

SPECIES DIVERGENCE IN SEXUALLY SELECTED TRAITS: INCREASE IN SONG ELABORATION IS RELATED TO DECREASE IN PLUMAGE ORNAMENTATION IN FINCHES

ALEXANDER V. BADYAEV,^{1,2} GEOFFREY E. HILL,³ AND BYRON V. WECKWORTH^{1,4}

¹Division of Biological Sciences, The University of Montana, Missoula, Montana 59812-1002

³Department of Biological Sciences, Auburn University, Auburn, Alabama 36849

⁴Department of Biological Sciences, Idaho State University, Pocatello, ID 83209-8007

Abstract.—Elaborate plumage and complex songs of male birds are two of the best-known examples of sexually selected traits, yet the interaction between these traits is poorly understood. Theory suggests that among a suite of potential displays, animals will emphasize traits that are most conspicuous, least costly, or best signal condition and reduce display of other traits. Here we examined the relationship between song and plumage elaborations in cardueline finches, songbirds that are highly variable in plumage displays and songs, but that share a similar mating system. We statistically controlled for body mass, habitat characteristics, and phylogenetic relationships and found that across species song complexity was strongly negatively related to elaboration of plumage ornamentation. When plumage coloration was partitioned into carotenoid-based and melanin-based components, song complexity was negatively related to elaboration of male carotenoid-based coloration but unrelated to elaboration of melanin-based coloration. These observations support the idea that, for condition-dependent traits, animal species trade off trait expression in response to changes in the costs or the information content of these traits. We discuss several alternative explanations for the observed pattern.

Key words.—Carduelinae, multiple sexual signals, plumage ornamentation, song elaboration.

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Elaborate plumage coloration of male birds and their complex songs are some of the best-known examples of sexually selected traits (Darwin 1871). Although numerous studies have investigated female preference for song and plumage characteristics (reviewed in Andersson 1994), the interaction between elaboration of these two kinds of traits is not well understood (Shutler and Weatherhead 1990).

Theory predicts that sexual selection on traits that indicate direct phenotypic benefits should favor display traits with greater detectability or with greater relevance to current environmental condition (Price et al. 1993; Schluter and Price 1993). Change in environmental conditions (e.g., diet or predation) that leads to change in the detectability or the cost of traits can strongly influence both preference for traits and trait elaboration (Darwin 1871; Gilliard 1956; Endler 1992). For example, if predation limits variation in sexual dichromatism, song elaboration may replace plumage characteristics as the target of sexual selection (Darwin 1871, p. 709; Shutler and Weatherhead 1990). Similarly, Bailey (1978) suggested that colors that are easily changed by behavioral displays depending on variable light conditions should be favored in dark habitats (see also Marchetti 1993; Endler and Théry 1996; Price and Birch 1996).

Thus, a change in environment can facilitate a preference for a novel, more informative, or cheaper trait (Endler 1992; Schluter and Price 1993; Price 1998). Whether the establishment of a novel sexual trait leads to elimination of the existing traits or to accumulation of multiple traits depends on cost of trait production and the mechanisms behind female choice (Iwasa and Pomiankowski 1994). If two sexual traits are condition dependent, females should prefer the one with

greater detectability in a particular environment, and this may be true even if this trait is less closely linked to individual condition (Schluter and Price 1993; Iwasa and Pomiankowski 1994). Over evolutionary time, selection should lead to the displacement of one type of condition-dependent trait by another (Hill 1994; Prum 1997; Badyaev and Hill 1999). This prediction is consistent with the observation that multiple traits are often less closely related to individual condition than single traits and that condition-dependence of sexual traits is most prevalent in species with a single sexual ornament (Møller and Pomiankowski 1993; Kusmiński et al. 1997).

Here we examined the relationship between two of the most prominent display traits of birds, song and colorful plumage, across 41 species of finches (Aves: subfamily Carduelinae). Both plumage ornamentation and song complexity vary widely across finch species, for example, from dull and monomorphic *Serinus donalsonii* to very colorful and dimorphic *Carpodacus rubicilla* and from species with no known courtship song (e.g., *Mycerobas carnipes* and Asian *Leucosticte arctoa*) to species with highly complex and lengthy vocalizations (e.g., *S. serinus* and *S. canaria*). Finches are uniquely suited for this study for several reasons. Most species of finches are nonterritorial, and song is primarily used for female attraction and female stimulation (e.g., Newton 1973) rather than for male competition. Female choice is consistently found to favor complex songs with larger repertoire size (reviewed in Searcy and Yasukawa 1996; see below). In most finch species, pairing occurs in winter and early spring flocks and thus, both plumage and song traits are used in similar, short-range communications with females (Cramp and Perrins 1994). Finally, close dependence of carotenoid-based plumage ornamentation and song complexity on individual condition has been established in many studies of

² Present address: Department of Biological Sciences, Auburn University, Auburn, Alabama 36849-5414; E-mail: abadyaev@selway.umn.edu.

finches (e.g., Nottebohm and Nottebohm 1978; Hill 1991; reviewed in Badyaev and Hill 1999 and Hill 1999; see also Nowicki et al. 2000), and plumage elaboration strongly varies with environmental conditions in these birds (Martin and Badyaev 1996; Badyaev 1997a,b; Badyaev and Ghalambor 1998).

