent breeding attempt (i.e. 20 more types and 10 exemplars per type). We used a two-tailed paired *t* test to test for differences in within-type consistency between samples.

RESULTS

Cross-sectional Analysis

Alpha males showed higher within-type consistency than beta males (Fig. 2; logistic regression model: predicted logit of (rank) = 116.89 − 134.32 × (within-type consistency); overall model evaluation: $G_1 = 8.533$, $P = 0.003$; individual test for within-type consistency: $Z = -2.23$, $P = 0.026$; Hosmer–Lemeshow's goodness-of-fit test: $\chi^2_8 = 11.98$, $P = 0.152$). No other factor explored in this analysis was a significant predictor of dominance rank (syllable bandwidth: $Z = -1.36$, $P = 0.172$; syllable duration: $Z = -0.24$, $P = 0.809$; within-type consistency*syllable bandwidth: $Z = 0.16$, $P = 0.865$; within-type consistency*syllable duration: $Z = -1.53$, $P = 0.125$).

We explored the differences between alpha and beta males by classifying each syllable type in our samples as low, intermediate or highly consistent on the basis of its mean SPCC. This classification revealed that the proportion of types performed with very high consistency (i.e. mean SPCC ≥ 0.9) was higher in alpha than in beta males (Fig. 3). To put this into context, different renditions of a type with a mean SPCC ≤ 0.8 (i.e. low consistency) are clearly different to an untrained human ear (and presumably to a bird receiver), but different renditions of a type with mean SPCC ≥ 0.9 are very difficult to perceive. Although this categorization is clearly arbitrary, it demonstrates that in principle, alpha and beta males can be easily

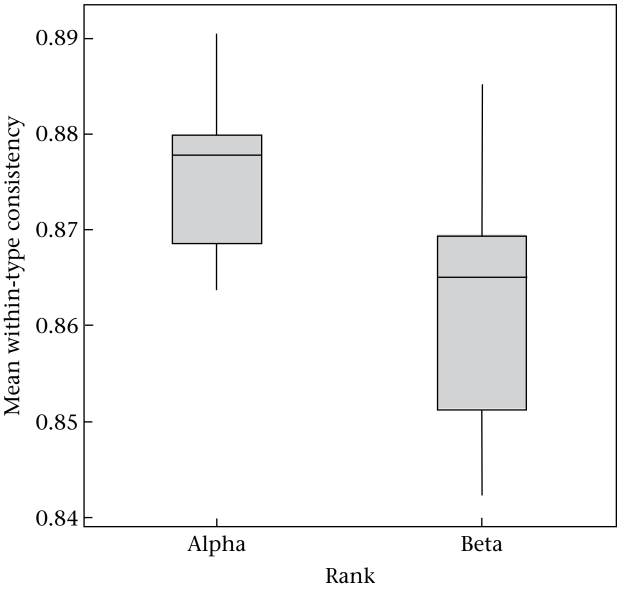

Figure 2. Mean within-type consistency (measured as the mean spectral cross-correlation coefficient across renditions of the same syllable type) as a function of social dominance. Boxes represent interquartile ranges, horizontal lines mark the medians, and vertical lines represent the general extent of the data. $N = 20$ alpha males and 12 beta males.

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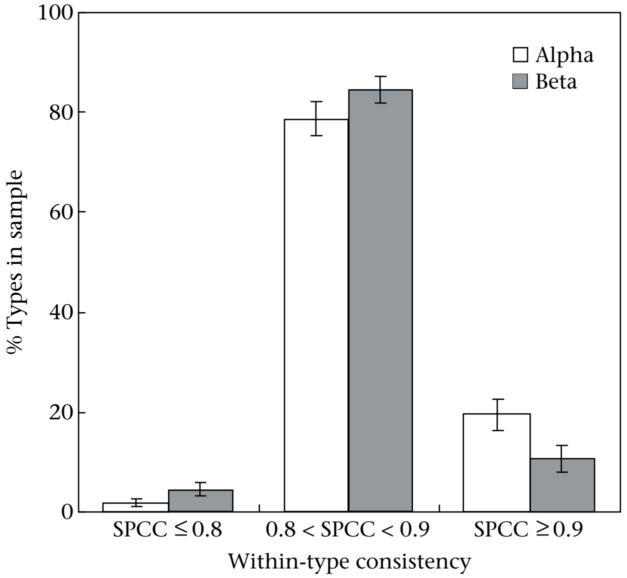

Figure 3. Distribution of syllable types with low ($SPCC \le 0.8$), intermediate ($0.8 < SPCC < 0.9$) and high ($SPCC \ge 0.9$) average within-type consistency, in alpha and beta male tropical mockingbirds.

distinguished on the basis of consistency alone even if, on average, their differences are very small.

