



RESEARCH PAPER

A Tradeoff Between Performance and Accuracy in Bird Song Learning

David C. Lahti*†, Dana L. Moseley* & Jeffrey Podos*

* Department of Biology, University of Massachusetts, Amherst, MA, USA

† Department of Biology, Queens College, City University of New York, Flushing, NY, USA

Correspondence

David C. Lahti, Department of Biology, Queens College, City University of New York, 65-30 Kissena Blvd., Flushing, NY 10541, USA.
E-mail: david.lahti@qc.cuny.edu

Received: March 2, 2011

Initial acceptance: April 14, 2011

Final acceptance: June 13, 2011
(L. Ebensperger)

doi: 10.1111/j.1439-0310.2011.01930.x

Abstract

Some of nature's most complex behaviors, such as human speech and oscine bird song, are acquired through imitative learning. Accurate imitative learning tends to preserve patterns of behavior across generations, thus limiting the scope of cultural evolution. Less well studied are the routes by which cultural novelties arise during development, beyond simple copy error. In this study we assess, in a species of songbird, the relationship in song learning between two potentially conflicting learning goals: accuracy in copying and maximization of vocal performance. In our study species, the swamp sparrow (*Melospiza georgiana*), vocal performance can be defined for a given song type and frequency range by the rate of note repetition ('trill rate'), with faster trills being more difficult to sing. We trained young swamp sparrows with song models with experimentally modified trill rates and characterized both the accuracy and performance levels of copies. Our main finding is that birds elevated the trill rates of low-performance models, but at the expense of imitative accuracy. By contrast, birds reproduced normal and high-performance models with typically high accuracy in structure and timing. Developmental mechanisms that enable songbirds to balance imitative accuracy and vocal performance are likely favored by sexual selection and may help explain some current patterns of variation in birdsong. Such mechanisms may also explain how behaviors that are learned by imitation can nevertheless respond to selection for high-performance levels in their expression.

Introduction

Imitative learning is a widespread means of acquiring patterns of behavior (Whiten 1992; Zentall 2006). When imitation is precise and rooted in an ecological function, the behavioral pattern tends to remain stable over time (Henrich & Boyd 1998; Claidière & Sperber 2010; Lindeyer & Reader 2010). This stability can preserve or even be vital to the effectiveness of a behavior, as in communication where signals are shared among individuals (Nowicki & Searcy 2005). Decades of research in the model systems of human speech and bird song, for example, have shown that juveniles memorize and accu-

rately reproduce sounds produced by their elders (Slater 1989; Kuhl & Meltzoff 1996; Brainard & Doupe 2002; Pagel 2009). Such accuracy is made possible not only by an advanced ability to imitate sounds, but also by an unlearned bias toward learning sounds of one's own species or genetic lineage (Marler & Peters 1977; Soha & Marler 2000; Dedić & Ladd 2007).

Accurate and species-specific imitation cannot explain the origins of behavioral novelty, about which less is known. In general, new variations in behavioral patterns can arise through creative departures from imitation. Some novelties might arise through random copy errors (Slater 1989). Another

possibility, explored here, is that animals under some circumstances might sacrifice imitative accuracy in favor of modifications that enhance behavioral function. For instance, chimpanzees and New Caledonian crows learn tool manufacture and use from each other through imitation, but new challenges might best be met by individual innovation (Sanz et al. 2009; Wimpenny et al. 2009). Likewise in courtship, individuals might benefit by elevating the performance levels of imitated displays, because sexual selection often favors individuals that distinguish themselves by producing displays with high proficiency or virtuosity (Patricelli et al. 2003; Clark 2009; Byers et al. 2010). Songbirds are known to assess the quality of rivals or prospective mates based on their songs, and sexual selection is thought to favor singers that display certain vocal characteristics that are difficult to produce (reviewed by Podos et al. 2009). While individuals might derive certain benefits from accurate imitation, they might also derive benefits by sacrificing imitative accuracy for the sake of increasing performance, however that may be defined for a given behavior and population (Kendal et al. 2005; Burkart et al. 2009). Thus, while accurate copying is central to imitative learning, superior individuals might be able to demonstrate their higher performance or competence only by departing from imitative accuracy during behavioral development.

In songbird species that produce trilled vocalizations, one component of vocal performance is trill rate, the rate at which syllables are repeated within trilled song components. All other song features being equal, songs with higher trill rates require more rapid modulations of the syrinxal, respiratory, and vocal tract motor systems (Podos 1997; Hoese et al. 2000; Suthers 2004; Riede et al. 2006). Consistent with predictions of sexual selection favoring vocal performance, female canaries (*Serinus canaria*) and swamp sparrows (*Melospiza georgiana*) have been found to produce more vigorous copulation solicitation displays (an indicator of mate preference) in response to playback of songs with higher trill rates (Vallent & Kreutzer 1995; Drăgănoiu et al. 2002; Ballentine et al. 2004; see also Caro et al. 2010). We hypothesize that sexual selection should thus drive male songbirds to increase the performance of songs they learn, even though any such increase in performance would necessarily represent a decrease in the accuracy of their imitation.

