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# SONG DIFFERENCES AMONG SUBSPECIES OF YELLOW-EYED JUNCOS (*JUNCO PHAEONOTUS*)

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ABSTRACT.—We compared 13 song features among three populations of Yellow-eyed Junco (*Junco phaeonotus*): *J. p. bairdi* from Baja California Sur, Mexico; *J. p. palliatus* from southeast Arizona, USA; and *J. p. phaeonotus* from Oaxaca, Mexico. Songs of *J. p. bairdi* differed significantly from those of *J. p. palliatus* in 11 of 13 features and differed significantly from those of *J. p. phaeonotus* in six of 13 features. Songs of *J. p. palliatus* differed significantly from those of *J. p. phaeonotus* in only four of 13 features. Discriminant function analysis clearly distinguished songs of *J. p. bairdi* from those of the two other subspecies, which were not clearly distinguishable from one another. Additional investigations using playback experiments and genetic analyses may be warranted to better evaluate the merits of promoting *J. p. bairdi* to species status. *Received 22 August 2010. Accepted 24 January 2011.*

Ornithologists have long hypothesized that geographic song variation affects gene flow and can lead to assortative mating, reproductive isolation, and population divergence (Grant and Grant 1996, Irwin et al. 2001, Slabbekoorn and Smith 2002). However, the relative extent to which geographic variation in bird song influences speciation remains controversial (Baker and Cunningham 1985, Slabbekoorn and Smith 2002). There are now several recent examples of song variation functioning as a reproductively isolating barrier among co-occuring cryptic species (e.g., Irwin et al. 2001, Toews and Irwin 2008), suggesting song variation may also act as a barrier to hybridization among populations that are currently separated, were they to become sympatric in the future.

The Yellow-eyed Junco (*Junco phaeonotus*) is a sedentary resident of arid conifer and pine (*Pinus*)-oak (*Quercus*) forests with a current distribution restricted to mountains between southeastern Arizona, USA and Guatemala (Sullivan 1999). Geographic song variation in the Yellow-eyed Junco is obvious to the ear and is one factor contributing to disagreement about how many species are involved in the complex. The fifth edition of the American Ornithologists' Union Checklist (AOU 1957) recognized two species: Baird's Junco (currently *J. p. bairdi*), isolated in the mountains of Baja California Sur, Mexico; and Yellow-eyed Junco (*J. p. palliatus* and *J. p. phaeonotus*), occurring in mainland Mexico and Arizona, USA. The AOU (1957) did not mention *J. p. fulvescens* or *J. p. alticola*, which occur in the mountains of Chiapas, Mexico and Guatemala, respectively. The 32nd AOU checklist supplement (AOU 1973) lumped Baird's Junco into Yellow-eyed Junco (*J. phaeonotus*, including *J. p. fulvescens* and *J. p. alticola*) without explaining the rationale for the change, although it cited authors who had lumped the groups (Paynter 1970) or recommended doing so (Mayr 1942). The AOU continues to treat all juncos with yellow eyes as a single species (AOU 1998). Howell and Webb (1995), however, recognized *J. p. bairdi* as a separate species from the rest of the Yellow-eyed Junco complex.

Howell and Webb (1995) describe marked differences in song between *J. p. bairdi* and mainland birds: *J. p. phaeonotus* sings ''a varied series of bright chips, often with trills or buzzes thrown in, typically the last note rising or upslurred… [that] can be confused with songs of Rufous-sided Towhee [*Pipilo* spp.] and Bewick's Wren [*Thryomanes bewickii*]'' (page 731), while *J. p. bairdi* sings ''a pleasant, tinkling, and trilled warble… [that] may suggest a small *Troglodytes* wren and strikingly different from mainland Yellow-eyed Juncos'' (page 730).