In addition to overall plumage brightness, we separately scored two easily distinguished types of ornamental plumage coloration: melanin and carotenoid pigmentation (Brush 1978). Carotenoids produce the red, orange, and yellow colors of feathers, whereas melanins produce the brown, gray, and black colors including the black caps, bibs, and wings patches (Brush 1978; Gray 1996). Because carotenoids or their precursors have to be acquired from the environment, carotenoid-based plumage coloration may be more dependent on environmental variation than other types of pigmentation (reviewed in Badyaev and Hill 1999). Consequently, significant dependence of carotenoid-based pigmentation on individual condition and health is frequently documented (reviewed in Hill 1999). In addition, carotenoid-based colors are often more conspicuous, and thus are more prominently featured in sexual displays, and may be under stronger and more frequent sexual selection compared to other types of pigmentation (Badyaev and Hill 2000). Similarly, many studies document that sexual selection favors longer songs with a higher number and diversity of notes, greater range of frequencies, and wider repertoire; across species, this preference results in more complex songs in species with more intense sexual selection (reviewed in Searcy and Yasukawa 1996). Elaboration of song complexity may be costly both in terms of anatomical, physiological, and mechanical adjustments (Read and Weary 1992; Lambrechts 1996; Nowicki et al. 2000), as well as in costs associated with transmissions in different environments (Morton 1975; Richards and Wiley 1980; Klump 1996; Zuk and Kolluru 1998).

If sexual selection favors reduction or elimination of former condition-dependent traits when elaborating a novel condition-dependent trait, then, across species, there should be a stronger inverse relationship between song complexity and carotenoid pigmentation compared to melanin pigmentation. In addition, difference in relationships between song elaboration and carotenoid versus melanin pigmentation is expected if carotenoid coloration, due to its greater conspicuousness, plays a more significant role in sexual displays compared to melanin coloration. Alternatively, elaboration of song complexity and plumage coloration may be unrelated if sexual selection incorporates redundancy in signaling systems (Møller and Pomiankowski 1993) or if the traits have different dependencies on individual condition (Schluter and Price 1993; Iwasa and Pomiankowski 1994).

MATERIALS AND METHODS

Song data were measures of published spectrograms of vocalizations that were described as breeding season or courtship song. Because our analyses were focused on among-taxa variation, we averaged data for each taxa across all individuals, song types, and locations (four to 15 sonograms per taxa; Appendices 1, 2). Each spectrogram was printed on standardized 0–10-KHz grid and magnified at 2 \times . We mea-

sured highest and lowest frequencies and mean range of frequencies across all notes (all in kHz); note length (averaged across all notes), internote interval (averaged across all notes), and song length (all in sec); and number of different notes. Data on male body mass, elevation of breeding, vegetation density, as well as source references for all taxa are in appendices 1 and 2 of Badyaev (1997a).

Data on plumage pigmentation and plumage elaboration for 41 taxa used in these analyses as well as the details of the methods are given in Badyaev and Hill (2000). Briefly, we used a spectrophotometer to record a hue (a point along 360° color circle that begins at red), saturation, and brightness scores (0–100%) for the crown, ventral region, and rump of males from color plates in Clement et al. (1993) that illustrates adult males of all extant species of cardueline finches. To test the assumption that color plates accurately reflect the carotenoid-based feather coloration, we measured the plumage coloration from specimens of 33 species of cardueline finches (all species available in the Museum of Natural Sciences at Louisiana State University) using the same method. Rump coloration was not measured for some species to prevent specimen damage. The book plate and specimen sets of measures were highly correlated: illustrations most accurately depicted color hue (Pearson $r = 0.99$, $n = 17$, $P < 0.0001$ for crown; $r = 0.99$, $n = 33$, $P < 0.0001$ for breast; $r = 0.99$, $n = 9$, $P < 0.0001$ for rump), color saturation ($r = 0.51$, $P = 0.04$ for crown; $r = 0.57$, $P = 0.0006$ for breast), and the composite measure of carotenoid-based plumage (see below; e.g., breast: $r = 0.71$, $n = 33$, $P = 0.04$). Thus, we concluded that depiction of cardueline finch coloration on the color plates in Clement et al. (1993) is suitable for our study (for details, see Badyaev and Hill 2000).