We tested this hypothesis in song learning experiments with swamp sparrows. Like many oscine songbirds, swamp sparrows learn to sing effectively

only if they hear songs of their species when they are young (Marler & Peters 1977; Dooling & Searcy 1980; Marler 1981). During their first spring and summer, they hear and memorize multiple conspecific song types. Each song type consists of a particular syllable (of two to five notes) repeated for approximately 2 s (Marler & Pickert 1984). Swamp sparrows do not learn songs they hear after their first summer (Marler & Peters 1988). During the following spring, they practice imitated song types aloud until the song types crystallize, i.e., achieve a final form that will persist virtually unchanged for the rest of the bird's life (Marler & Peters 1982; Clark et al. 1987). Swamp sparrows reared without exposure to model songs still develop trilled syntax – suggesting a central motor program for this attribute (Marler 1984) – although syllables within isolate-reared songs tend to show an aberrant, non-species-typical acoustic structure (Marler & Sherman 1985).

We trained young swamp sparrows on songs with experimentally modified trill rates. Given that higher trill rates indicate higher performance in this species (all other song features being equal), training young birds on song models with experimentally elevated trill rates alone would not allow us to distinguish predictions based on performance vs. imitative accuracy. In this case, attempts to maximize both accuracy and high performance would lead individuals to sing the songs the way they had heard them. Therefore, to help tease apart the relative importance of accuracy vs. performance, we trained hand-reared male swamp sparrows with song models in which trill rates were artificially diminished, the accurate imitation of which should require comparatively low vocal proficiency. Young birds were also trained with control models at natural trill rates, and with models at elevated trill rates (as in Podos 1996; Podos et al. 1999). Model trill rates were modified by the addition or deletion of silent intervals between notes and syllables, thus preserving the original frequency and amplitude structure of individual notes (Podos et al. 2004). If birds emphasize imitative accuracy over performance, we would predict that (1) birds would learn and reproduce slowed models with high accuracy. On the other hand, if birds emphasize vocal performance at the expense of accuracy, we would predict that (2) birds would memorize slowed models yet reproduce them at higher trill rates. Another possible outcome is that experimental manipulations would render songs inappropriate as models, so that (3) birds would ignore song models with diminished trill rates. Distinguishing among these outcomes

allows us to draw inferences about the relative importance of learning accuracy and vocal performance in song development.

Methods

Study Animals and Housing

We collected swamp sparrow nestlings of five to 7 d post-hatching, from nests in a population at the Quabbin Reserve in Franklin County in western Massachusetts, in June 2005 and June–July 2007. We hand-reared birds in sterilized swamp sparrow nests until fledging, then in groups of 5–8 in common cages ($84 \times 74 \times 44$ cm) to independence, at which time males were moved into individual cages ($46 \times 22 \times 26$ cm). Birds were kept at the natural light/dark schedule throughout the study and had access to perches and biweekly baths. Nestlings and fledglings were fed a blended mixture of commercial turkey feed, carrots, eggs, ground beef, calcium derived from oyster shells, and vitamin powder. As the birds grew to independence, this diet gradually transitioned to *ad libitum* access to a commercial finch seed mixture supplemented with egg food, mealworms, and a vitamin spray. Birds were housed in a walk-in acoustic isolation chambers for daily song training, which began at 11–29 d of age and continued until 118–148 d of age. This time period encompasses the sensitive period for song acquisition in this species (Marler & Peters 1988). Five males were raised and trained in 2005, and 11 males in 2007. Males were kept in captivity for 10 mo for this study and retained in captivity following the experiments. All activities were performed with the approval of University of Massachusetts Institutional Animal Care and Use Committee (protocol #28-10-02).

Song Training Regimes

Models were constructed from ten swamp sparrow songs recorded from another population (Millbrook, New York, as in Podos 1996; Podos et al. 1999). Naturally occurring songs used to construct training songs ranged in trill rate between 4.6 and 11.7 Hz. It is important to note that trill rate by itself does not provide a comprehensive measure of performance levels required for the production of swamp sparrow song. This is because trills in nature also vary in other performance-related parameters, such as frequency bandwidth (the range of frequencies represented in a song), the structure of notes within

syllables, and the number of notes per syllable. These aspects of performance interact: for instance, songs with faster trill rates tend to have narrower frequency bandwidths (Podos 1997; Ballentine et al. 2004; Liu et al. 2008) and fewer notes per syllable (e.g., songs of 4–5 Hz typically contain four or five notes per syllable, whereas songs of 10–12 Hz contain only two notes per syllable). For these reasons, different song types may entail similar levels of performance, in spite of large differences in trill rate. The most direct assessment of vocal performance is thus not among different song types, but among different versions of a given song type (e.g., Ballentine et al. 2004; DuBois et al. 2011). Our study focuses on this latter type of comparison— we ask how birds reconstruct particular model song types with manipulated trill rates (thereby altering required performance levels).