Differences between the songs of mainland *J. p. phaeonotus* and peninsular *J. p. bairdi* may be obvious to the human ear, and contributed to Howell and Webb's (1995) treatment of the populations as separate species, but the distinction has not been investigated quantitatively. The objective of this study was to investigate the extent and nature of vocal differences between *J. p. bairdi* Yellow-eyed Juncos and mainland Yellow-eyed Juncos from two regions (Arizona,

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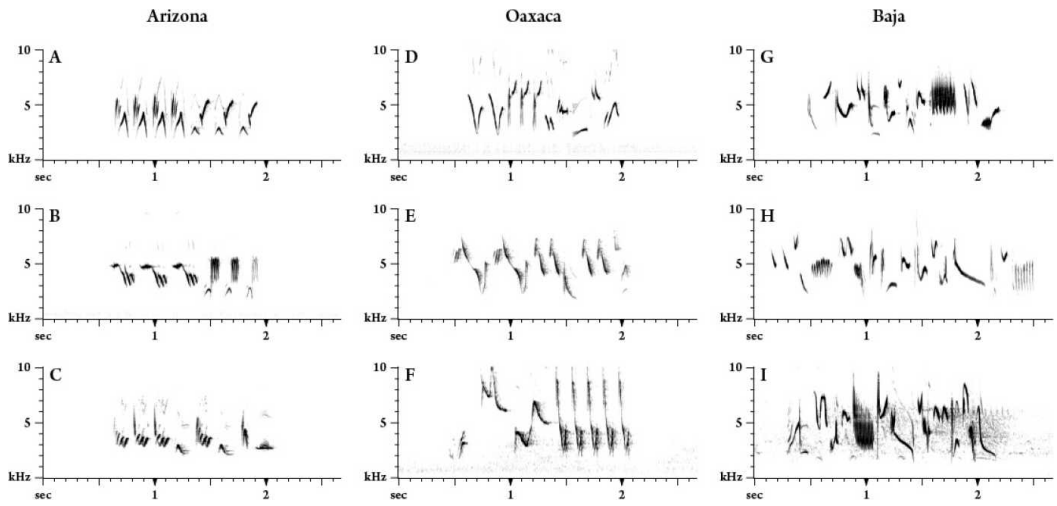


FIG. 1. Spectrograms of Yellow-eyed Junco songs from Arizona (A–C), Oaxaca, Mexico (D–F), and Baja California Sur, Mexico (G–I). All recordings by NDP except D (courtesy of Florida Museum of Natural History), E (Charlie Vogt), and F (Peter Boesman 2006). Complexity of song syntax increases from left to right.

USA and Oaxaca, Mexico). This study represents an initial quantitative assessment of differences between these taxa to identify potential barriers to gene flow between the isolated populations and to examine if re-evaluation of the taxonomic status of *J. p. bairdi* may be warranted.

## METHODS

*Recordings.*—Songs of *J. p. bairdi* were recorded on a Western Field Ornithologists and Sonoran Joint Venture expedition to the Sierra La Laguna, Baja California Sur, Mexico, during 14–19 July 2008. Songs of *J. p. palliatus* were recorded in the Huachuca and Chiricahua mountains, Arizona in May 2009. We considered the difference in the month of recording unlikely to influence study results, as both study sites were visited during the lengthy active breeding season; Arizona Yellow-eyed Juncos raise up to three broods per year from late April to the beginning of August (Sullivan 1999), while juncos in Baja California during the 2008 expedition were at all stages of breeding from nest-building to independent young (Carol Beardmore et al., unpubl. data).

Recordings were made in 24-bit WAV format with a sample rate of 44.1 kHz on a Fostex FR2-LE recorder with a 55-cm Telinga parabola and stereo DAT microphone. Additional recordings of *J. p. bairdi* from Baja California Sur, *J. p. palliatus* from Arizona, and nominate *J. p. phaeonotus* from Oaxaca were assembled from the collections of the Macaulay Library at the Cornell Laboratory of Ornithology, the Florida Museum of Natural History, the Borror Laboratory of Bioacoustics, the Xeno-Canto online collection, and the private collections of S. N. G. Howell, Andrew Spencer, and Richard Webster, as well as the commercially published audio collection of Boesman (2006). Recordings from the Macaulay Library, the Borror Laboratory of Bioacoustics, Xeno-Canto, and Boesman (2006) were originally obtained in MP3 format and converted to WAV format at 44.1 kHz for analysis. Recordings by S. N. G. Howell were digitized in WAV format at 44.1 kHz from the original cassette tape by NDP. Typical songs from each region are illustrated in Fig. 1.