This approach to color analysis allowed us to quantify the plumage coloration of all study species and to generate quantitative descriptors of color. Our approach, however, ignored the ultraviolet (UV) component of the coloration. In previous studies, the reflectance spectrum from UV through infrared of carotenoid-based plumage coloration of both yellow and red finches was examined with a spectrophotometer and no significant UV signal was observed (McGraw and Hill 2000; for further discussion of this topic, see Hill 1998). Thus, we proceed under the assumption that our tristimulus color scores were a reasonable representation of the ornamental plumage of the species that we studied.

Carotenoid-based coloration of plumage was the first eigenvector (PC1) of the zero-mean transformed covariance matrix of hue, saturation, and brightness for each body part; overall carotenoid-based plumage coloration was a sum of standardized values for each body part (Badyaev and Hill 2000). The extent of melanin-based pigmentation was scored (by two independent observers from Auburn University) as the percent of the entire male plumage (profile view of perched birds, wings folded) with black pigmentation from color plates and museum skins. Data on overall plumage brightness of males are in appendix 1 of Badyaev (1997a). Briefly, plumage brightness was assessed (by two independent observers from the University of Montana) from illustrations in Clement et al. (1993). The overall brightness was scored on a scale from 1 to 6. Full details of all analyses are in Badyaev and Hill (2000).

TABLE 1. Effects of potential covariates on song attributes of cardueline finches. Species with higher PC1 scores sing longer and more complex songs over a wide range of frequencies. Species with higher PC2 scores sing songs with fewer and more widely spaced notes. Phylogenetic relationships across taxa are accounted by the method of independent linear contrasts. Standardized partial regression coefficients (b_{ST}) are shown.

Predictor	Dependent variable	
	PC1	PC2
Body mass	-0.57*	-0.01
Vegetation density	-0.19	+0.40*
Elevation of breeding	-0.12	-0.06

* Significance at $\alpha = 0.01$ level after modelwide Bonferroni correction.

Our phylogenetic hypothesis of subfamily of cardueline finches was constructed by summarizing most recent data available for each clade and is published elsewhere (Badyaev 1997a). This composite phylogeny of the subfamily is well supported by molecular studies of both the basal nodes (Marten and Johnson 1986) and within-clade analyses (e.g., Arnaiz-Villena et al. 1998, 1999). We did not have consistent estimates of branch lengths because data came from studies using different methods. However, because all extant cardueline species were included in the phylogenetic tree and plots of standardized contrasts against the variances of the untransformed contrasts showed no significant correlation, the use of equal branch lengths is justified (Garland et al. 1992; Purvis and Rambaut 1995). We analyzed data using the independent contrast method of Felsenstein (1985) and incorporated the methods of Purvis and Garland (1993) for incompletely resolved phylogenies, based on the software described in Purvis and Rambaut (1995). By using this method, we assumed that different clades are equally likely to develop similar proportional changes in each variable included in independent contrast computations. None of the regressions of absolute values of contrasts versus their estimated nodal values showed slopes that significantly differed from zero, thus validating the assumption (Purvis and Rambaut 1995; for further details of phylogenetic analyses, see Martin and Badyaev 1996). All regressions were forced through the origin (Garland et al. 1992). All data were log transformed, and body mass was cube-root transformed before statistical analyses. We provide results of analyses of phylogenetically untransformed data (i.e., taxa means, see Appendices 1, 2) in addition to analyses of phylogenetically transformed data (i.e., contrasts values).

RESULTS

Song elements were strongly intercorrelated within and across species. Thus, to facilitate comparisons across taxa we constructed linear principal components of original song variables. The first principal component (PC1) accounted for 47.3% of total variation in the song variables, and an increase in PC1 scores was associated with an increase in song length (vector loading: +0.59), range of dominant frequencies (+0.55), the highest frequency (+0.53), and the number of different notes in a song (+0.42). Species with higher PC1 had longer songs with greater number of notes, so PC1 score is hereafter used as an index of song complexity. The second