Using Signal Software (Engineering Design 2003), we constructed a regime of ten training songs for each set of birds. Two control songs in each regime were constructed at the same trill rate as the original wild-recorded songs (natural trill rate), and the remaining eight songs in each regime were the experimentally modified songs. For the 2005 birds ('slowed' regime), trill rates of the eight experimental training models were decreased to between 25% and 95% of their wild-recorded (natural) trill rates. We opted for a broad range of values for trill rate reductions here because we did not know the minimum degree of slowing that would affect learning, nor the maximum degree of slowing that would still permit the song to be considered a conspecific signal. For the 2007 birds ('slowed and sped' regime), trill rates were decreased for four models to 65% to 95% of their natural trill rates (following our finding from 2005 birds that models slower than this are not copied; see Results). For the other four experimental models, trill rates were increased to 105% to 135% of their natural trill rates. This range of trill rate increases was chosen because past research (Podos 1996; Podos et al. 1999) showed that increases beyond this level can drive birds to restructure their songs into 'broken' syntax (to compensate for motor constraints), which presents a level of complexity to the analyses that we wished to avoid here. Trill rates were adjusted by adding or deleting silent intervals between notes and syllables, thus preserving the original structure of individual notes (Podos et al. 1999).

Six of the resulting song type copies were produced by birds that had been trained on the 'slowed' regime. The other 14 copies were produced by birds

that had been trained on the ‘slowed and sped’ regime (Fig. 1).

Analysis of Learned Songs

From 294–304 to 362–372 d of age, we recorded the vocalizations of each bird for three morning hours 2 d each week, rotating birds from the walk-in acoustic chamber through eight individual recording chambers. Between recording sessions, individual birds thus were able to hear and interact with other birds in the experiment. The ability to engage in social interactions likely enriched birds’ general welfare, as well as their specific ability to develop songs previously memorized. At the same time, we recognize that interactions during sensorimotor learning could potentially bias birds’ vocal phenotype, especially the choice of song models crystallized (e.g., Nelson 1992; Liu & Nottebohm 2007; Templeton et al. 2010). One indication that birds housed in groups affect each other’s song output would be convergence on similar song types; however, in our study (see below), as in other studies on this species in which birds were housed in groups (Podos 1996; Podos et al. 1999), different sets of training models were copied by different birds, which suggests that social interactions during sensorimotor learning had minimal if any effects on the final song phenotype.

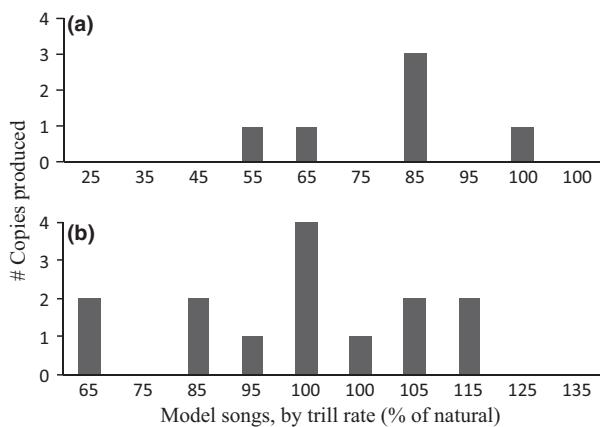


Fig. 1: Numbers of imitated song types produced by hand-reared swamp sparrows, binned according to which model songs they copied. Each numbered point on the x-axis represents a model song, which was experimentally modified from the natural (wild recorded) trill rate by the percent indicated. Note that two control songs (unmodified from the natural trill rate) were presented to each group of males. The y-axis indicates how many copies males rendered of each model song. Panel a is the slowed trill rate group, and panel b is the sped trill rate group.

Birds were recorded using Shure microphones and Marantz PMD-660 audio recorders, using a 44.1-kHz sample rate. Recordings were made until birds had crystallized their song-type repertoires, which was evident when the structure of notes and syllables in songs was consistent across successive days of recording. We scanned crystallized recordings to identify each bird’s repertoire of song copies. The three authors independently assigned models to specific copies, by visual inspection of note structure and sequences within syllables from spectrograms (as in Podos 1996; Podos et al. 1999). For each copy of a model song by a given bird, five renditions were chosen from the last day of recording for quantitative analysis. Parameter values from all calculations below were averaged to produce grand means for each song type. One bird in 2005–2006 and four birds in 2007–2008 learned no songs, although they did produce vocalizations, especially single repeated notes, not attributable to any model. In three cases in 2005–2006 and in one case in 2007–2008, birds that did learn songs also occasionally produced repetitions of notes that were not attributable to any model.