We randomly selected five songs of the same song type from each recording for each individual sampled. The recording contained a single song type in almost all cases; if a recording included more than one song type, we randomly selected five songs of the song type that was most common on the recording. We used Marler and Isaac's (1961) definitions of junco song features: a note is a continuous vocal utterance, a syllable is two or more notes grouped to form a single coherent unit, a trill is a syllable repeated at least twice consecutively, and a phrase is one or more dissimilar syllables that are separated from other phrases by a trill. We measured 13 song features (Fig. 2): song length (sec), total number of

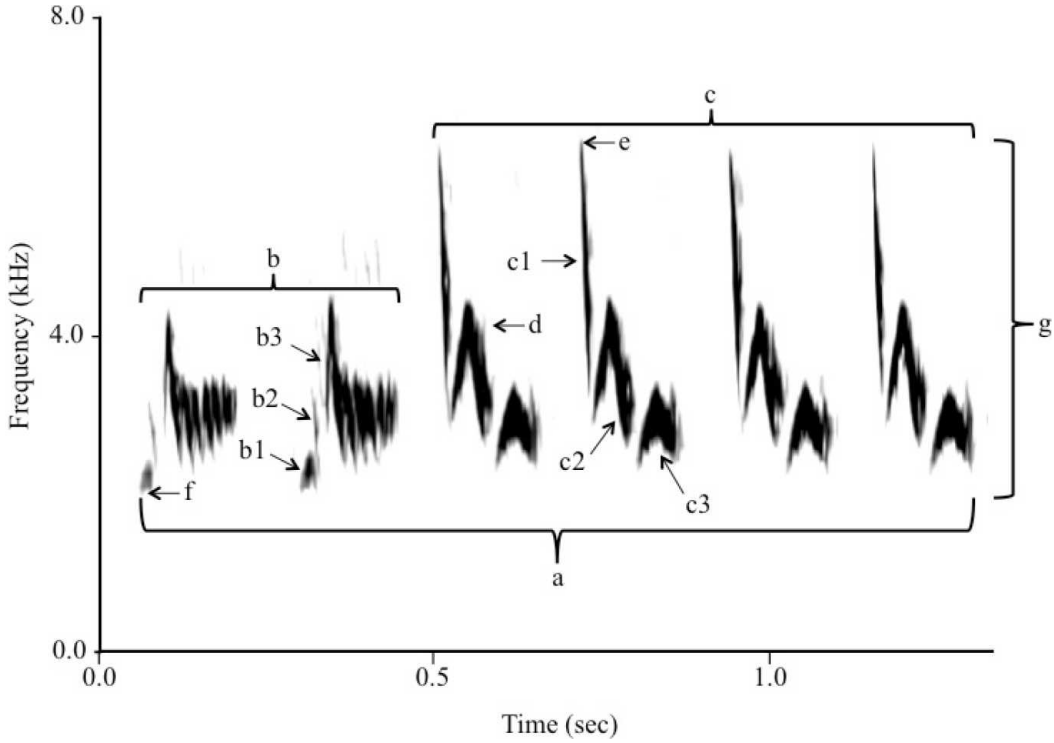


FIG. 2. Annotated spectrogram of a single Yellow-eyed Junco song from Arizona, USA, illustrating the measurements used in song analysis: (a) song length (sec), (b) two repeats of first unique syllable/trilled unit and its three unique notes (b1–3), (c) four repeats of the second unique syllable/trilled unit and its three unique notes (c1–3), (d) peak frequency, (e) highest frequency, (f) lowest frequency, and (g) frequency bandwidth. This song has six syllables, two of which are unique, resulting in a song average of three repeats per syllable. In this particular example, the number of unique trills is the same as the number of unique syllables and the number of repeats per trill is three, just as per syllable. This particular song does not have any phrases. Figure 1D, F, G–I illustrate sample phrases (continuous utterances of unrepeated, dissimilar syllables).