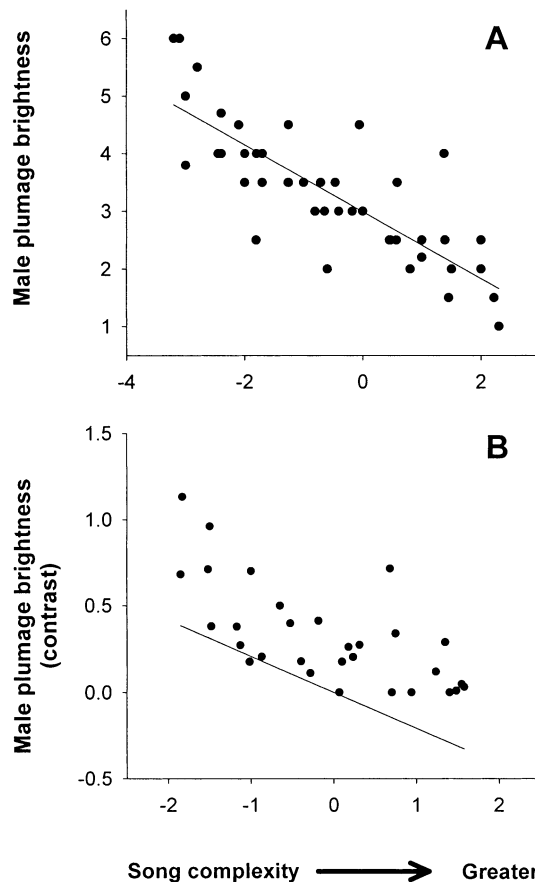


FIG. 1. Song complexity in relation to overall plumage brightness in 41 taxa of cardueline finches. Shown are partial regression plots where effects of body mass, vegetation density, and elevation of breeding were statistically controlled. (A) Raw data, (B) data transformed by the method of standardized independent linear contrasts.

principal component (PC2) accounted for 34.8% of total variation, and an increase in PC2 scores was associated with an increase in duration of internote intervals (+0.62) and note length (+0.56), but with a decrease in the number of notes in a song (-0.48). Because most variation in PC2 was accounted by changes in vegetation density (Table 1), it will be examined elsewhere. Here we will focus on explaining variation in the index of song complexity (PC1).

To examine the relationship between song complexity and plumage ornamentation, we statistically controlled for effects of body mass, vegetation density, and elevation of breeding because these factors covary with both plumage ornamentation and song complexity in cardueline finches (Badyaev 1997a; Table 1). Across species, overall male plumage brightness, which combined the contribution of melanin and carotenoid pigmentation, was strongly negatively correlated with song complexity, both when we used raw data (partial $b_{ST} = -0.83$, $P = 0.0001$; Fig. 1A) and independent linear contrasts (partial $b_{ST} = -0.52$, $P = 0.003$; Fig. 1B). However, the relationship between plumage ornamentation and song elaboration was distinct for carotenoid and melanin pigmentation (Fig. 2). Although increase in song complexity was strongly negatively correlated with elaboration of male carotenoid ornamentation (raw data: $b_{ST} = -0.56$, $P < 0.001$;