We assessed the accuracy of copies relative to their models, in three ways. First, we documented qualitatively the syntax and note composition of each copy. In particular, we documented note omissions (in which model notes were not replicated in copies) and deviations from simple trilled syntax (Podos et al. 1999). Second, we assessed the accuracy of note and syllable reproduction, using spectrogram cross-correlation analysis. This method assesses the similarity between model songs and their copies, in terms of frequency and amplitude structure over time. We performed this analysis at the level of individual notes (averaging the results of all notes within a syllable) as well as for each syllable as a whole, for each copy. Cross-correlation scores generally match subjective impressions of song similarity based on visual examination of spectrograms (Clark et al. 1987; Podos et al. 1999). Spectrogram cross-correlation calculations were performed without frequency shifting, on spectrograms constructed with 256-point fast Fourier transformations and 150 time steps, within a frequency range of 1–9 kHz (Engineering Design 2003). Third, we calculated trill rates of song copies, as assessed across the eight central syllables of each song (or fewer if eight were not available). We then compared the average trill rate of each copy to that of its model and represented this value as a percentage. From the original 20 song copies, we excluded one from analysis that had

'broken' (non-continuous) song syntax. We excluded three additional copies from the trill rate analysis, for which trill rates were not consistent across any given song (and thus for which a meaningful trill rate value could not be obtained).

We tested for an interaction between our experimental manipulations and changes in frequency bandwidth. Although copied songs tended to have a more restricted frequency bandwidth than their models ($t = -2.6$, $df = 19$, $p = 0.017$), this effect was found here to be unrelated to other measures of copy fidelity, to the degree to which the model trill rate was manipulated, and to copy trill rate ($p > 0.1$ in all cases). Thus, we restrict further analysis and discussion to trill rate as an indicator of performance in this study, while recognizing that song performance can be described by additional song features as well.

We quantified how model trill rate manipulations may have shaped copy accuracy in terms of (1) note structure, (2) syllable structure, and (3) trill rates, using three regression analyses (SYSTAT 10; SPSS, Chicago, IL, USA). Non-significant regression models would indicate that our manipulation of model trill rates did not influence the accuracy of song model reproduction, whereas models with statistical significance would identify systematic biases in song reproduction expressed during vocal learning.

Results

Overall Patterns of Learning

Study subjects produced 20 copies of song models (e.g., Fig. 2). Our attributions of copies to models

were corroborated in all cases by spectrogram cross-correlation analysis: mean spectral similarity among notes was 0.74 (± 0.08) between copies and their models, as compared with 0.31 (± 0.04) between copies and other training songs. When a given model was copied by more than one bird, the separate copies did not differ in any measure of similarity to the model ($p > 0.1$ in all four cases). Ten of 20 copies omitted a single model note, and an additional copy omitted two model notes. These notes were nearly always of comparatively short duration; a tendency for birds to fail to reproduce short model notes has been observed in prior learning studies on this species (Podos 1996; Podos et al. 1999). The syntax of copies was altered relative to the model in three instances. Two copies (one of a model song slowed to 85% of its natural trill rate, and another of a control model at the natural rate) were reproduced as two-part songs, in which one half of the song was a recognizable copy of a model song and the other half consisted of repeated notes that were not recognizable copies. One copy, of a model sped to 115% of its natural trill rate, was reproduced with broken syntax, such that syllables were not reproduced at a constant rate but very rapidly with periodic pauses (as in Podos et al. 1999).

Model Song Choice

Birds did not copy any of the three models that were slowed most severely, at 45% of their original trill rates or less. No further biases were evident in terms of song model selection (Fig. 1).

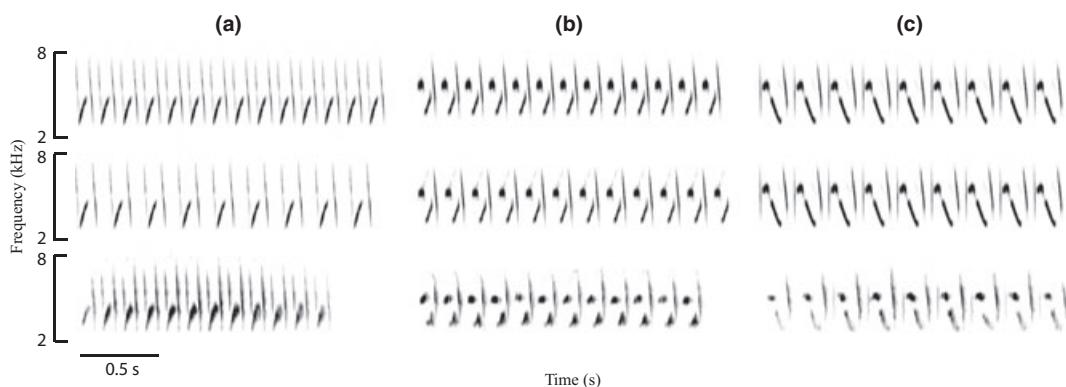
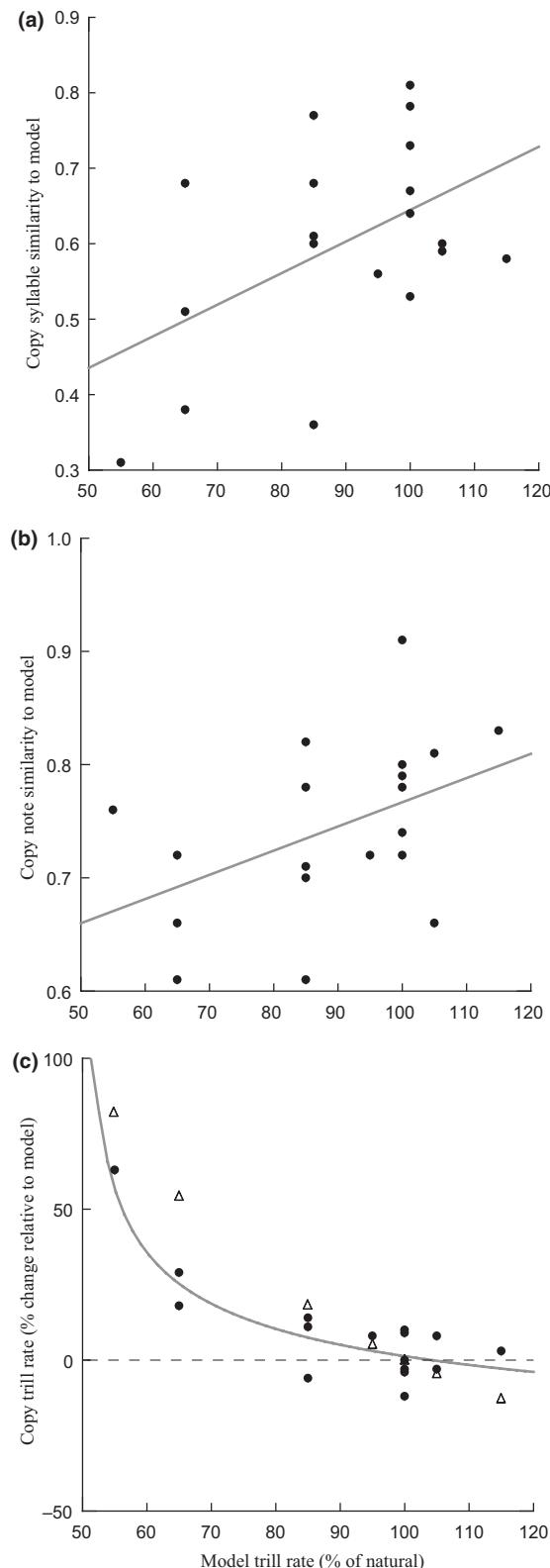