Within-group Reproductive Success

All but one of the nestlings included in this analysis were fully genetically compatible with the alpha males in their natal groups under the assumption that eggs were incubated by their mothers (only one female mockingbird incubates each brood). In contrast, beta males were fully genetically compatible with only four nestlings in their own territories and showed two or more allelic mismatches with the other 19. In the four cases (two nests) in which both the alpha and beta male from the natal territory were compatible with the offspring, the alpha male had a higher nonexclusion probability and a higher logarithm of the odds (LOD) score than the beta male, suggesting that the alpha male was the most likely parent. Given that all but one offspring could be parsimoniously attributed to the alpha males and that we have already shown that these same alpha males have higher within-type consistency than beta males, no further statistical test to correlate within-type consistency with within-group reproductive success was performed.

Longitudinal Analysis

The consistency with which male tropical mockingbirds repeated each syllable type improved over time (paired *t* test: $t_{11} = -4.14$, $N = 12$ birds, $P = 0.0002$). Furthermore, such improvement was significantly correlated with the time elapsed between samples (Pearson correlation: $r_{10} = 0.75$, $P = 0.005$; Fig. 4). There were no significant differences between samples in mean frequency bandwidth (General Linear Mixed Model with individual as a random factor: $F_{1,411} = 0.09$, $P = 0.763$) or duration ($F_{1,411} = 0.10$, $P = 0.751$) of syllable types. As in the cross-sectional analysis, higher consistency was achieved by increasing the proportion of syllable types performed with high consistency. In this case, the proportion of types performed with low consistency was also reduced (Fig. 5).

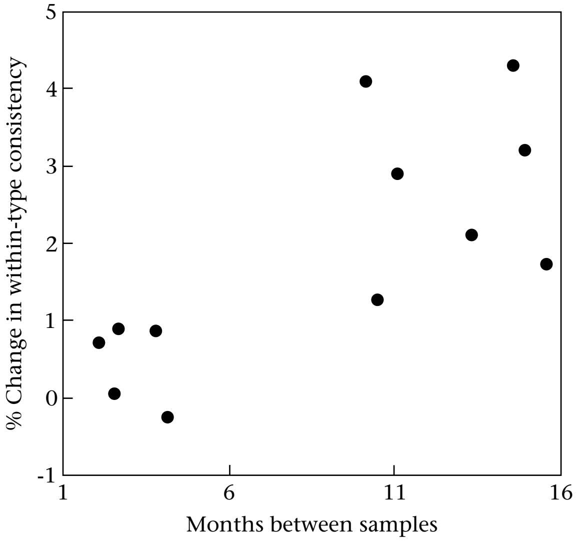

Figure 4. Individual changes in within-type consistency (i.e. 2nd sample − 1st sample) as a function of the time elapsed between the two samples.

DISCUSSION

Male tropical mockingbirds with high within-type consistency tended to be socially dominant over less consistent males and to achieve greater reproductive success within their own social groups. A similar result was reported recently for the chestnut-sided warbler, *Dendroica pensylvanica*, in which males with lower coefficients of variation for pitch and intersong interval tend to father more extrapair young (Byers 2007). Our study adds to these results by showing that variability in syllable type performance is determined not solely by an individual's quality but also by its age. Furthermore, it suggests that the consistency with which learned types are performed may also be important in species that are being selected for high vocal versatility.

The individual changes in within-type consistency observed in our longitudinal analysis suggest that vocal consistency may be an

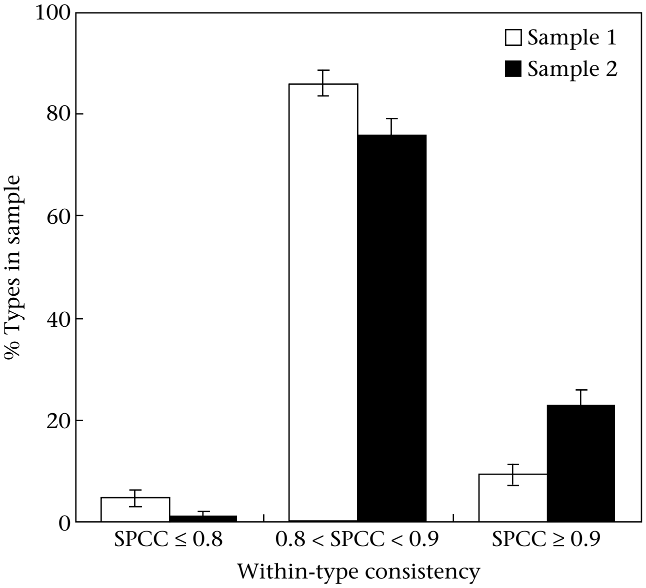

Figure 5. Change in the distribution of types with low ($SPCC \le 0.8$), intermediate ($0.8 < SPCC < 0.9$) and high ($SPCC \ge 0.9$) average within-type consistency, between breeding attempts.