syllables, number of unique syllables, mean number of repetitions per syllable, number of trills, mean number of repeated syllables per trill, number of unique notes per trill, number of phrases, mean of number of notes per phrase, peak frequency (frequency of the maximum amplitude), lowest frequency, highest frequency, and bandwidth (highest frequency minus lowest frequency). We calculated the mean for each song feature for each vocalizing individual, and a single mean value represented each variable for an individual bird. All song measurements were performed manually in RavenPro 1.3 (Charif et al. 2008) using a Hamming window and a fast Fourier transformation (FFT) length of 1,024, providing a spectral resolution of 43 Hz.

*Statistical Analyses.*—We used two complementary methods to analyze differences in song characteristics among juncos from the three regions: (1) Kruskal-Wallis one-way analysis of variance with *post-hoc* comparisons based on pairwise Mann-Whitney *U*-tests and the studentized range (Sokal and Rohlf 1995), and (2) linear discriminant function analysis (DFA) to classify individuals to regions based on song features. The latter analysis may be biased towards correctly assigning groups, and we used a jackknifed classification matrix as a more conservative grouping method. All analyses were conducted in Program R (R Development Core Team 2009). Significance thresholds were adjusted to 0.0038 following a Bonferroni correction for multiple comparisons. Results are presented as means ± SE unless labeled otherwise.

## RESULTS

Eleven of the 13 features of Yellow-eyed Junco song differed among the three regions (all, $\chi^2 \geq 11.15$, $P \leq 0.0037$; Table 1). The only features that did not differ among regions were the number

TABLE 1. Song features (means ± SE) of Yellow-eyed Juncos from Baja California Sur, Mexico, Arizona, USA, and Oaxaca, Mexico.

| Song feature | Baja | Arizona | Oaxaca | $\chi^{2}$ [a] | $P$ [b] | *Post-hoc* [c] |
|---|---|---|---|---|---|---|
| Song length (sec) | 1.78±0.06 | 1.52±0.05 | 1.37±0.11 | 11.29 | <0.004 | B-A (<0.001), B-O (0.005), A-O (0.005) |
| Syllables per song | 11.52±1.02 | 10.24±0.83 | 8.18±0.98 | 17.37 | <0.001 | B-A (<0.001), B-O (<0.001), A-O (<0.001) |
| Number of unique syllables | 13.06±0.68 | 3.26±0.23 | 3.73±0.60 | 33.47 | <0.001 | B-A (<0.001), B-O (<0.001), A-O (0.72) |
| Repeats per syllable | 1.22±0.04 | 3.31±0.20 | 2.44±0.27 | 34.73 | <0.001 | B-A (<0.001), B-0 (<0.001), A-O (<0.001) |
| Number of trills | 1.73±0.25 | 2.01±0.12 | 2.00±0.41 | 2.69 | 0.26 | |
| Number of syllables per trill | 2.47±0.25 | 4.45±0.33 | 3.71±0.61 | 17.55 | <0.001 | B-A (<0.001), B-O (0.02), A-O (0.004) |
| Number of unique notes per trill | 1.47±0.22 | 2.96±0.22 | 3.30±0.60 | 22.85 | <0.001 | B-A (<0.001), B-O (<0.001), A-O (0.30) |
| Number of phrases | 2.00±0.13 | 0.32±0.08 | 0.50±0.19 | 34.03 | <0.001 | B-A (<0.001), B-O (<0.001), A-O (0.68) |
| Number of notes per phrase | 12.26±1.37 | 5.34±0.57 | 6.95±4.29 | 12.11 | 0.002 | B-A (<0.001), B-O (0.04, A-0 (0.39) |
| Peak frequency (Hz) | 5,290.46±154.28 | 4,631.59±99.34 | 4,384.19±283.61 | 14.75 | <0.001 | B-A (<0.001), B-O (0.003), A-O (0.07) |
| Lowest frequency (Hz) | 2,218.49±59.13 | 2,183.77±63.47 | 2,126.26±86.06 | 1.09 | 0.58 | |
| Highest frequency (Hz) | 7,959.87±161.34 | 7,063.27±173.82 | 7,749.82±377.44 | 12.40 | 0.002 | B-A (<0.001), B-O (0.27), A-O (<0.001) |
| Song bandwidth (Hz) | 5,741.38±194.69 | 4,879.50±184.70 | 5,623.56±408.50 | 11.15 | <0.004 | B-A (<0.001), B-O (0.58), AZ-O (<0.001) |