Fig. 2: Representative songs at natural (wild recorded) trill rates (top row), those same songs with experimentally modified trill rates as presented to juvenile swamp sparrows in the laboratory (middle row), and copies of those songs produced by the tutored birds (bottom row). The model songs in columns a and b were slowed to 65% and 85% of the trill rate of the natural songs, respectively. Birds increased the trill rates of these copies nearly to the rates of the natural songs from which the models were derived. Column c depicts a control, where the model song was presented at the natural trill rate, which was also matched by the copy.



Copy Accuracy

The accuracy of song copies varied with our modification of the trill rate of the model songs, in both magnitude and direction. The higher the trill rates of manipulated models relative to their natural (wild recorded) trill rates, the greater was the accuracy of their copies, in both syllable and note structure (regression; syllables: $F = 5.59$, $R^2 = 0.25$, $N = 19$, $p = 0.03$, Fig. 3a; notes: $F = 4.46$, $R^2 = 0.21$, $N = 19$, $p = 0.05$, Fig. 3b).

We also detected significant effects of our manipulation on the accuracy of trill rate reproduction (Fig. 3c). When models were at or above natural (wild recorded) trill rates, trill rates of copied songs were similar to those of model songs. By contrast, copies of slowed models were reproduced with above-model trill rates. Moreover, the greater the degree to which models were experimentally slowed, the greater the increase in copy trill rate relative to the model ($F = 21.8$, $R^2 = 0.61$, $N = 16$, $p = 0.0004$; Fig. 3c). The pattern of residuals indicated a non-linear relationship (see Fig. 3c for the best-fit exponential curve). This model retained significance ($F = 9.90$, $R^2 = 0.43$, $N = 15$, $p = 0.008$) and nonlinearity when the single copy of the 55% model was excluded. A regression model based only on copies

Fig. 3: Accuracy of syllable, note, and trill rate copying of experimental model songs by hand-reared swamp sparrows. Each filled circle represents a song type that was a clearly recognizable copy of a particular model song. Structural similarity of copied syllables (a) and notes (b) to their models is represented by spectrogram cross-correlation scores (y-axis) as a function of the degree to which model trill rates had been experimentally altered from natural (wild recorded) trill rates (x-axis). Learned songs were of higher accuracy in both syllable and note structure when copied from models at or above natural trill rates, as compared to copies of models with slowed trill rates. Each solid line is the best-fit line to the copies. Panel c represents the degree to which copies differed in trill rate from their models (y-axis) as a function of the degree to which model trill rates had been experimentally altered from natural (wild recorded) trill rates (x-axis). The dashed line represents the copy trill rate that would have matched that of the model (perfect imitation). Open triangles indicate the copy trill rates that would have matched the natural (wild recorded) trill rates of the models. The solid line is the best-fit exponential curve to the copies. Birds copying experimentally slowed models tended to increase trill rate relative to the models proportionally, though not to the rate of natural songs. Copies of models at or above natural trill rates had similar trill rates to their models, copies of sped models even exceeding the trill rate of natural songs.

of slow models was also significant and nonlinear ($F = 10.3$, $R^2 = 0.67$, $N = 7$, $p = 0.02$).

