

Ecological gradient of sexual selection: elevation and song elaboration in finches

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Abstract Ecological gradients in natural and sexual selection often result in evolutionary diversification of morphological, life history, and behavioral traits. In particular, elevational changes in habitat structure and climate not only covary with intensity of sexual selection in many taxa, but may also influence evolution of mating signals. Here we examined variation in courtship song in relation to elevation of breeding across cardueline finches—a subfamily of birds that occupies the widest elevational range of extant birds and shows extensive variation in life histories and sexual selection along this range. We predicted that decrease in sexual selection intensity with elevation of breeding documented in this clade would result in a corresponding evolutionary reduction in elaboration of courtship songs. We controlled for the effects of phylogeny, morphology, and habitat structure to uncover a predicted elevational decline in courtship song elaboration; species breeding at lower elevations sang more elaborated and louder songs compared to their sister species breeding at higher elevations. In addition, lower elevation species had longer songs

with more notes, whereas frequency components of song did not vary with elevation. We suggest that changes in sexual selection account for the observed patterns of song variation and discuss how elevational gradient in sexual selection may facilitate divergence in mating signals potentially reinforcing or promoting speciation.

Keywords Bird song · Sexual selection · Environmental gradient · Cardueline finches · Speciation

Introduction

Divergence in mating signals can play an important role in premating isolation and speciation (Darwin 1859; Mayr 1940; West-Eberhard 1983; Coyne and Orr 2004). Within an ecological context, the divergence of signals across environmental gradients may promote or reinforce local adaptation of morphological or physiological traits (review Schluter 2000; e.g., Haavie et al. 2004; Servedio 2004). First, environmental constraints on the development or propagation of signals often result in signal variation across populations (Ryan and Brenowitz 1985; Endler 1992; Grether et al. 1999; Irwin 2000; Patten et al. 2004; Patricelli and Blickley 2006). Second, variation in the intensity of sexual selection commonly leads to the divergence of mating signals (review Andersson and Simmons 2006; Badyaev and Snell-Rood 2006; Svensson et al. 2006). Whereas the correspondence between the degree of sexual selection intensity and interspecific divergence of mating signal is commonly documented (Chenoweth and Blows 2003; Snook et al. 2005; Møller et al. 2006), it remains unclear how variation in sexual selection intensity promotes signal divergence within an ecological context (Shuster and Wade 2003).

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Ecological gradients provide an opportunity to examine the contribution of selection pressures to variation in mating signals, morphology, and life history (Boyce 1979; Berven 1982; Grant and Dunham 1990; Mathies and Andrews 1995). For example, elevational changes in habitat structure and climate have strong effects on life histories and mating systems of animals, generating environmental gradients in sexual selection intensity (Zang 1980; Badyaev 1997a; Badyaev and Hill 2003). In birds breeding at higher elevations, colder climate, distinct nesting and foraging habitats, and shorter breeding seasons result in frequent and distant foraging trips during nesting, and the reproductive success of both males and females depends more on investment in care of within-pair young than on multiple extra-pair matings (Badyaev and Ghalambor 2001; rev. Magrath and Komdeur 2003). Consequently, the ecological conditions at high elevations favor greater monogamy, similar levels of parental care between males and females, and lesser variation in mating success between the sexes compared to species breeding at lower elevations (Howard and Wallace 1985; Badyaev 1997a). The resulting negative covariation between elevation of breeding and sexual selection intensity (Wynne-Edwards 1998; Badyaev and Ghalambor 2001) provides an opportunity to test the hypothesis that environmental variation in sexual selection intensity promotes divergence in sexual displays (Badyaev 1997a, b; Irwin 2000).

Bird songs are an ideal system in which to investigate how intraspecific processes of sexual selection result in interspecific divergence in song structure (Searcy and Andersson 1986; Read and Weary 1990; Slabbekoorn and Smith 2002; Rugg et al. 2006). First, numerous studies have considered the role of female preference in the elaboration and diversification of song characteristics (Andersson 1994; Podos et al. 2004; Nowicki and Searcy 2005), allowing a priori predictions of how song components should diverge with variation in sexual selection intensity. Females generally prefer songs that are difficult to produce or learn (Nowicki et al. 1998; Ward et al. 2003; Garamszegi et al. 2006), such as songs with rapid trill rate, greater energy output, rapid frequency modulation, and greater complexity (Ballentine et al. 2003; Draganoiu et al. 2002; Forstmeier et al. 2002; Nolan and Hill 2004; Reid et al. 2005). Second, a wide range of selection pressures on bird song have been documented, allowing a priori prediction of proper controls in comparative studies. For instance, body size (Morton 1975; Ryan and Brenowitz 1985; Badyaev and Leaf 1997) and habitat structure (Richards and Wiley 1980; Endler 1992) strongly influence production and propagation of songs.

