

GEOGRAPHIC VARIATION IN THE SONG OF WILLOW FLYCATCHERS: DIFFERENTIATION BETWEEN *EMPIDONAX TRAILLII ADASTUS* AND *E. T. EXTIMUS*

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ABSTRACT.—The vocal signatures of the primary song form (“fitz-bew”) of the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) and its northern counterpart, *E. t. adastus*, are distinctive. Songs of the *extimus* subspecies are longer (total song, note, inter-note) and frequencies at maximum amplitude are lower than those of *adastus*. I used vocal evidence to clarify the distributional limits of the Southwestern Willow Flycatcher and that of the geographically adjacent subspecies, *E. t. adastus*. Unweighted pair-group method using averaging (UPGMA) cluster analysis and canonical discriminant analysis revealed that (1) low elevation, southerly desert populations (Arizona, New Mexico, and southern Utah) have a unique vocal identity corresponding to populations in the range of *E. t. extimus*; (2) northerly song groups (Oregon, Colorado, and northern Utah) share a different song type corresponding to populations in the range of *E. t. adastus*; and (3) a departure from vocal and morphological congruence occurs for a population of high-elevation Arizona birds that, although in the currently accepted range of *E. t. extimus*, sings songs acoustically similar to more northern populations (*E. t. adastus*). Multiple regression of song distance on latitude and elevation, and a comparison of a matrix of song distances with a matrix of latitude and elevation dissimilarities, demonstrated that song populations sort out by both latitude and elevation: birds with the vocal identity of *extimus* occur as far north as 37°N if at low elevation, and those acoustically similar to *adastus* occur as far south as 33.7°N if at high elevation. The vocal background of northern New Mexico birds appears to be intermediate between that of *extimus* and *adastus*, suggesting that northern New Mexico is a zone of intermixing and intergradation between the subspecies. Pure forms of *E. t. extimus* apparently do not occur in Colorado because even the southernmost populations are acoustically similar to more northerly populations of *adastus*. A low-elevation population in western Colorado, however, stands apart from other *adastus* populations, suggesting moderate introgression of *extimus* genes into the *adastus* gene pool. Received 28 January 2000, accepted 16 September 2000.

THE WILLOW FLYCATCHER (*Empidonax traillii*) is a common migratory species that breeds in a variety of usually shrubby, often wet habitats from Maine to British Columbia and as far south as southern Arizona and southern California. Either four or five subspecies are recognized (*E. t. traillii*, *E. t. brewsteri*, *E. t. adastus*, *E. t. extimus*, and some also recognize *E. t. campestris*), but subspecific differentiation based on morphology and plumage is often indeterminate (Phillips 1948, Aldrich 1951, Behle 1985, Hubbard 1987, Unitt 1987, Browning 1993). Subspecific taxonomy and, as a corollary, distributional limits of the races of Willow Flycatcher have been clouded by minor differences in morphology, subtle and complex variation in plumage, and relatively few breeding-season

specimen records, especially in parts of the western and southwestern United States. The distributional limits between the endangered Southwestern Willow Flycatcher (*E. t. extimus*) and the geographically adjacent *E. t. adastus* race are especially unclear: the northern extent of pure forms of *extimus* in New Mexico, its occurrence in Colorado, and the possible occurrence of *adastus* in Arizona remain unresolved on the basis of morphological taxonomy.

Geographic variation in bird song can be used in much the same way that variation in morphological characters is used to study avian systematics (Baker 1975, Payne 1986, Kroodsma 1989). For example, avian song has been used to delimit species ranges (Marshall 1967, 1978), to confirm the distinctiveness of species (Johnson 1963, 1980), to infer historical founding processes (Baker and Thompson 1985), as an indicator of evolutionary diver-

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gence for morphologically indistinct populations (Kroodsma 1989, Moldenhauer 1992), and has led to the recognition of sympatric sibling species (Stein 1963, Ratti 1979, Nuechterli 1981; for review, see Payne 1986).

Willow Flycatchers are particularly appropriate for acoustic analysis because they do not imitate their vocalizations from other individuals; the song of hand-reared birds raised in isolation has an adult-like pattern and does not derive from earlier sounds (Kroodsma 1984). Because avian song is either innate, acquired through learning, or is partly genetically and partly culturally based (Kroodsma 1989, Baptista and Gaunt 1994), there is a great deal of variability in the usefulness of avian song in systematics (Payne 1986, Slater 1989). Studies of acoustic variation to examine taxonomic relationships are perhaps most useful for species where the song is innate. Innate songs are highly stereotyped, and clues to genetic identity are not complicated by song-learning from different tutors at different times. Learned song, which is not genetically based, is less likely to be a good indicator of genotype, because cultural evolution may obscure species relationships (but see, e.g. Baker and Thompson 1985, and Kroodsma 1989). Because the vocal displays of Willow Flycatchers are innate, they provide evidence of genetic background (Kroodsma et al. 1995), and vocal differentiation may be used to make taxonomic inference.