[a] $\chi^{2}$ values for Kruskal-Wallis tests comparing variation in song features among the three regions. Sample sizes for all features except number of notes per phrase were: Arizona, $n = 30$; Baja California, $n = 16$; Oaxaca, $n = 8$. Sample sizes for number of notes per phrase were Arizona, $n = 13$; Baja California, $n = 16$; Oaxaca, $n = 4$.

[b] Significance at $\alpha = 0.05$ when Bonferroni corrected was adjusted to $P \leq 0.0038$.

[c] Pairwise *post-hoc* comparisons are denoted as B-A for Baja vs. Arizona, B-O for Baja vs. Oaxaca, and A-O for Arizona vs. Oaxaca.

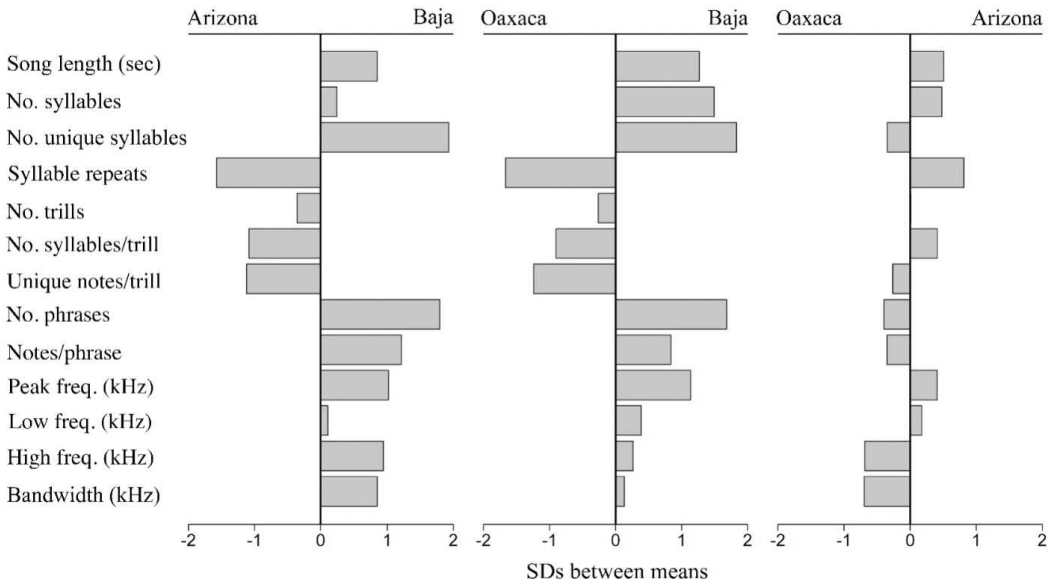


FIG. 3. Difference in song features among juncos from Arizona, USA, Baja California Sur, Mexico, and Oaxaca, Mexico. The size of the bar for each pair of regions reflects the number of pooled standard deviations (pooled from paired regions) between the means of the two regions under comparison. Bar size reflects how distinguishable the two regions are using the corresponding song feature; the direction of bar from center indicates the region with the larger mean value for the feature. Baja California songs are more distinguishable from those of Arizona and Oaxaca than Arizona songs are from Oaxaca songs.

of trills per song and the lowest frequency. Four features differed between Oaxaca and Arizona songs (all, $P < 0.001$); Baja California songs were different from those in Arizona for 11 features (all, $P < 0.001$) and were different from Oaxaca songs for six features (all, $P < 0.001$; Table 1, Fig. 3). Values for the number of unique syllables and the number of repeated syllables of the Baja California population did not overlap with values from the two mainland populations. Baja California songs had more unique and total syllables per song, and included more phrases than songs from the other two regions. Songs from Baja California had fewer repeats per syllable than those from Arizona or Oaxaca, which coincides with fewer trills and fewer repeated syllables per trill than songs from the two other regions. Baja California songs also were longer and had lower peak and highest frequencies and a narrower bandwidth than Arizona songs. Spectral features of Baja California and Oaxaca songs differed only in terms of peak frequency, while songs from Oaxaca were higher pitched in terms of highest frequency and had a broader bandwidth than those from Arizona.