While copies of slowed models were produced with elevated trill rates, they did not recover completely the trill rates of the natural songs from which training models had been derived. Similarly, birds did not slow copies of sped models down to original trill rates. These patterns are evident in the offset between copy and natural trill rates (filled circles vs. triangles in Fig. 3c). A multiple linear regression model considering both natural and model trill rates and their interaction explains virtually all of the variation in copy trill rates ($F = 259$, $R^2 = 0.98$, $N = 16$, $p < 0.00001$).

Discussion

Three main results emerge from our study. First, the slowest song models were not copied at all by young swamp sparrows (Fig. 1). Second, slowed models were reproduced with reduced copying accuracy, relative to the accuracy of copies of control and rapid models (Fig. 3a, b). Third, slowed models were reproduced with elevated trill rates, approaching those of the natural songs from which models were derived (Fig. 3c). These latter two effects varied quantitatively: the greater our model trill rate reduction, the more pronounced the impact on copy accuracy.

Our observation that birds did not copy the most extremely slowed models may indicate that these songs are so unlike typical swamp sparrow songs that males do not consider them as targets for learning. For any song feature, such as trill rate, we expect there to be a range of values, equal to or greater than the range of values in nature, beyond which a song is not recognized as a conspecific signal, whether during learning or actual communication. In swamp sparrows, trill rate reductions by 45% or more seem to move swamp sparrow models into this category with respect to learning. Heterospecific songs are likewise ignored by young swamp sparrows in laboratory tests (Marler & Peters 1977).

The poorer copying of slowed models suggests that within the range of our experimental training songs, mechanisms of song acquisition and memorization favor the accurate imitation of faster (higher performance) songs. If there were no such biases, we would have expected to see slowed model notes and syllables reproduced with normal or even greater copy accuracy. This is because the greater temporal spacing between notes and syllables in the slowed models should have given birds improved opportuni-

ties to perceive and memorize those elements accurately. Moreover, there are no *a priori* reasons to believe that notes or syllables within slowed models would be harder to reproduce from a motor standpoint, and in fact, males were observed singing songs more slowly than the crystallized version during early song development. It is unknown whether the bias observed here is perceptual or cognitive in nature, i.e., whether swamp sparrows are deficient in their ability to hear or to encode slow trill models.

The elevation of trill rates of slowed models supports the hypothesis that birds calibrate learned vocal output to match their individual performance capabilities (Podos et al. 2004, 2009). The calibration hypothesis predicts that copies will differ from models in certain cases because of performance differences between learners and models. Prior work in swamp sparrows showed calibration in response to song models with elevated trill rates: in the face of motor constraints, birds adjusted song structure to more attainable levels, e.g., by reducing trill rates (Podos et al. 2004). The present study, by contrast, shows that birds can also calibrate their songs so as to improve the performance of their songs relative to models, e.g., by increasing trill rates. However, this increase in performance can be achieved only at the expense of imitative accuracy.

Taken together, our results reveal that vocal ontogeny can be shaped not only by the well-established premium on imitative accuracy, but also by a premium on high performance. Again, performance in this case refers to the trill rate of songs, all other features being equal, and high performance being that of typical songs recorded from the field as compared with our experimentally slowed versions. Our experimental regime allowed us to separate the influences of imitative accuracy vs. high performance on song learning and demonstrated that they act concurrently. The combined influence of these two factors should manifest as a tradeoff in the wild. Young birds hearing songs of varying levels of performance might copy higher-performance models with greater accuracy (Fig. 3a, b). Moreover, birds learning songs from tutors of inferior quality might not merely mimic tutor songs faithfully, but instead enhance song parameters related to performance (Fig. 3c).

We can interpret these developmental patterns as mechanisms by which birds respond to sexual selection favoring vocal performance. Sexual selection, which is thought to be central in shaping bird song structure (Searcy & Yasukawa 1996; Collins 2004),

operates on genetic variation. However, for birds that learn their songs, population-level changes in song are often attributable to cultural rather than genetic evolution (Payne 1996). This raises the question of how structural features of song can respond to sexual selection. The learning biases documented here in swamp sparrows suggest two specific mechanisms toward this end. Both of these are consistent with a history of sexual selection for faster trill rates, given that female swamp sparrows prefer them (Ballentine et al. 2004). First, our data imply that selection has favored birds with an inherited tendency to attend to model songs with faster trill rates, such that birds copy these songs with greater accuracy. Second, our data imply that selection has favored birds that balance two objectives during song development: reproduction of memorized models with maximum accuracy and production of trill rates that maximize birds' vocal capabilities. A premium on accurate imitation ensures that individuals will develop songs with parameters that females and other males will consider conspecific and local (Baker et al. 1981; Searcy et al. 2002). A bias toward increasing the performance level of songs would enable birds to indicate their performance capacities; otherwise, the quality of a tutor's song would set a ceiling on the performance level a learner could attain.

