

Male response to historical and geographical variation in bird song

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In many species, individuals discriminate among sexual signals of conspecific populations in the contexts of mate choice and male–male competition. Differences in signals among populations (geographical variation) are in part the result of signal evolution within populations (temporal variation). Understanding the relative effect of temporal and geographical signal variation on signal salience may therefore provide insight into the evolution of behavioural discrimination. However, no study, to my knowledge, has compared behavioural response to historical signals with response to current signal variation among populations. Here, I measured the response of male white-crowned sparrows (*Zonotrichia leucophrys*) to historical songs compared with current songs from their local population, a nearby non-local population and a distant population. Males responded most strongly to current local songs, less, but equally, to historical local and current non-local songs, and least to songs of the distant population. Moreover, response to both temporal and geographical variation in song was proportional to how much songs differed acoustically from current local songs. Signal evolution on an ecological time scale appears to have an effect on signal salience comparable to differences found between current neighbouring populations, supporting the idea that behavioural discrimination among learned signals of conspecific populations can evolve relatively rapidly.

Keywords: behavioural discrimination; historical signals; geographical variation; birdsong; signal evolution; white-crowned sparrow

1. INTRODUCTION

Sexual signals, such as bird song, often exhibit considerable variation among conspecific populations. Signal divergence between populations can lead to a reduction in signal recognition, and many studies suggest that individuals discriminate among signals from conspecific populations, preferring the signal of their local population [1]. As these signals are used in important functional contexts, such as mate-choice and male–male competition, a reduction in signal recognition can promote the evolution of behavioural isolation [2]. Despite the widespread occurrence of behavioural discrimination among conspecific signals,

relatively little is known about the tempo and mode of this process. At least one study suggests that signal evolution on an ecological time scale can affect signal recognition [3]; however, the question remains whether the effect of temporal variation on signal salience is comparable to the differences found between current neighbouring populations.

To address this question in the context of male–male competition, I examine behavioural responses to temporal and geographical song variation in white-crowned sparrows (*Zonotrichia leucophrys*). In this species, males learn their song and typically sing one song type. Most males within a population sing the same song type, whereas songs from different populations vary in note type and order (song syntax) [4]. Males respond most to their local song and less to songs that vary in syntax (e.g. [5]). Over more than three decades, syntax has been relatively stable in many populations but songs have changed in acoustic features, such as tempo and frequency, which are subject to habitat-dependent selection [6,7].

I describe temporal and geographical song variation for a set of populations. I then measure the response of males to historical songs compared with current songs from their local population, a nearby non-local population and a distant population of a different subspecies. As response to unfamiliar signals may be affected by how individuals generalize knowledge about the signals with which they are familiar [8], I also explore whether variation in response to both temporal and geographical variation in song can be explained by acoustic dissimilarity between unfamiliar songs (e.g. playback songs) and familiar songs (e.g. the current songs of the local population).

2. MATERIAL AND METHODS

Songs of 106 males were used to analyse acoustic variation. These included 64 males from Tioga Pass, CA (local population) at four time points: 7 in 1970, 23 in 1979, 19 in 1996, and 15 in 2003; 32 males from Sonora Pass, CA (neighbouring population, approx. 50 km from Tioga) at three time points: 7 in 1970, 15 in 1996 and 10 in 2005; and 10 males from Manzanita, OR (distant population, approx. 600 km from Tioga) in 2005 (see the electronic supplementary material, figure S1).

Recordings in 1970 and 1978 were made using Uher 4000 S Report recorders and parabolic reflectors [9]. Recordings in 1996, 2003 and 2005 were made using Sony TCM-5000EV cassette recorders with directional microphones [6,7]. Historical and current recordings were similar in sound quality [3]. All songs were digitized with 16-bit precision at a 25 kHz sampling rate.

For each song, I measured 13 parameters, including the duration (ms) and dominant, maximum and minimum frequencies (Hz) of the whole song and of each major section of the song (whistle, complex note and trill; see the electronic supplementary material, figure S2) from digital spectrograms (256 pt transform, frequency resolution = 97.7 Hz) using SIGNAL v. 3.1 [10]. Variables were transformed to *z*-scores and reduced using a principal component analysis.