Discriminant function analysis was based on all song features except number of notes per phrase because many songs from Oaxaca and Arizona lacked phrases. The analysis correctly assigned 87% of the songs to the correct region: 100% were correctly assigned to the Baja California region, 90% were correctly assigned to the Arizona region, and 50% were correctly assigned to the Oaxaca region. Three songs from Arizona were misclassified as from Oaxaca and four Oaxaca songs were misclassified as from Arizona. No Arizona or Oaxaca songs were misclassified as Baja California songs. The Baja California songs were easily distinguishable from Arizona and Oaxaca songs based on the first discriminant axis (97.5% of variance), but Arizona and Oaxaca songs were not easily identifiable based on this axis, nor on the second discriminant axis (2.5% of variance; Fig. 4). Variables with strong loadings on the first axis were song length (1.23) and number of phrases (1.48); those with strong loadings on the second axis were number of trills (1.09) and song length (−2.03; values of all other loadings are in Table 2).

## DISCUSSION

We found strong systematic differences between songs of *J. p. bairdi* and those of two

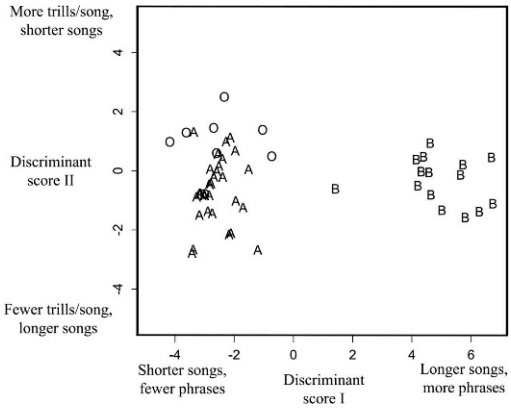


FIG. 4. DFA results of song variation of Yellow-eyed Juncos from Arizona, USA (A), Baja California Sur, Mexico (B), and Oaxaca, Mexico (O). Song features included as variables in the DFA included all features (Table 1) except number of notes per phrase. Discriminant score I explains 97.5% of the variance in the data and discriminant score II explains 2.5%. Baja California songs are easily distinguishable based on discriminant score I. Arizona and Oaxaca songs are not easily distinguishable from each other by either score.

TABLE 2. Percent variance explained and loadings of each song feature for discriminant axis I (DA I) and DA II.

| Variance explained/song feature | DA I | DA II |
|---|---|---|
| Percent variance explained | 97.50 | 2.50 |
| Song length (sec) | 1.23[a] | −2.03[a] |
| Syllables per song | −0.04 | −0.37 |
| Number of trills | −0.90 | 1.09[a] |
| Number of syllables per trill | −0.71 | 0.69 |
| Number of unique notes per trill | −0.43 | 0.04 |
| Number of unique syllables | 0.43 | 0.47 |
| Repeats per syllable | 0.58 | −0.33 |
| Number of phrases | 1.48[a] | −0.39 |
| Peak frequency (Hz) | 0.00 | 0.00 |
| Lowest frequency (Hz) | 0.00 | 0.00 |
| Highest frequency (Hz) | 0.00 | 0.00 |
| Song bandwidth (Hz) | 0.00 | 0.00 |

[a] Denote song features with strong loadings for that discriminant axis.

mainland Yellow-eyed Junco subspecies (*J. p. palliatus* and *J. p. phaeonotus*). The number of unique syllables per song and the number of repeated syllables are diagnostic because there is no overlap in these features between *J. p. bairdi* and mainland subspecies. In contrast, there were fewer differences between songs of the two mainland subspecies and they were not easily distinguishable from one another through discriminant function analysis.