In light of past work, our data also provide a possible explanation for why swamp sparrows sing at the trill rates that they do. Performance constraints prevent trill rates from increasing beyond certain upper limits (Podos 1996; Podos et al. 1999), whereas the learning biases demonstrated here should prevent trill rates from decreasing below certain lower limits. The latter effect derives from birds' tendencies to increase trill rates of slowed models and to copy note and syllable structure of faster songs with greater accuracy. The concurrent operation of both sets of influences should lead trill rates to be fairly circumscribed and stable across generations. Over longer time frames, the evolution of morphological components of the vocal apparatus, of female choice and male competition, and of learning mechanisms such as those shown here, should yield the range of trill rates expressed by populations in nature.

Acknowledgements

We thank Steve L. Johnson for essential help in the field; Stephanie Wallace, Cosmo Laviola, Ana Gabela, Christine Rega, Chrissy Breed, Merry Bixby, Nicole Dewberry, Greg LeBoeuf, Princess Gilbert,

and several undergraduate assistants for field and laboratory assistance and bird care. We thank the staff at the Podos laboratory for helpful discussion, and two anonymous reviewers for their insightful comments. This project was supported by the OEB Darwin Fellows Program at the University of Massachusetts, National Institutes of Health NRSA fellowship 5F32DC7539 to DCL, and National Science Foundation grant IOB-0347291 to JP.

Literature Cited

- Baker, M. C., Spitler-Nabors, K. J. & Bradley, D. C. 1981: Early experience determines song dialect responsiveness of female sparrows. *Science* **214**, 819–821.
- Ballentine, B., Hyman, J. & Nowicki, S. 2004: Vocal performance influences female response to male bird song: an experimental test. *Behav. Ecol.* **15**, 163–168.
- Brainard, M. S. & Doupe, A. J. 2002: What songbirds teach us about learning. *Nature* **417**, 351–358.
- Burkart, J. M., Strasser, A. & Foglia, M. 2009: Tradeoffs between social learning and individual innovativeness in common marmosets, *Callithrix jacchus*. *Anim. Behav.* **77**, 1291–1301.
- Byers, J., Hebert, E. & Podos, J. 2010: Female mate choice based upon male motor performance. *Anim. Behav.* **79**, 771–778.
- Caro, S. P., Sewall, K. B., Salvante, K. G. & Sockman, K. W. 2010: Female Lincoln's sparrows modulate their behavior in response to variation in male song quality. *Behav. Ecol.* **21**, 562–569.
- Claudière, N. & Sperber, D. 2010: Imitation explains the propagation, not the stability of animal culture. *Proc. Biol. Sci.* **277**, 651–659.
- Clark, C. J. 2009: Courtship dives of Anna's hummingbird offer insights into flight performance limits. *Proc. Biol. Sci.* **276**, 3047–3052.
- Clark, C. W., Marler, P. & Beaman, K. 1987: Quantitative analysis of animal vocal phonology: an application to swamp sparrow song. *Ethology* **76**, 101–115.
- Collins, S. 2004: Vocal fighting and flirting: the functions of birdsong. In: *Nature's Music: The Science of Bird Song* (Marler, P. & Slabbekoorn, H., eds). Elsevier, San Diego, CA, pp. 39–79.
- Dediu, D. & Ladd, D. R. 2007: Linguistic tone is related to the population frequency of the adaptive haplogroups of two brain size genes, *ASPM* and *Microcephalin*. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 10944–10949.
- Dooling, R. & Searcy, M. 1980: Early perceptual selectivity in the swamp sparrow. *Dev. Psychobiol.* **13**, 499–506.
- Drăgănoiu, T. I., Nagle, L. & Kreutzer, M. 2002: Directional female preference for an exaggerated male trait