Over four successive weeks during the 2005 breeding season (pre-incubation to pre-fledging), the response of free-living, paired adult males in Tioga Pass, CA was measured using territorial playbacks, a standard experimental design that quantifies male response to simulated intrusion on their territories [11]. Songs were played at a natural rate of six songs per minute from a speaker in the centre of the focal male's territory. The focal male's distance from the speaker was recorded at 10 s intervals during a 3 min playback period and a 9 min post-playback period (see [3]). Average distance from the speaker was the sole response measure, and males who approached the speaker more closely were considered to have a stronger response to the stimulus [12].

I contrasted (Experiment 1) historical (1978) and current Tioga songs in two trials, (Experiment 2) historical Tioga and current Sonora songs and (Experiment 3) historical Tioga and current

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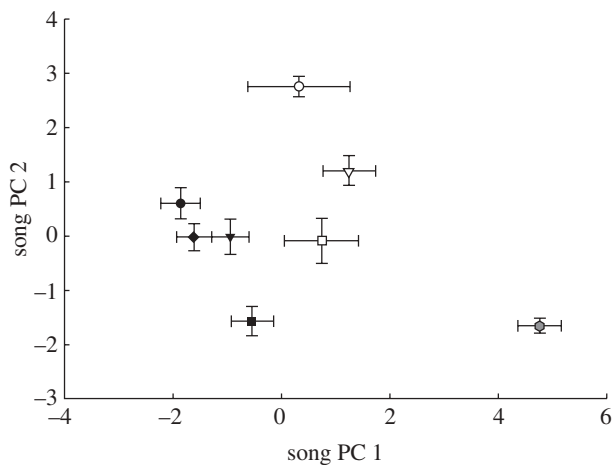


Figure 1. Plot of the first two principal components (PCs) of acoustic variation in historical and current songs from three populations. Error bars represent standard errors. Representative sonograms of each population at each time point can be found in the electronic supplementary material, figure S1 (filled circle, 1970 Tioga; filled diamond, 1978 Tioga; filled inverted triangle, 1996 Tioga; filled square, 2003 Tioga; open circle, 1970 Sonora; open inverted triangle, 1996 Sonora; open square, 2005 Sonora; filled hexagon, 2005 Manzanita).

Manzanita songs. I used a balanced, pairwise design with 10 exemplars for each song category and 10 males tested in each trial (20 total in Experiment 1). Response to exemplars was averaged across trials in Experiment 1 to avoid pseudoreplication. Owing to limited historical exemplars and testable males, the same 10 historical song exemplars were used in each experiment, and some males were tested in multiple experiments. Experiments were analysed (i) separately using Wilcoxon matched-pairs signed-ranks tests and (ii) as a group using a standard least-squares model with response distance as the dependent variable, song category as the independent variable and male tested as a random effect. To avoid pseudoreplication of response to historical and current songs in the group analysis, 10 responses to each were chosen randomly. Power analyses of non-significant results were conducted at an alpha of 0.05; power was adjusted for non-parametric tests by 95 per cent. Results from Experiment 1 have been published but are included here to allow a more complete analysis of response to song [3].

I used linear regression to determine whether variation in male response was explained by acoustic dissimilarity between unfamiliar and familiar songs. Acoustic dissimilarity was measured as the average Euclidean distance between playback songs and each current local song based on the 13 acoustic parameters. I averaged male response to historical exemplars, as songs and not test subjects were the unit of comparison. To meet model assumptions, I transformed data using the Box-Cox method in the R package [13].

3. RESULTS

Measurements of the 13 acoustic variables can be found in the electronic supplementary material, table S1. Principal component analysis reduced song variation from 13 variables to four axes (see the electronic supplementary material, table S2). A plot of the first two principal components revealed that the Tioga Pass (local) song and the Sonora Pass (non-local) song have undergone similar acoustic changes over time but have remained distinct (figure 1), such that historical (1978) Tioga and current Sonora are approximately equidistant from current local songs in Tioga.