Here we examine the relationship between elaboration of courtship song and elevation of breeding in cardueline finches—a group of 126 species with the widest elevational distribution of all extant avian subfamilies (Clement et al.

1993). We controlled for the effects of habitat structure, body size, and bill size to test the hypothesis that song elaboration varies with elevational changes in sexual selection intensity. We predicted that because species breeding at lower elevations are often subject to stronger sexual selection, they should have more elaborated courtship songs compared to related species at higher elevations. Based on within-species studies of female choice, we specifically predicted that elaborated songs would be those with long total length, more notes, shorter internote interval length, shorter notes, and wider frequency ranges. Because elevational variation in other environmental variables may contribute to interspecific variation in signals, we contrast our results with predictions of several alternative hypotheses. Because bill size (Bowman 1979; Podos et al. 2004) and ambient noise (Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006) also affect song characteristics, we tested whether variation in bill length or wind speed could produce a spurious correlation between elevation and song characteristics that was not caused by variation in sexual selection intensity.

Materials and methods

We collected data on the ecology, breeding elevation, morphology, and song characteristics of all extant species of cardueline finches (appendices in Badyaev 1997c; Badyaev et al. 2002). First, we collected qualitative data on the general song type of a species (references in appendix B, Badyaev 1997c). Song types were classified into three categories: (1) no known courtship or loud song, (2) quiet song in close proximity to a female, (3) loud courtship song (data were available on 64 species and subspecies, Online Appendix 1). Second, we measured seven song characteristics from spectrograms (minimum 15 individuals per species, see appendices in Badyaev et al. 2002): lowest and highest frequencies and mean range of frequencies across all notes, average note length, average length of internote interval, number of different notes, and total song length (data were available for 25 species, Online Appendix 2). Song measurements were averaged across all individuals, song types, and locations or recordings for each species. Song types of high and low sister species pairs are presented in Online Appendix 1. Online Appendix 2 contains data on song characteristics, maximum breeding elevation, habitat, body mass, and bill length. Based on the original habitat types, we categorized habitat type as: (1) open (e.g., steppe, meadows); (2) semi-open (e.g., hedges, subalpine bushes); and (3) closed (e.g., forests) (see appendices in Badyaev 1997c). Such habitat classifications are comparable to those used in previous studies (review Boncoraglio and Saino 2007) and allowed inclusion of species found in remote regions.

We used SAS (SAS Institute 1996) and JMP-IN 5.1 for all analyses. All song component variables were tested for normality with the Shapiro–Wilks' test and then log transformed to achieve normal distribution. The analyses were performed with the transformed data, although results were qualitatively identical when untransformed variables were used. In this dataset, bird species were evenly distributed across the elevational gradient (i.e., 30 species fell below and 33 species fell above the elevation midpoint, see Online Appendix 1). Variables were analyzed individually and then as composites using two principal component analyses (PCAs). One PCA included all three frequency characteristics (highest frequency, lowest frequency, and range of frequencies), and one PCA included all four temporal characteristics (average note length, average internote interval length, number of notes, and song length). The first PC from each PCA was used in subsequent analyses. We investigated effects of several independent variables including maximum elevation at which breeding occurs, habitat type, and male body mass.

In addition to body mass and habitat, several other morphological and ecological factors may vary with elevation and could produce correlations between elevation and song characteristics that are not caused by variation in sexual selection intensity. First, bill size can affect song components (Bowman 1979; Podos et al. 2004); thus, elevational variation in bill morphology would affect the relationship between breeding elevation and song characteristics. We examined this possibility and found that inclusion of bill length as a factor (see Online Appendix 3) did not change the results concerning temporal components of song (e.g., song length, number of notes, temporal elaboration). Further, bill size did not affect song characteristics of species in our dataset ($P > 0.10$). Thus, bill size was not included in the final analyses. Second, ambient noise can affect amplitude and frequency of bird song (Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006). Thus, elevational variation in ambient noise, such as wind speed, could confound the relationship between elevation and song characteristics. For a subset of the dataset, North American cardueline finches (20% of the dataset, see Online Appendix 2), we measured ambient noise associated with wind speed using a grayscale averaging function in Image J (NIH), as the average annual wind intensity over the geographical range of a species. In general linear models that included body size, elevation, and average wind speed, the relationship between elevation and song characteristics were qualitatively identical to those from analyses that did not control for wind speed.