The study of acoustic variation as a guide to species relatedness may be especially worthwhile when the evolution of morphology and vocalizations has become decoupled. In the case of *Empidonax* flycatchers, the evolution of song has outpaced that of plumage and morphology (Zink and Johnson 1984): morphologic uniformity contrasts with striking differences in song, pointing to more rapid evolutionary rates for vocalizations. The discordance of morphological and vocal evolution is nowhere more evident than for the Willow Flycatcher. Its convoluted taxonomic history is a consequence of close morphological similarity to the Alder Flycatcher (*E. alnorum*), and disentanglement of the two forms of Traill's Flycatcher (AOU 1973) rested not on morphological differentiation, but on differences in song (Stein 1963).

I report results of a vocal survey of the endangered Southwestern Willow Flycatcher and the geographically adjacent *E. t. adastus*. Using

vocal evidence, I describe the pattern of geographic variation in advertising song, suggest subspecies limits between *E. t. adastus* and *E. t. extimus*, and compare the taxonomies inferred from vocal and morphological data.

METHODS

Study areas.—Recordings of Willow Flycatcher songs were secured from within the currently defined ranges of *E. t. adastus* and *E. t. extimus* in Arizona, New Mexico, Colorado, Utah, and Oregon, mostly in 1994, 1995, and 1998. Song samples encompass nearly the entire range of latitudes and elevations over which the two subspecies are found. Songs were recorded at 45 locations and organized by geographical proximity into 16 different populations or song groups for analysis (Table 1, Fig. 1). I conservatively assigned subspecific identity according to geographic location and currently accepted taxonomy (Phillips 1948, Aldrich 1951, Hubbard 1987, Unitt 1987, Browning 1993). Northerly populations, generally thought to be *E. t. adastus* ($n = 44$ individuals), were recorded in Oregon (population A1), north-central and northeastern Utah (populations A2 and A3), and in northern Colorado (population A4). Southerly populations, believed to be *E. t. extimus* ($n = 41$ individuals), were recorded in south-central and southwestern New Mexico (population E1), southwestern Utah (population E2), and in Arizona (populations E3–E5). Assignment of songs to the northern (= *adastus*) and southern (= *extimus*) populations correspond to published ranges and known specimens of those two subspecies (Browning 1993, Unitt 1987, 1999). Because the northern extent of *E. t. extimus* is in question, central song populations ($n = 69$ individuals), including birds in western, west-central, southwestern, and southern Colorado, and those in northern New Mexico and south-central Utah (populations U1–U6) were conservatively recorded as birds of unknown taxonomic status (Table 1, Fig. 1). In addition, a high-elevation population of birds in east-central Arizona (population U7), whose taxonomic status has recently been reconsidered (Sedgwick 1997), was also included in the group of birds of uncertain taxonomy. In all, I recorded and analyzed the advertising songs of 154 different males.

Field recording.—Most vocalizations were recorded with a Sony TC-D5 PRO II cassette recorder and Pre-amp coupled with a Sennheiser ME20 omnidirectional microphone mounted in a 61-cm Roche graphite parabolic reflector. Five songs from New Mexico were recorded with a Sony Pro-Walkman WM-D6C cassette recorder and Dan Gibson 46 cm parabola microphone setup, and two songs from Arizona were recorded with a Sony TCM-5000 cassette recorder, coupled with a Sennheiser ME20 microphone

TABLE 1. Geographical song groups of Willow Flycatchers. Northern (A1–A4) and southern (E1–E5) song groups are known to be *E. t. adastus* and *E. t. extimus*, respectively, based on currently accepted taxonomy. Status of the central song groups (U1–U7) is less certain.