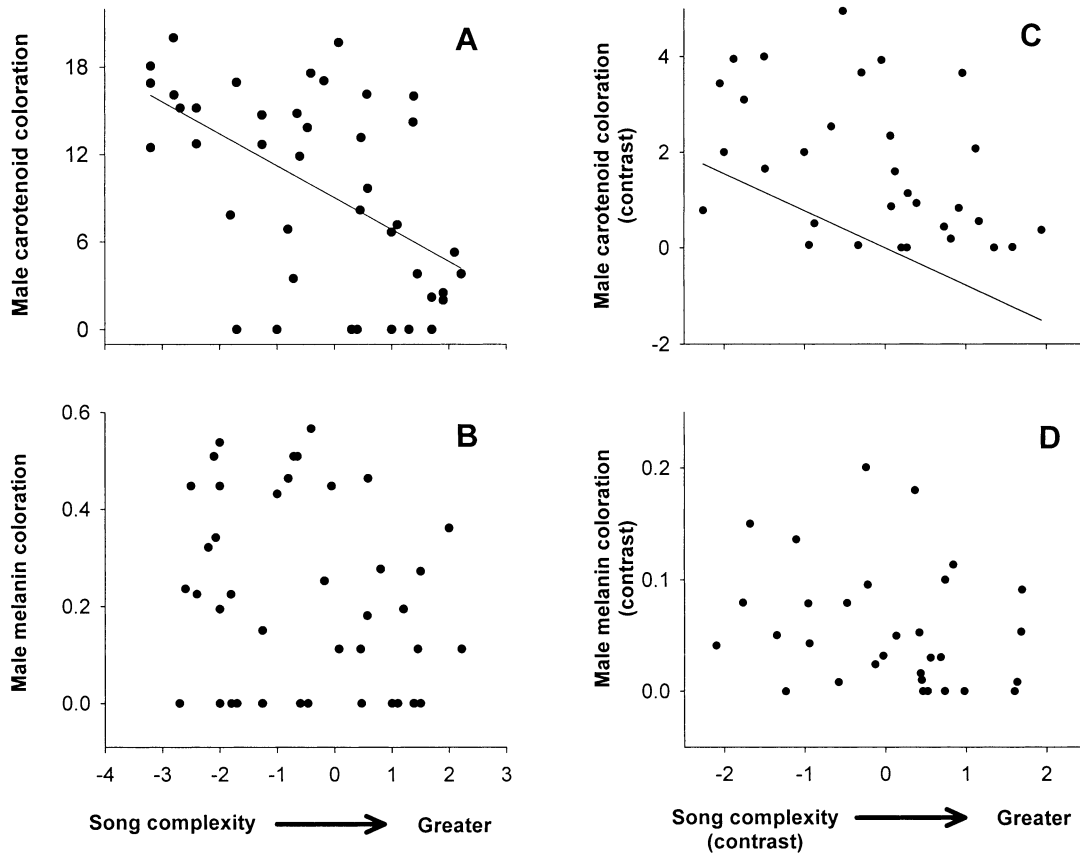


FIG. 2. Song complexity in relation to elaboration of male carotenoid- and melanin-based ornamentation. Shown are partial regression plots where effects of body mass, vegetation density, and elevation of breeding were statistically controlled. Greater song complexity is associated with lower elaboration of carotenoid ornamentation (A), but not with elaboration of melanin ornamentation (B). Plots on (C) and (D) are partial regressions of data transformed by the method of standardized independent linear contrasts.

contrasts: $b_{ST} = -0.68$, $P < 0.0001$; Fig. 2A, C), it did not correlate with elaboration of melanin ornamentation (raw data: $b_{ST} = -0.22$, $P = 0.15$; contrasts: $b_{ST} = -0.15$, $P = 0.42$; Fig. 2B, D).

DISCUSSION

We documented a strong negative relationship between song complexity and elaboration of carotenoid-based plumage coloration in cardueline finches. This relationship is consistent with several alternative explanations. First, both song complexity and carotenoid-based plumage traits may be closely related to overall individual condition and costly to produce and maintain (Schluter and Price 1993; Iwasa and Pomiankowski 1994). Indeed, previous within-species studies have shown that carotenoid pigmentation and song complexity are condition-dependent signals used in mate choice (Hill 1991; Hasselquist et al. 1996; Nowicki et al. 2000). Likewise, a lack of a relationship between melanin-based coloration and either song complexity (Fig. 2) or carotenoid-based coloration (Badyaev and Hill 2000) may suggest greater developmental constraints of melanin-based plumage coloration and corresponding weaker association between melanin-based ornamentation and individual condition. If the difference in the relationship between song complexity and plumage pigmentation elaboration is based on relative dif-

ferences in condition dependence of carotenoid and melanin plumage, then our observations would simultaneously confirm a difference in the signal content of carotenoid versus melanin pigmentation (Gray 1996; Owens and Hartley 1998) and support the idea of transference of elaboration from one condition-dependent signal to another (Darwin 1871; Gilliard 1956; Schluter and Price 1993).

However, these results do not suggest the lack of condition dependence in melanin pigmentation. Indeed, in species with melanin-based sexual ornaments, the condition dependence of melanin-based coloration is well documented (Møller 1987; Gustafsson et al. 1995; Veiga and Puetra 1996; Griffith et al. 1999; Qvarnström 1999). Neither do these results suggest that carotenoid-based coloration is always closely linked to individual condition (e.g., Badyaev et al. 2001). These results instead suggest that when both carotenoid- and melanin-based coloration are present in the ornamentation of the same species (as found in most cardueline finches), carotenoid pigmentation will be relatively less developmentally constrained, more dependent on environmental variation and individual condition, and thus more likely to be selected as a signal of individual condition than melanin-based coloration.

Second, the observed negative relationship between song complexity and carotenoid-based ornamentation may reflect

differing signaling strategies in variable environments (Endler 1992; Price 1998). For example, detectability and costs of both types of traits vary with vegetation density (Ryan and Brenowitz 1985; Marchetti 1993; Badyaev and Leaf 1997; Götmark 1999), mechanistic constraints of body size (Read and Weary 1992; Lambrechts 1996; Badyaev 1997a), elevation of breeding (Boehme and Banin 1994), and predation risk (Martin and Badyaev 1996). We found that the negative relationship between song complexity and plumage ornamentation persists across all habitat types and when variation due to body mass and elevation of breeding is statistically controlled (Figs. 1, 2). Thus, the negative trade-off between song complexity and plumage displays is likely to be mediated either by their common condition dependence or by a greater role of the more conspicuous carotenoid-based ornament play in sexual selection. Alternatively, additional environmental factors not controlled in this study may favor the use of different signals.