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acquired skill that can improve through practice. Nevertheless, there was a clear difference between males that were resampled in the same versus in different breeding seasons (i.e. <5 months versus >5 months in Fig. 4), suggesting that most changes could take place during the phase of neuroanatomical restructuring that occurs between breeding seasons (see Nottebohm 1981). If this is the case, vocal consistency may be considered more a signal of age than of singing experience.

Although the differences observed in this study appear small, there are at least three reasons why they may be biologically relevant. First, specialization of cochlear structures (reviewed in Bradbury & Vehrencamp 1998) may allow birds to perceive differences that escape the human ear. Second, consistency may be used to distinguish between classes that differ by much more than the reported averages (e.g. between first-year males and older, more experienced ones). Third, mockingbirds may classify types into broad categories (as we did in the Results) and distinguish between dominance or age classes on the basis of the proportion of highly consistent (or conspicuously inconsistent) types they hear.

Our study provides preliminary evidence that sexual selection in species with very large vocal repertoires rewards not only high vocal diversity but also the ability to sing each type in a consistent fashion. Selection for high vocal diversity via female choice is thought to be the main driving force behind the exaggerated repertoires of mockingbirds, nightingales, *Luscinia megarhynchos*, and other songbirds with very large repertoires (reviewed in Catchpole & Slater 1995). However, if vocal diversity was the only parameter of interest for female receivers in these species, then males would benefit from learning how to improvise novel sounds without going through the trouble of memorizing specific song or syllable types. Our results suggest that the ability to deliver each type in a consistent fashion could also be a target of selection in mockingbirds as an honest indicator of dominance status and age. This hypothesis could explain why all mockingbird species in the genus *Mimus* and most other mimids repeat the same syllable type multiple times within a short period (Brewer & MacKay 2001) instead of maximizing their apparent vocal diversity by presenting new types more often. Short-term repetition of syllable types may not only facilitate the assessment of within-type variability but also emphasize individual differences in the ability to cope with exhaustion (Lambrechts & Dhondt 1988).

Within-type consistency could also be a target of selection in agonistic contexts as is the case with other displays of singing ability (Lambrechts & Dhondt 1988; Podos 1997; Illes et al. 2006). Male mockingbirds often engage in countersinging interactions in which rivals match each other's songs and the songs become highly repetitive (Botero & Vehrencamp 2007). Repetitiveness in song sequences facilitates the assessment of performance variability and, thus, could be used to signal relative quality to rivals or even to female eavesdroppers (Mennill et al. 2002).

We hypothesize that, besides indicating age and dominance status, syllable type consistency may also indicate brain integrity. Recent findings suggest that adult birds constantly monitor their own songs and make the necessary adjustments to maintain a consistent outcome (Tumer & Brainard 2007). Furthermore, male finches tend to do most of this motor exploration when females are not present (Kao & Brainard 2006; Sakata et al. 2008), possibly because females show strong preferences for more consistent males (for effects of consistency on female preference see Woolley & Doupe 2008). Given that lesions to the anterior forebrain pathway (AFP) can strongly diminish a bird's ability to perform this type of motor exploration (Kao & Brainard 2006), our hypothesis predicts that AFP-lesioned birds will also be less capable of maintaining a consistent directed song in long-term studies, and that they will be less able to cope with disruptive stimuli such as the one used by Tumer & Brainard (2007). If that is the case, then it is possible that the assessment of within-type variability in syllable type performance is a simple index of the integrity of brain function in birds. A similar type of assessment is found in human medicine, where neuropsychological methods rely on the speed, coordination and pacing of simple motor tasks to determine the likelihood of certain types of brain damage (see the 'finger tapping test' in Dodrill 1978; Miller 1992; Christianson & Leathem 2004; Patton & Black 2005; de Groot-Driessen et al. 2006; Perfahl et al. 2007). Given that enumerating the number of syllable types in a large repertoire is time consuming and neurologically taxing (Botero et al. 2008), it seems possible that mockingbird receivers use other indicators of individual quality than repertoire size, such as the consistency with which different syllable types are performed over time.

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