| Group | <i>n</i> | Location | Morphological taxonomy | Latitude | Elevation (m) | County |
|-----------------------------|----------|-------------------------|------------------------|---------------|---------------|--------------------------------|
| Northern song groups | | | | | | |
| A1 | 12 | Southeastern Oregon | <i>E. t. adastus</i> | 42°52' | 1270 | Harney |
| A2 | 9 | North-central Utah | <i>E. t. adastus</i> | 39°46'–40°53' | 1460–2740 | Carbon, Morgan, Weber, Wasatch |
| A3 | 8 | Northeastern Utah | <i>E. t. adastus</i> | 40°21' | 1550 | Uintah |
| A4 | 15 | Northern Colorado | <i>E. t. adastus</i> | 40°05'–40°32' | 1830–2470 | Rio Blanco, Jackson |
| Central song groups | | | | | | |
| U1 | 14 | West-central Colorado | ? | 38°52'–39°13' | 2500–2680 | Gunnison, Mesa |
| U2 | 9 | Western Colorado | ? | 38°45' | <1500 | Delta |
| U3 | 13 | Southwestern Colorado | ? | 37°39'–37°47' | 2430–2830 | Dolores |
| U4 | 15 | South-central Colorado | ? | 37°17'–37°26' | 2290–2300 | Alamosa, Conejos |
| U5 | 2 | South-central Utah | ? | 38°20'–38°22' | 2130–2740 | Sevier, Wayne |
| U6 | 11 | Northern New Mexico | ? | 35°59'–36°53' | 2000 | Taos, Rio Arriba, San Juan |
| U7 | 5 | East-central Arizona | ? | 33°40'–33°49' | >2400 | Apache |
| Southern song groups | | | | | | |
| E1 | 8 | Southwestern New Mexico | <i>E. t. extimus</i> | 32°58'–33°49' | <1340 | Socorro, Grant |
| E2 | 1 | Southwestern Utah | <i>E. t. extimus</i> | 37°05' | 820 | Washington |
| E3 | 5 | West-central Arizona | <i>E. t. extimus</i> | 34°13'–34°38' | <200 | Mohave |
| E4 | 13 | South-central Arizona | <i>E. t. extimus</i> | 33°27'–33°35' | <700 | Gila |
| E5 | 14 | Southeastern Arizona | <i>E. t. extimus</i> | 32°51'–32°52' | <700 | Cochise |

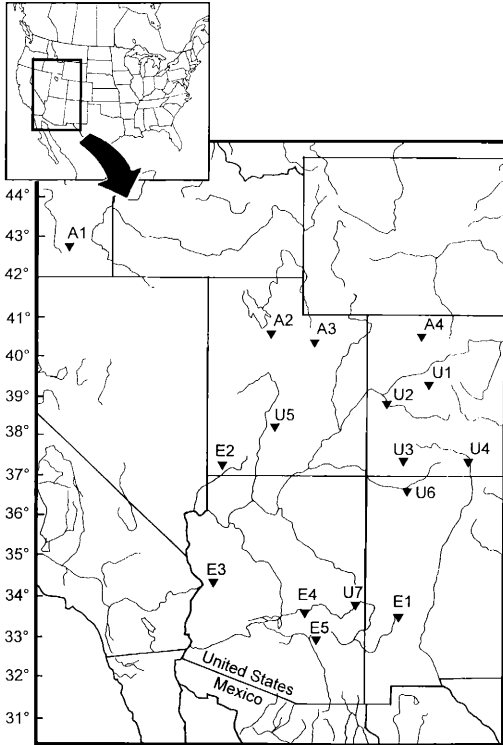


FIG. 1. Localities where Willow Flycatchers were recorded. A1–A4 = *E. t. adastus*; E1–E5 = *E. t. extimus*; and U1–U7 = unknown subspecies. Details of site locations are in Table 1.

mounted in a 61 cm parabolic reflector. Those minor differences in recording system configurations are not thought to affect interpretation or analysis of spectrograms.

Most recordings were made in June and July during the peak of breeding activity. Some southern populations, which initiate nesting earlier, were recorded in late May; songs of a few individuals were recorded as late as August. Because Willow Flycatchers may sing during spring migration, the possibility of recording a singing migrant of one subspecies in the breeding range of another becomes an issue. Spring song by migrant Willow Flycatchers is thought to be relatively uncommon (Stein 1963, Sedgwick 2000, J. Travis pers. comm.) but may become more frequent as birds approach their breeding grounds (Unitt 1987). I took the following precautions to guard against recording migrants: (1) recordings were secured only from birds singing at high rates and which appeared to be territorial; (2) recordings were made only at known, historical breeding sites; (3) at sites where recordings were made during periods of potential temporary occupancy by passage migrants, the continued presence (≤ 3 days) of birds in territories on successive re-

cording visits suggested resident status, and; (4) most recordings (68%) were secured during the relatively short interval (10 June–17 July) between the majority of spring and fall migratory activity in this species (Ely 1970, Hussell 1991a, b; Sedgwick 2000). Birds recorded in August, near the onset of fall migration, were almost certainly territorial occupants because singing during the fall passage has not been reported for this species (Sedgwick 2000). Females also occasionally sing the advertising song (Seutin 1987), but such vocalizations are given only infrequently (Sedgwick 2000). In any event, songs of females are spectrographically similar to (Kroodsmma 1984) and sound like those of males.