To control for species relatedness within the subfamily, we analyzed data using both pairwise comparisons and independent linear contrasts. Our phylogenetic hypothesis

of subfamily of cardueline finches is published elsewhere (Badyaev 1997a, c) and is well supported by molecular studies of both the basal nodes (Marten and Johnson 1986) and within-clade divergence patterns (Arnaiz-Villena et al. 1998, 1999). First, we used pairwise comparisons, where pairs of closely related species based on our phylogenetic hypothesis were ranked by elevation of breeding and then compared with respect to a song type. The concordance with the directional prediction was then tested with a one-tailed sign test. Clades with more than two species with non-missing data were omitted from this analysis. This method provides the most direct test of concordance between elevation and life history traits, because it makes fewer assumptions about phylogenetic relations among clades in the subfamily, and is statistically more powerful than analysis of covariance on independent contrasts when phylogeny has unresolved nodes with multiple species (see Martin and Badyaev 1996). Second, we analyzed the data using independent linear contrast. However, in concordance with other analyses of elevational gradients (Badyaev and Ghalambor 2001; Badyaev et al. 2002) and theoretical expectations for analyses of ecological data (Price 1997), we found no difference between results of independent contrasts and raw data, thus we present relationships based on raw data only.

Results

Song type

In sister species pairs that differed in song type, species breeding at lower elevations were more likely to sing elaborate and loud courtship songs than their sister taxa at high elevation ($n_1 = 32$ species, $n_2 = 16$ pairs, $k = 2$, sign test, $P = 0.02$).

Temporal components of song

Species breeding at lower elevation had a greater number of notes and longer songs compared to high-elevation species (Table 1, Fig. 1). Structurally larger species sang shorter songs (Table 1). Habitat closeness did not influence temporal characteristics of song (Table 1). A PC of temporal characteristics of song accounted for 48.9% of the variance among note length, internote interval length, number of notes, and song length (eigenvectors: -0.19 , -0.47 , 0.66 , 0.54 , respectively) and tended to vary with elevation of breeding. Species breeding at higher elevations tended to sing shorter songs with longer notes, longer internote intervals, and fewer notes (Table 2, Fig. 2). Temporal elaboration of songs did not vary with habitat closeness or body size (Table 2).

Table 1 Variation in temporal and frequency components of song in relation to breeding elevation, body size, and habitat type. Habitat was treated as a categorical variable; the least-squared means are presented

| Song variables | Factors | | | | | | | | | | | |
|-------------------|---------------------------|----------|-------------|---------------------------|----------|--------------|--------------|----------|----------|--------------|------------|--------------|
| | Elevation of breeding | | | Body mass | | | Habitat type | | | Model values | | |
| | $b_{st} (\times 10^{-5})$ | <i>F</i> | <i>P</i> | $b_{st} (\times 10^{-3})$ | <i>F</i> | <i>P</i> | LS Mean | <i>F</i> | <i>P</i> | r^2 | $F_{4,24}$ | <i>P</i> |
| Note length | −0.40 | 1.04 | 0.31 | −0.34 | 1.27 | 0.27 | 3, 2, 1 | 0.88 | 0.42 | 0.20 | 1.23 | 0.33 |
| Interval length | −0.01 | 0.00 | 0.99 | 0.40 | 1.15 | 0.29 | 2, 3, 1 | 1.06 | 0.36 | 0.18 | 1.14 | 0.36 |
| Number of notes | −1.30 | 4.76 | 0.04 | −0.45 | 0.73 | 0.40 | 1, 2, 3 | 0.94 | 0.40 | 0.28 | 1.95 | 0.14 |
| Song length | −1.30 | 7.04 | 0.01 | −0.87 | 4.21 | 0.05 | 1, 2, 3 | 2.20 | 0.13 | 0.45 | 4.07 | 0.01 |
| Maximum frequency | −0.20 | 1.24 | 0.27 | −0.41 | 6.82 | 0.01 | 1, 2, 3 | 0.62 | 0.54 | 0.38 | 3.07 | 0.04 |
| Minimum frequency | 0.20 | 1.20 | 0.28 | 0.03 | 0.03 | 0.85 | 1, 3, 2 | 1.14 | 0.34 | 0.13 | 0.73 | 0.58 |
| Frequency range | −0.40 | 2.55 | 0.12 | −0.70 | 10.56 | 0.004 | 1, 2, 3 | 0.52 | 0.60 | 0.47 | 4.55 | 0.008 |