Male approach distance to playback of historical Tioga (H) and current Sonora (S) songs did not differ significantly (H (mean distance (m) \pm s.e.m.):

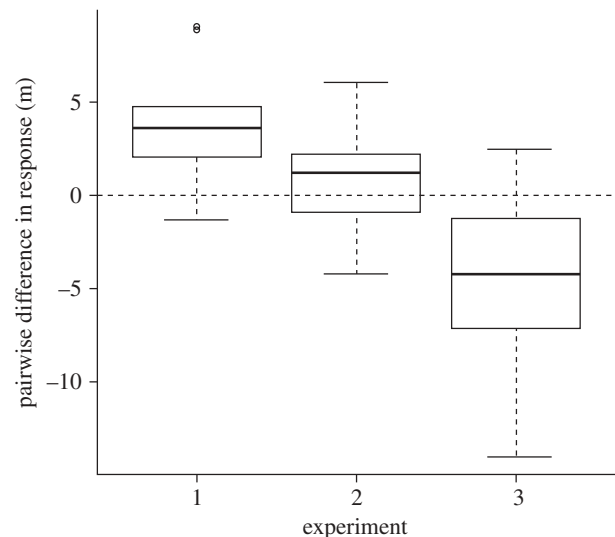


Figure 2. Results of male playback experiments presented as boxplots. Experiments compared response to historical local songs with response to: current local songs (Experiment 1), current songs of a neighbouring population (Experiment 2) and current songs of a distant population (Experiment 3). Results are presented as pairwise differences in response, such that values above the dotted line demonstrate a weaker response to historical local songs.

5.8 ± 1.4 ; S : 5.7 ± 1.1 ; $n = 8$, $Z = 0.05$, $p < 0.96$, power = 0.91; figure 2). By contrast, males approached historical Tioga songs significantly more closely than songs from the distant population of Manzanita (M) (H : 5.6 ± 1.0 ; M : 10.4 ± 1.7 ; $n = 8$, $Z = 2.4$, $p < 0.018$) but less closely than current Tioga songs (C) (H : 10.5 ± 0.8 ; C : 6.8 ± 0.7 ; $n = 10$, $Z = 2.61$, $p < 0.009$) [3]. Using Kruskal-Wallis tests, I found no significant differences in response across historical Tioga exemplars ($n = 36$, d.f. = 9, $H = 10.4$, $p = 0.32$, power = 0.29) or across males tested ($n = 72$, d.f. = 20, $H = 29$, $p = 0.10$, power = 0.98), but there was significant variation in overall strength of response across trials ($n = 72$, d.f. = 3, $H = 7.9$, $p = 0.048$; Experiment 1: Trial 1: 10.4 ± 1.2 , Trial 2: 7.0 ± 0.8 ; Experiment 2: 5.8 ± 0.8 ; Experiment 3: 8.0 ± 1.1).

When experiments were analysed as a group, song category explained significant variation in male response ($n = 36$, $r^2 = 0.81$, $F_{17,18} = 4.53$, $p = 0.0013$; song category: $p < 0.0001$; male (random effect): $p < 0.005$). Males responded most strongly to current Tioga, equally strongly to historical Tioga and current Sonora, and least strongly to Manzanita (post hoc Tukey HSD: $C = 3.4 \pm 0.9$ (least squares mean \pm s.e.m.), $H = 6.8 \pm 0.8$, $S = 8.1 \pm 1.1$, $M = 12.8 \pm 1.1$, $\alpha = 0.05$).

There was a significant correlation between response to playback songs and the distance of each playback song from current variation in local songs ($n = 36$, $r^2 = 0.17$, $p < 0.01$; electronic supplementary material, figure S3). Response distance was power transformed, with values raised to the power of 0.6.

4. DISCUSSION

Comparing results from the three experiments suggests that male white-crowned sparrows respond most

strongly to current local songs, less, but equally, to historical local and current non-local songs, and least to the songs of a distant population. This finding provides the first sense of how changes over time within populations map onto differences among populations in sexual signals and in recognition of those signals. At least in white-crowned sparrows, changes in signals on an ecological time scale are as salient as differences in signals between neighbouring populations but not as salient as differences between distant populations. Because historical songs appear as effective as neighbouring non-local songs, the magnitude of behavioural discrimination found between neighbouring populations could arise in as short a time period as 12–24 generations (assuming a generation time of 1–2 years).