Sound analysis.—Digital sound acquisition, storage, and analysis were performed using Real Time Spectrogram (RTS) version 1.23, and SIGNAL version 3.0 programs and hardware (Beeman 1996). Songs were stored as digitized waveforms in computer files using RTS (sample rate = 25 kHz). Twenty measures of duration and 14 measures of frequency were taken from each song (Tables 2 and 3, Fig. 2). Acoustic features of duration comprised measures of song, phrase, note, frequency modulation (FM), and internote lengths determined in RTS. Parameters of frequency included measures of song, phrase, and note frequencies at maximum amplitude or at -20 db below maximum amplitude; those measures of the distribution of sound energy among frequencies (hertz) were determined from power spectrums (frequency vs. amplitude displays) in SIGNAL. Hard-copy spectrograms were produced from SIGNAL (sample rate = 25 kHz, frequency range = 10 kHz, transform size = 128 points).

The song.—Three different song forms are used by the Willow Flycatcher, the “fizz-bew”, a slightly more buzzy “fizz-bew”, and the “creet” (after Stein 1963). All three types are part of the song repertoire, with the *fitz-bew* being given most frequently (Sedgwick 2000). This study examines only the *fitz-bew* song form, which, based on earlier analyses, demonstrated more differences across subspecies. *Fitz-bew* songs are composed of three phrases (Fig. 2). Phrase I is composed of two notes (continuous traces on a spectrogram)—the first ascending in frequency and averaging 40–75 ms in duration. The second note of phrase I is shorter in duration but often of higher peak frequency. Phrase II typically consists of three notes, all usually lower in frequency than phrase I notes and all of relatively short duration, typically lasting from 6–27 ms. Phrase III consists of two parts, the first made up of a series of 10–15 closely spaced FM sounds, each lasting only 4–5 ms. The second part of phrase III consists of FMs (usually 5–10) of longer duration (15–35 ms).

Statistical analysis.—For all but one of the analyses, spectrograms were grouped according to geographical proximity (Table 1, Fig. 1). That resulted in 16 song groups for analysis. I first compared variable

TABLE 2. Most univariate differences in acoustic features of duration (msec) and counts of frequency modulations (FMs) occurred between populations of *E. t. extimus* (E1–E5) and either *E. t. adastus* (A1–A4) or unknown song groups (U1–U7). Unknown and *adastus* song groups were nearly always similar to one another for any given song character.

| Song variable | F | P | Bonferroni difference among groups |
|--|-------|--------|---|
| Features of Duration (msec) | | | |
| Total song (Sd) | 4.80 | 0.0001 | (E3 = E4) > (A2 = U7) ^a |
| Phrase I | | | |
| Phrase I (P1d) | 2.74 | 0.0010 | nd ^b |
| First note (P1n1d) | 3.14 | 0.0002 | (U4 = E4) > U7 |
| First to second note interval (P1i1) | 1.90 | 0.0285 | nd |
| Second note (P1n2d) | 2.65 | 0.0015 | U1 > E2 |
| Phrase I to phrase II interval (Ipi1) | 2.30 | 0.0060 | nd |
| Phrase II | | | |
| Phrase II (P2d) | 3.80 | 0.0001 | nd |
| First note (P2n1d) | 4.37 | 0.0001 | E5 > (A2 = E2) |
| First to second note interval (P2i1) | 3.15 | 0.0002 | E3 > (A3 = U1) |
| Second note (P2n2d) | 0.55 | 0.9054 | nd |
| Second to third note interval (P2i2) | 7.08 | 0.0001 | U5 > (E1 = E3 = E4 = E5); (A2 = U5) > (E3 = E4 = E5); (A2 = A4 = U5) > (E3 = E4) |
| Third note (P2n3d) | 4.84 | 0.0001 | E2 > (A2 = U7) |
| Phrase II to phrase III interval from end of first note (Ipi21) | 3.04 | 0.0003 | E3 > (A3 = U1 = U7) |
| Phrase II to phrase III interval from end of second note (Ipi22) | 1.18 | 0.2912 | nd |
| Phrase III | | | |
| Phrase III (Pd3) | 2.29 | 0.0064 | nd |
| First part (P3ad) | 3.34 | 0.0001 | U2 > E5 |
| Second part (P3bd) | 2.27 | 0.0068 | nd |
| FM 3 of second part (P3bc3d) | 80.94 | 0.0001 | (E1 = E2 = E3 = E4 = E5) > (A1 = ... = A4 = U1 = ... = U7) |
| Number of frequency modulations | | | |
| First part of phrase III (P3afm) | 3.64 | 0.0001 | U2 > E5 |
| Second part of phrase III (P3bfm) | 10.67 | 0.0001 | U4 > (E1 = E2 = E3 = E4 = E5); (U4 = A1) > (E2 = E4 = E5); (A1 = ... = A4 = U1 = ... = U5) > E4; (A1 = A2 = A3 = U1 = U2 = U4 = U5) > (E4 = E5) |