Similarly to this study, Shutler and Weatherhead (1990) found that more dimorphic wood warblers sang shorter songs. However, contrary to our study of finches, in wood warblers plumage dimorphism did not correlate with song complexity as measured by the number of notes and repertoire size. Also, contrary to our study, more dimorphic species had songs with higher maximum frequency. For example, lower plumage dimorphism in ground-nesting warblers was not associated with greater song complexity in this group (Shutler and Weatherhead 1990). However, in both wood warblers and cardueline finches, difference in sexual dichromatism between ground- and off-ground-nesting species did not result from decreased male brightness, as previously assumed (Shutler and Weatherhead 1990), but instead resulted from an increase in female brightness in ground-nesting birds related to their reduced risk of nest predation as compared to shrub-nesters (Martin and Badyaev 1996). Thus, an association between male plumage and song complexity should provide a more appropriate comparison between the two studies. More generally, if variation in sexual dichromatism is used as a measure of sexual selection in a group, it needs to be shown whether it is contributed by male or female plumage variation (e.g., Irwin 1994; see also Catchpole and McGregor 1986; Badyaev and Hill 1999).

In summary, we documented that across cardueline finch species song complexity was strongly negatively related to elaboration of plumage ornamentation. This result provides broad evidence that common dependence on individual condition and environmental variation is likely to mediate the historical relationship between coexistence and elaboration of sexual traits. We showed that the relationship between elaborations of song and plumage is distinct for different types of plumage pigmentation, providing additional empirical support for the trade-offs between condition-dependent sexual traits. We hope that the documentation of this broad evolutionary pattern will stimulate detailed within-species studies of the proximate mechanisms that contribute to it.

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APPENDIX 1. Frequency characteristics of cardueline finches' songs. Mean (CV) values are shown. HF, highest frequency (kHz); LF, lowest frequency (kHz); Range, average range of frequencies across all notes (i.e., an approximation of the dominant frequency for each song; kHz).

Species	HF	LF	Range
<i>Carduelis cannabina</i>	6.538 (2.4)	1.628 (16.7)	2.422 (42.9)
<i>Carduelis carduelis</i>	7.220 (0.5)	2.226 (3.4)	2.627 (49.4)
<i>Carduelis chloris</i>	6.444 (3.6)	1.815 (6.5)	2.599 (23.4)
<i>Carduelis flammea</i> ¹	5.068 (17.4)	1.793 (11.0)	2.921 (28.5)
<i>Carduelis flammea</i> ²	4.296 (0.4)	1.679 (7.0)	3.805 (10.6)
<i>Carduelis flavirostris</i> ³	7.222 (0.4)	1.630 (6.4)	3.748 (20.1)
<i>Carduelis flavirostris</i> ⁴	6.985 (5.5)	1.126 (24.3)	3.687 (29.2)
<i>Carduelis hornemanni</i>	5.037 (1.0)	2.024 (2.0)	2.543 (19.4)
<i>Carduelis lawrencei</i>	8.542 (3.9)	0.938 (4.0)	5.604 (18.9)
<i>Carduelis pinus</i>	14.778 (4.8)	2.074 (8.7)	10.704 (45.0)
<i>Carduelis psaltria</i>	7.741 (7.0)	2.123 (8.9)	4.618 (31.0)
<i>Carduelis sinica</i>	6.305 (6.7)	2.016 (11.3)	2.673 (37.8)
<i>Carduelis spinoides</i>	5.778 (6.0)	2.148 (9.7)	2.706 (29.2)
<i>Carduelis spinus</i>	6.731 (3.9)	2.180 (18.4)	3.060 (34.7)
<i>Carduelis tristis</i>	8.667 (7.0)	1.889 (10.0)	4.778 (19.4)
<i>Carduelis yemenensis</i>	5.497 (5.1)	1.708 (8.0)	1.752 (59.3)
<i>Carpodacus cassinii</i>	7.649 (27.5)	1.313 (18.3)	4.336 (30.1)
<i>Carpodacus erythrinus</i> ⁵	5.463 (7.8)	1.934 (17.6)	1.933 (45.8)
<i>Carpodacus erythrinus</i> ⁶	4.992 (6.7)	1.938 (6.2)	1.977 (46.2)
<i>Carpodacus mexicanus</i>	6.128 (7.0)	1.481 (18.5)	2.647 (3.3)
<i>Carpodacus purpureus</i>	9.910 (17.4)	0.934 (35.2)	6.975 (22.2)
<i>Carpodacus rubicilla</i>	3.556 (1.0)	2.123 (1.7)	1.183 (10.5)
<i>Carpodacus synoicus</i>	5.856 (14.0)	1.812 (14.0)	2.941 (48.9)
<i>Coccothraustes coccothraustes</i>	6.630 (5.8)	2.785 (38.0)	3.269 (40.8)
<i>Loxia curvirostra</i>	7.000 (2.7)	1.370 (40.9)	3.232 (45.2)
<i>Loxia leucoptera</i> ⁷	5.778 (12.7)	2.356 (3.1)	1.765 (65.5)
<i>Loxia leucoptera</i> ⁷	5.264 (8.3)	2.472 (7.5)	1.637 (55.8)
<i>Loxia leucoptera</i> ⁸	7.604 (12.0)	2.593 (10.0)	4.012 (30.0)
<i>Loxia pytyopsittacus</i> ⁷	5.489 (7.1)	2.349 (15.2)	1.430 (66.8)
<i>Loxia pytyopsittacus</i> ⁹	4.259 (12.0)	2.716 (11.0)	1.088 (21.2)
<i>Loxia scotica</i>	6.209 (10.9)	1.301 (24.9)	1.759 (71.9)
<i>Pinicola enucleator</i>	3.846 (2.4)	2.007 (10.9)	1.244 (34.3)
<i>Pyrrhula pyrrhula</i>	4.965 (22.6)	1.761 (15.3)	1.927 (78.4)
<i>Rhodopechys githaginea</i>	6.002 (12.3)	1.245 (13.1)	2.554 (52.9)
<i>Rhodopechys obsoleta</i>	6.440 (2.3)	1.005 (8.8)	2.015 (60.8)
<i>Rhodopechys sanguinea</i>	4.596 (4.7)	1.485 (6.1)	1.797 (39.0)
<i>Serinus canaria</i>	7.222 (12.0)	1.778 (18.0)	2.704 (41.5)
<i>Serinus citrinella</i>	7.462 (4.6)	2.148 (9.8)	2.684 (45.8)
<i>Serinus pusillus</i>	6.074 (8.0)	1.481 (6.0)	2.634 (35.9)
<i>Serinus serinus</i>	13.926 (11.0)	3.185 (8.9)	9.741 (4.0)
<i>Serinus syriacus</i>	6.409 (5.3)	1.586 (19.9)	2.979 (34.6)