Bold values indicate statistical significance at $P < 0.05$

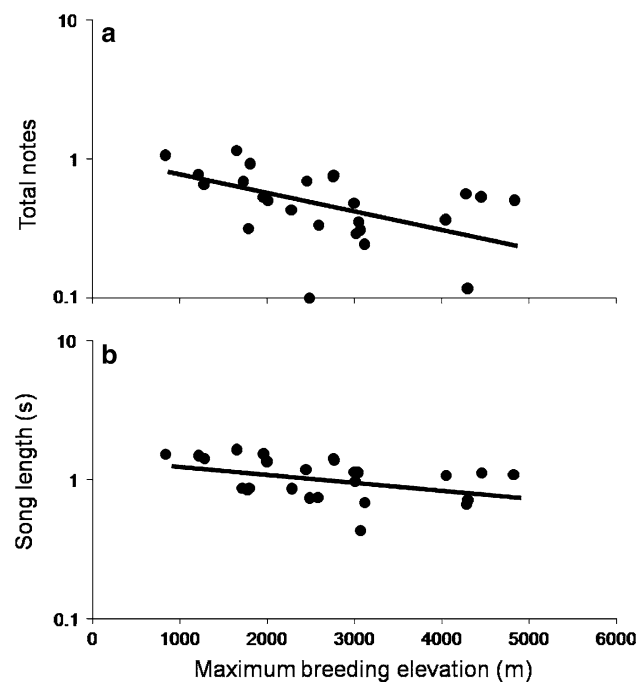


Fig. 1 Effects of breeding elevation on **a** total number of notes and **b** song length. Both song variables were log-transformed and are displayed on a logarithmic scale. Shown are residuals from a general linear model for the effects of breeding elevation, body size, and habitat type on each song characteristic

Frequency components of song

Elevation of breeding did not affect maximum frequency, minimum frequency or frequency range of songs (Table 1). Larger species sang lower frequency notes and had narrower frequency ranges (Table 1), but habitat closeness had no effect on frequency components of song (Table 1). A PC of frequency characteristics of song accounted for 66.4% of the variance in highest frequency, lowest frequency, and

from lowest to highest values [open (1), semi-closed (2), closed (3)]. b_{st} —standardized regression coefficient

Table 2 Effects of breeding elevation, body mass, and habitat type on temporal and frequency characteristics of songs. For habitat categories, least square means were highest for closed habitats and lowest for open habitats

| Factor | Temporal elaboration | | | Frequency elaboration | | |
|---------------------------------------|---------------------------|----------|-------------|---------------------------|----------|--------------|
| | $b_{st} (\times 10^{-5})$ | <i>F</i> | <i>P</i> | $b_{st} (\times 10^{-3})$ | <i>F</i> | <i>P</i> |
| Elevation | −4.0 | 3.24 | 0.08 | −2.0 | 2.42 | 0.13 |
| Body mass | −2.30 | 1.78 | 0.19 | −3.57 | 9.19 | 0.006 |
| Habitat type | | 1.18 | 0.32 | | 0.43 | 0.65 |
| Total (r^2 , <i>F</i> , <i>P</i>) | 0.31 | 2.19 | 0.10 | 0.45 | 4.04 | 0.01 |

Bold values indicate significance at $P < 0.05$, *bold italicized* values indicate $P < 0.10$

frequency range (eigenvectors: 0.68, −0.17, 0.71, respectively) and did not vary with elevation of breeding (Table 2, Fig. 2). Larger species sang songs with lower maximum frequency, higher minimum frequency, and narrower frequency range (Table 2), and habitat closeness was not related to the PC for frequency components of song.

Discussion

Signal divergence along ecological gradients often reinforces local adaptation and can facilitate speciation (Coyne and Orr 2004). Our results suggest that variation in sexual selection intensity along an elevational gradient may drive variation in acoustic signals. Capitalizing on previous intra-specific documentation of greater bi-parental care and lower sexual selection intensity in high-elevation species (Badyaev 1997a, b, c; Badyaev and Ghalambor 2001), we predicted that signal elaboration would decrease with elevation of breeding across species.