- in canary (*Serinus canaria*) song. Proc. Biol. Sci. **269**, 2525–2531.
- DuBois, A. L., Nowicki, S. & Searcy, W. A. 2011: Discrimination of vocal performance by male swamp sparrows. Behav. Ecol. Sociobiol. **65**, 717–726.
- Henrich, J. & Boyd, R. 1998: The evolution of conformist transmission and the emergence of between-group differences. Evol. Hum. Behav. **19**, 215–241.
- Hoese, W. J., Podos, J., Boetticher, N. C. & Nowicki, S. 2000: Vocal tract function in birdsong production: experimental manipulation of beak movements. J. Exp. Biol. **203**, 1845–1855.
- Kendal, R. L., Coolen, I., van Bergen, Y. & Laland, K. N. 2005: Tradeoffs in the adaptive use of social and asocial learning. Adv. Study Behav. **35**, 333–379.
- Kuhl, P. K. & Meltzoff, A. N. 1996: Infant vocalizations in response to speech: vocal imitation and developmental change. J. Acoust. Soc. Am. **100**, 2425–2438.
- Lindeyer, C. M. & Reader, S. M. 2010: Social learning of escape routes in zebrafish and the stability of behavioural traditions. Anim. Behav. **79**, 827–834.
- Liu, W. C. & Nottebohm, F. 2007: A learning program that ensures prompt and versatile vocal imitation. Proc. Natl. Acad. Sci. U.S.A. **104**, 20398–20403.
- Liu, I. A., Lohr, B., Olsen, B. & Greenberg, R. 2008: Macrogeographic vocal variation in subspecies of swamp sparrow. Condor **110**, 102–109.
- Marler, P. 1981: Birdsong: the acquisition of a learned motor skill. Trends Neurosci. **4**, 88–94.
- Marler, P. 1984: Song learning: innate species differences in the learning process. In: The Biology of Learning (Marler, P. & Terrace, H. S., eds). Springer-Verlag, Berlin, pp. 289–309.
- Marler, P. & Peters, S. 1977: Selective vocal learning in a sparrow. Science **198**, 519–521.
- Marler, P. & Peters, S. 1982: Structural changes in song ontogeny in the swamp sparrow *Melospiza georgiana*. Auk **99**, 446–458.
- Marler, P. & Peters, S. 1988: Sensitive periods for song acquisition from tape recordings and live tutors in the swamp sparrow, *Melospiza georgiana*. Ethology **77**, 76–84.
- Marler, P. & Pickert, R. 1984: Species-universal microstructure in the learned song of the swamp sparrow, *Melospiza georgiana*. Anim. Behav. **32**, 673–689.
- Marler, P. & Sherman, V. 1985: Innate differences in singing behaviour of sparrows reared in isolation from adult conspecific song. Anim. Behav. **33**, 57–71.
- Nelson, D. A. 1992: Song overproduction and selective attrition lead to song sharing in the field sparrow (*Spizella pusilla*). Behav. Ecol. Sociobiol. **30**, 415–424.
- Nowicki, S. & Searcy, W. A. 2005: Song and mate choice in birds: how the development of behavior helps us to understand function. Auk **122**, 1–14.
- Pagel, M. 2009: Human language as a culturally transmitted replicator. Nat. Rev. Gen. **10**, 405–415.
- Patricelli, G. L., Uy, J. A. C. & Borgia, G. 2003: Multiple male traits interact: attractive bower decorations facilitate attractive behavioural displays in satin bowerbirds. Proc. Biol. Sci. **270**, 2389–2395.
- Payne, R. B. 1996: Song traditions in indigo buntings: origin, improvisation, dispersal, and extinction in cultural evolution. In: Ecology and Evolution of Acoustic Communication in Birds (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, NY, pp. 198–220.
- Podos, J. 1996: Motor constraints on vocal development in a songbird. Anim. Behav. **51**, 1061–1070.
- Podos, J. 1997: A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). Evolution **51**, 537–551.
- Podos, J., Nowicki, S. & Peters, S. 1999: Permissiveness in the learning and development of song syntax in swamp sparrows. Anim. Behav. **58**, 93–103.
- Podos, J., Peters, S. & Nowicki, S. 2004: Calibration of song learning targets during vocal ontogeny in swamp sparrows, *Melospiza georgiana*. Anim. Behav. **68**, 929–940.
- Podos, J., Lahti, D. C. & Moseley, D. L. 2009: Vocal performance and sensorimotor learning in songbirds. Adv. Study Behav. **40**, 159–195.
- Riede, T., Suthers, R. A., Fletcher, N. H. & Blevins, W. E. 2006: Songbirds tune their vocal tract to the fundamental frequency of their song. Proc. Natl. Acad. Sci. U.S.A. **103**, 5543–5548.
- Sanz, C., Call, J. & Morgan, D. 2009: Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). Biol. Lett. **5**, 293–296.
- Searcy, W. A. & Yasukawa, K. 1996: Song and female choice. In: Ecology and Evolution of Acoustic Communication in Birds (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, pp. 454–473.
- Searcy, W. A., Nowicki, S., Hughes, M. & Peters, S. 2002: Geographic song discrimination in relation to dispersal distances in song sparrows. Am. Nat. **159**, 221–230.
- Slater, P. J. B. 1989: Bird song learning: causes and consequences. Ethol. Ecol. Evol. **1**, 19–46.
- Soha, J. A. & Marler, P. 2000: A species-specific acoustic cue for selective song learning in the white-crowned sparrow. Anim. Behav. **60**, 297–306.
- Suthers, R. A. 2004: How birds sing and why it matters. In: Nature's Music: The Science of Birdsong (Marler, P. & Slabbeekoor, H., eds). Elsevier Academic Press, San Diego, CA, pp. 272–295.
- Templeton, C. N., Akcay, C., Campbell, S. E. & Beecher, M. D. 2010: Juvenile sparrows preferentially eavesdrop on adult song interactions. Proc. Biol. Sci. **277**, 447–453.

- Vallet, E. & Kreutzer, M. 1995: Female canaries are sexually responsive to special song phrases. *Anim. Behav.* **49**, 1603—1610.
- Whiten, A. 1992: On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Adv. Study Behav.* **21**, 239—283.
- Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C. & Kacelnik, A. 2009: Cognitive processes associated with sequential tool use in New Caledonian crows. *PLoS ONE* **4**, 8.
- Zentall, T. R. 2006: Imitation: definitions, evidence, and mechanisms. *Anim. Cogn.* **9**, 335—353.