¹ Subalpine population.² Forest population.³ *C. f. pipilans*.⁴ *C. f. montanella*.⁵ *C. e. erythrinus*.⁶ *C. e. ferganensis*.⁷ Northern Europe.⁸ North America.⁹ Central Europe.

APPENDIX 2. Temporal characteristics of cardueline finches' songs. Mean (CV) values are shown. NTLEN, note length (averaged across all notes; sec); INT, internote interval (averaged across all notes; sec); NT, number of notes; SLEN, song length (sec).

Species	NTLEN	INT	NT	SLEN
<i>Carduelis cannabina</i>	0.079 (88.7)	0.109 (104.7)	28.03 (33.0)	5.970 (29.6)
<i>Carduelis carduelis</i>	0.051 (69.3)	0.086 (105.9)	13.42 (11.3)	3.524 (15.9)
<i>Carduelis chloris</i>	0.057 (83.8)	0.195 (157.3)	6.90 (4.6)	6.963 (8.5)
<i>Carduelis flammea</i> ¹	0.115 (96.7)	0.221 (92.9)	7.92 (42.0)	6.178 (38.3)
<i>Carduelis flammea</i> ²	0.373 (92.3)	0.316 (41.0)	4.00 (1.1)	4.820 (1.5)
<i>Carduelis flavirostris</i> ³	0.074 (88.2)	0.155 (76.3)	28.00 (0.9)	9.970 (1.0)
<i>Carduelis flavirostris</i> ⁴	0.319 (136.0)	0.330 (91.3)	15.50 (29.8)	11.768 (32.2)
<i>Carduelis hornemanni</i>	0.262 (125.0)	0.275 (62.0)	3.00 (0.5)	2.260 (0.5)
<i>Carduelis lawrencei</i>	0.073 (70.8)	0.068 (85.0)	12.00 (12.0)	2.550 (15.0)
<i>Carduelis pinus</i>	0.060 (67.3)	0.124 (51.1)	24.0 (10.0)	6.100 (12.0)
<i>Carduelis psaltria</i>	0.060 (106.9)	0.080 (87.2)	12.00 (8.5)	2.350 (9.0)
<i>Carduelis sinica</i>	0.133 (149.9)	0.181 (151.4)	3.22 (46.0)	2.563 (67.1)
<i>Carduelis spinoides</i>	0.066 (94.2)	0.127 (170.6)	6.00 (0.5)	5.280 (1.0)
<i>Carduelis spinus</i>	0.142 (127.8)	0.191 (100.7)	9.89 (23.2)	3.468 (27.8)
<i>Carduelis tristis</i>	0.038 (43.1)	0.278 (84.5)	7.00 (8.0)	2.360 (10.0)
<i>Carduelis yemenensis</i>	0.055 (59.1)	0.078 (119.9)	13.20 (19.0)	4.416 (10.5)
<i>Carpodacus cassinii</i>	0.117 (148.6)	0.111 (64.4)	28.46 (21.9)	7.064 (53.3)
<i>Carpodacus erythrinus</i> ⁴	0.068 (28.0)	0.160 (62.9)	5.38 (14.8)	1.211 (4.1)
<i>Carpodacus erythrinus</i> ⁶	0.072 (35.4)	0.203 (59.9)	4.00 (2.0)	1.010 (13.1)