This study also provided some insight into the potential mechanism underlying response to both temporal and geographical variation in song. Males appear to respond to songs based on how different these songs are from their current experience of local variation in songs. For example, historical (1978) Tioga and current Sonora songs are equidistant from current Tioga songs and Tioga males gave a similar level of response to these songs. Thus, response to unfamiliar signals may be explained by how males are generalizing their knowledge of familiar signals. Males appear to generalize in part based on frequency and tempo differences from current variation in song. Both frequency and duration characteristics appear to change over time in relation to changes in habitat structure in this species [6]. If songs within each population are under selection pressure to adapt to the local environment, then the magnitude of behavioural discrimination between populations could be associated in part with the degree to which populations have experienced different environments over time.

Similar new insights into the evolution of behavioural discrimination might be made in other species by comparing response to temporal and geographical variation in sexual signals. Changes over time in acoustic sexual signals have been documented in many different taxa (e.g. [14,15,16]), making comparisons between temporal and geographical variation possible for a wide diversity of species. Such studies may begin to reveal whether signals evolve along different trajectories under historical versus geographical processes and how these evolutionary trajectories might affect signal recognition. One important question is how the effects of temporal processes on signal evolution and recognition influence the relative strength of behavioural isolation between populations over time. Replicates across species will provide further insight into the effects of signal variation on signal salience, and ultimately the evolution of behavioural discrimination among conspecific populations.

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- Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
- Coyne, J. A. & Orr, H. A. 2004 *Speciation*. Sunderland, MA: Sinauer Associates.
- Derryberry, E. P. 2007 Evolution of bird song affects signal efficacy: an experimental test using historical and current signals. *Evolution* **61**, 1938–1945. (doi:10.1111/j.1558-5646.2007.00154.x)
- Marler, P. & Tamura, M. 1964 Culturally transmitted patterns of vocal behavior in sparrows. *Science* **146**, 1483–1486. (doi:10.1126/science.146.3650.1483)
- Nelson, D. A. & Soha, J. A. 2004 Perception of geographical variation in song by male Puget Sound white-crowned sparrows, *Zonotrichia leucophrys pugetensis*. *Anim. Behav.* **68**, 395–405. (doi:10.1016/j.anbehav.2003.08.027)
- Derryberry, E. P. 2009 Ecology shapes birdsong evolution: variation in habitat and morphology explains variation in white-crowned sparrow song. *Am. Nat.* **174**, 24–33. (doi:10.1086/599298)
- Harbison, H., Nelson, D. A. & Hahn, T. P. 1999 Long-term persistence of song dialects in the mountain white-crowned sparrow. *Condor* **101**, 133–148. (doi:10.2307/1370454)
- Shepard, R. N. 1987 Toward a universal law of generalization for psychological science. *Science* **237**, 1317–1323. (doi:10.1126/science.3629243)
- Baptista, L. F. & King, J. R. 1980 Geographical variation in song and song dialects of Montane white-crowned sparrows. *Condor* **82**, 267–284. (doi:10.2307/1367392)
- Beeman, K. 1999 *SIGNAL*. Belmont, MA: Engineering Design.
- McGregor, P. K. *et al.* 1992 Design of playback experiments: the Thornbridge Hall NATO ARW consensus. In *Playback and Studies of Animal Communication* (ed. P. K. McGregor), pp. 1–9. New York, NY: Plenum Press.
- Searcy, W. A., Anderson, R. C. & Nowicki, S. 2006 Bird song as a signal of aggressive intent. *Behav. Ecol. Sociobiol.* **60**, 234–241. (doi:10.1007/s00265-006-0161-9)
- R Development Core Team 2008 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org>.
- Cerchio, S., Jacobsen, J. K. & Norris, T. F. 2001 Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Anim. Behav.* **62**, 313–329. (doi:10.1006/anbe.2001.1747)
- Goodale, E. & Podos, J. In press. Persistence of song types in Darwin's finches, *Geospiza fortis*, over four decades. *Biol. Lett.* (doi:10.1098/rsbl.2010.0165)
- Zuk, M., Rotenberry, J. T. & Tinghitella, R. M. 2006 Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biol. Lett.* **2**, 521–524. (doi:10.1098/rsbl.2006.0539)