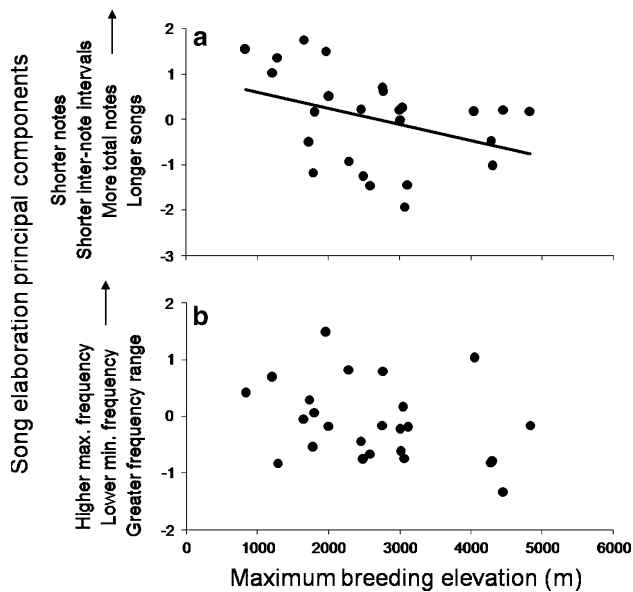


Fig. 2 Effects of breeding elevation on principal components for song elaboration. **a** Temporal components of song: species at higher elevations sang songs with longer notes, longer internote intervals, less total notes, and shorter total length. **b** Frequency components of song: species at higher elevations did not differ from those at lower elevations in maximum or minimum frequency, or in total frequency range. Shown are residuals from a general linear model for the effects of breeding elevation, body size, and habitat type

We found that songs diverged along an elevation gradient in a manner consistent with sexual selection for more elaborate, harder-to-produce songs at lower elevations. First, total song output varied with elevation, and species at high elevations sang quieter, less intense songs (Online Appendix 1). Second, song structure varied with elevation—low elevation species tended to have longer songs with more total notes (Table 1, Figs. 1, 2, Online Appendix 2).

Divergence in songs may play a particularly important role in population divergence and speciation (Grant and Grant 1996, 1997; Price 1998; Lachlan and Servedio 2004; Qvarnström et al. 2006; Ruegg et al. 2006), because of both strong natural selection on components of song production that often indicate local adaptation (Podos 2001) and self-reinforcing mechanisms of cultural inheritance of local song preference and production (Irwin and Price 1999; Lachlan and Feldman 2003). The results of this study further suggest that displays may diverge along ecological gradients due not only to differences in display transmission in different environments (Endler 1992; Slabbekoorn and Smith 2002), but also due to differential investment in displays under variable sexual selection (Badyaev and Qvarnström 2002).

Because elevation affects not only the intensity of sexual selection, but also variation in body size and habitat structure (Traylor 1950; Potapov 2004), we controlled statistically for interspecific variation in body size and habitat.

Our results corroborate findings of other studies (Podos et al. 2004) that larger species sing songs with lower maximum, higher minimum frequencies, and a smaller frequency range, as well as shorter song lengths (Table 1). However, contrary to other studies (Richards and Wiley 1980) we found no effects of habitat structure on song characteristics. Two observations may explain this result. First, cardueline finches often perform display flights while singing, and this might lessen habitat constraints on song elaboration. Display flights reduce the sound-degrading effects of habitats because the song is either delivered above the habitat or in close proximity to the female. Second, habitat types are replicated across the elevational gradient such that a roughly equal proportion of open, semi-closed, and closed habitat is typically found at high and low elevations. That is, lower elevations have open, semi-open, and closed habitats (e.g., meadows and steppe, bushes and shrub-steppe, deciduous forests), while higher elevations have a corresponding distribution of such habitat types (e.g., alpine meadows, sub-alpine bushes, coniferous forests). Such replication might obscure the relationship between habitat structure and song elaboration across an entire elevational range of cardueline finches.

Environmental conditions associated with elevation, not considered in this study, might contribute to the interspecific patterns of song elaboration documented here. For example, oxygen concentration becomes lower as elevation increases which can constrain the length of bird song (Podos et al. 2004) and provide an alternate explanation for the negative relationship between song length and elevation (Tables 1, 2). However, this alternate hypothesis also predicts that, for a given song length, birds at higher elevations should take breaths more frequently, resulting in more notes and/or shorter notes, a prediction that is unsupported by our data (Table 1).

Ambient noise and wind often increase at higher elevations exerting an additional selection pressure on song structure, possibly providing an alternative hypothesis for the negative relationship between song temporal complexity and elevation documented in this study (Tables 1, 2). High ambient noise would favor songs with longer note lengths (Lohr et al. 2003; Patricelli and Blickley 2006) and a broad frequency range (Richards and Wiley 1980; Wiley and Richards 1978), predictions not met in our study (Table 1). Furthermore, we found that wind speed did not affect the relationship between song and elevation in a subset of North American cardueline finches.

Elevational gradients in natural and sexual selection provide an opportunity to examine evolution of morphological, life history, and behavioral traits. Our results suggest that an elevational gradient in sexual selection may drive divergence in mating signals and thus significantly facilitate and reinforce ecological diversification of morphological and life history traits.

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