<i>Carpodacus mexicanus</i>	0.059 (63.9)	0.084 (70.0)	22.18 (9.1)	3.168 (0.6)
<i>Carpodacus purpureus</i>	0.142 (147.4)	0.130 (51.5)	14.17 (37.3)	4.370 (58.2)
<i>Carpodacus rubicilla</i>	0.122 (48.5)	0.076 (36.3)	7.00 (1.0)	1.430 (0.5)
<i>Carpodacus synoicus</i>	0.197 (65.6)	0.145 (54.5)	3.80 (10.9)	1.367 (22.7)
<i>Coccothraustes coccothraustes</i>	0.298 (43.6)	0.052 (37.7)	5.20 (19.9)	1.554 (12.0)
<i>Carduelis cannabina</i>	0.079 (88.7)	0.109 (104.7)	28.03 (33.0)	5.970 (29.6)
<i>Loxia curvirostra</i>	0.062 (82.4)	0.068 (89.9)	11.14 (67.4)	1.987 (18.4)
<i>Loxia leucoptera</i> ⁷	0.080 (222.4)	0.042 (65.2)	7.20 (13.8)	6.762 (37.3)
<i>Loxia leucoptera</i> ⁷	0.076 (89.5)	0.063 (96.4)	4.13 (54.5)	3.093 (57.9)
<i>Loxia leucoptera</i> ⁸	0.067 (46.4)	0.051 (71.2)	5.00 (31.2)	3.970 (20.0)
<i>Loxia pytyopsittacus</i> ⁷	0.130 (88.3)	0.057 (88.7)	5.52 (55.7)	2.205 (30.8)
<i>Loxia pytyopsittacus</i> ⁹	0.070 (76.4)	0.094 (61.0)	2.00 (15.0)	1.550 (14.0)
<i>Loxia scotica</i>	0.082 (86.8)	0.082 (115.8)	12.70 (47.4)	2.188 (2.6)
<i>Pinicola enucleator</i>	0.040 (66.2)	0.095 (55.7)	19.37 (27.3)	2.624 (34.9)
<i>Pyrrhula pyrrhula</i>	0.230 (134.9)	0.150 (78.8)	6.00 (0.0)	2.319 (15.4)
<i>Rhodopechys obsoleta</i>	0.100 (155.7)	0.108 (145.6)	22.25 (35.6)	4.354 (31.9)
<i>Rhodopechys githaginea</i>	0.130 (86.4)	0.321 (174.8)	5.58 (36.6)	3.587 (32.3)
<i>Rhodopechys sanguinea</i>	0.065 (79.2)	0.074 (63.7)	14.45 (21.3)	2.571 (25.8)
<i>Serinus canaria</i>	0.073 (83.0)	0.114 (113.7)	58.00 (87.9)	23.020 (54.5)
<i>Serinus citrinella</i>	0.058 (98.1)	0.121 (83.9)	20.08 (10.8)	5.240 (45.8)
<i>Serinus pusillus</i>	0.049 (78.0)	0.065 (121.7)	14.00 (13.1)	3.440 (15.0)
<i>Serinus serinus</i>	0.021 (48.4)	0.066 (61.8)	39.00 (9.0)	4.310 (8.7)
<i>Serinus syriacus</i>	0.069 (108.6)	0.145 (112.0)	17.87 (38.5)	6.163 (24.9)

¹ Subalpine population.

² Forest population.

³ *C. f. pipilans*.

⁴ *C. f. montanella*.

⁵ *C. e. erythrinus*.

⁶ *C. e. ferghanensis*.

⁷ Northern Europe.

⁸ North America.

⁹ Central Europe.