Vocal features, like other phenotypic traits, are expected to diverge among species and subspecies over time for a variety of reasons (Irwin 2000). One potential explanation for the difference in song is that signal features have diverged in response to unique habitat features (*acoustic adaptation hypothesis*; e.g., Morton 1975, Boncoraglio and Saino 2007). However, because both mainland and peninsular populations inhabit structurally similar pine-oak forests and arid woodlands (Sullivan 1999), it is unlikely that habitat features would differ sufficiently to account for significant differences in song features.

A more probable explanation for the distinctly different *J. p. bairdi* song may be that sexual selection pressures have differed for *J. p. bairdi* relative to mainland populations (e.g., Irwin et al. 2001). It is not clear whether the difference in song would constitute a behavioral barrier to gene flow upon secondary contact among these currently allopatric populations. Song can be used in combination with other tools to identify taxonomic boundaries (Irwin et al. 2001, Päckert et al. 2004, Toews and Irwin 2008), and our results provide initial support for re-evaluating the taxonomic status of *J. p. bairdi*. However, several key pieces of information are still needed to clarify taxonomic limits. A phylogenetic analysis of the genus *Junco* by Milá et al. (2007) concluded the genus represents a case of extremely rapid diversification following a postglacial range expansion. Unfortunately, individuals from Baja California Sur (*J. p. bairdi*) were not included in their analysis, and knowledge of this population's phylogenetic relationship with the rest of the genus is lacking.

The largest differences in song were between *J. p. bairdi* and the two mainland subspecies, but our results also show some variation within the songs of mainland Yellow-eyed Juncos. Oaxaca birds sing slightly shorter songs with fewer repeated syllables and shorter trills (fewer syllables per trill) than birds from Arizona. Overall, there appears to be a gradual trend towards increased song complexity (e.g., an increased number of unique syllables and a decrease in the number of repeated syllables) with decreasing latitude among populations included in this study and throughout the ranges of all *Junco* taxa in western North America (NDP, pers. obs.). Most taxa currently included in the Dark-eyed Junco (*J. hyemalis*) complex sing simple songs consisting

of a single trill (a single syllable rapidly repeated), while songs of the 'Red-backed' form in northern Arizona (*J. hyemalis dorsalis*) frequently consist of two or three trills, or a trill with one or two buzzy notes (Thatcher 1968, Sibley 2000, Christian Nunes recordings), and are apparently intermediate in complexity between the songs of other Dark-eyed Juncos and those of *J. p. palliatus* Yellow-eyed Juncos in southeastern Arizona. This trend of increasing complexity may continue south at least to Oaxaca. It is presently unknown whether songs of the Yellow-eyed Junco subspecies south of the Isthmus of Tehuantepec (*J. p. fulvescens* and *J. p. alticola*) differ from those north of the Isthmus, and we do not know of any recordings of these taxa. Howell and Webb (1995: 731) describe the song of *J. p. alticola*, which resides south of the isthmus, as ''a varied series of bright chips, usually the last note rising… much like *phaeonotus*.'' Additional recordings from the two southernmost subspecies are needed to understand vocal variation among juncos.

It is clear the song of *J. p. bairdi* is distinct from that of other Yellow-eyed Junco subspecies, but whether this difference is indicative of an important reproductive barrier is unknown. Still needed are field and molecular studies. Playback experiments are necessary to ascertain whether and how individuals of *J. p. bairdi* respond to songs from other regions and vice versa. Molecular analyses comparing mitochondrial and nuclear DNA of *J. p. bairdi* with those groups included in Milá et al. (2007) may provide insight on whether gene flow exists between Baja California juncos and populations on the mainland and, if it does not, how long the population has been genetically isolated and how it is related to the rest of the clade. Promotion to species status may be warranted if field and molecular studies confirm that *J. p. bairdi* is behaviorally and genetically distinct from mainland juncos.

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