^a A greater-than sign (>) indicates a significant Bonferroni difference between groups. An equal sign (=) indicates no Bonferroni difference among groups.

^b No Bonferroni differences among any groups.

means with one-way ANOVA, using Bonferroni's multiple-comparison test to determine specific differences among group means. To summarize differences among song groups and reduce the dimensionality of the data, I used canonical discriminant analysis (CDA). Scores on canonical variables, plots of scores, and squared distances between class means (Mahalanobis distances) in discriminant "song space" were used to explore the pattern of vocal similarity among songs and song groups. Reduction of the original variable set before performing the CDA entailed (a) discarding variables not signifi-

cantly different ($P > 0.05$) in the univariate ANOVA or not demonstrating Bonferroni differences across groups, (b) elimination of one of pairs of variables correlated at $r > 0.7$, and, (c) further variable reduction with stepwise discriminant analysis, which selected a subset of song variables able to discriminate among the song groups.

I performed a UPGMA (unweighted pair-group method using averaging) cluster analysis to further evaluate the geographic patterning of the song groups. A linkage-tree diagram was constructed from the song (Mahalanobis) distance matrix of the

TABLE 3. Most univariate differences in acoustic features of frequency (kilohertz) at maximum amplitude occurred between populations of *E. t. extimus* (E1–E5) and either *E. t. adastus* (A1–A4) or the unknown song groups (U1–U7). Unknown and *adastus* song groups were nearly always similar to one another for any given song character.

| Song Variable (frequency [kHz] at maximum amplitude) | F | P | Bonferroni difference among groups |
|--|------|--------|--|
| Total song (Sf) | 4.85 | 0.0001 | nd ^a |
| Total song ^c (Sflo) | 5.18 | 0.0001 | (U5 = U7) > (E1 = E2 = E3); (A3 = A4 = U5 = U7) > (E1 = E3) ^b |
| Total song ^d (Sfhi) | 9.46 | 0.0001 | (A3 = U1 = U4) > (E1 = E2 = E3 = E5); (A3 = U1 = U3 = U4) > (E1 = E3); (A3 = U1 = U3 = U4 = U7) > E1 |
| Phrase I | | | |
| Phrase I (P1f) | 6.01 | 0.0001 | U5 > (E1 = E2 = E3); (A3 = U3 = U5) > E2 |
| First note (P1n1f) | 5.22 | 0.0001 | U5 > (E1 = E2 = E3 = E4 = E5); (A3 = U5) > (E1 = E2 = E3) |
| Second note (P1n2f) | 3.28 | 0.0001 | (A3 = A4 = U1 = U3 = U4) > E3 |
| Phrase II | | | |
| Phrase II (P2f) | 2.57 | 0.0021 | A2 > (E2 = E3) |
| First note (P2n1f) | 2.15 | 0.0107 | nd |
| Second note (P2n2f) | 7.98 | 0.0001 | (A2 = A3) > (E2 = E3 = E4 = E5); (A2 = A3 = U5) > (E2 = E3 = E4); (A2 = A3 = A4 = U5) > (E3 = E4) |
| Third note (P2n3f) | 0.52 | 0.9269 | nd |
| Phrase III | | | |
| Phrase III (P3f) | 1.99 | 0.0197 | nd |
| First part (P3af) | 3.65 | 0.0001 | (A1 = ... = A4 = U1 = ... = U7) > E2 |
| Second part (P3bf) | 2.30 | 0.0061 | nd |
| First FM of second part (P3bc1f) | 7.10 | 0.0001 | U5 > (E1 = E2 = E3 = E4 = E5); (A2 = U5) > (E1 = E2 = E3 = E5); (A1 = ... = A4 = U3 = U4 = U5) > (E1 = E2); (A1 = ... = A4 = U2 = ... = U6) > E2 |

^a No Bonferroni differences among any groups.

^b A greater-than sign (>) indicates a significant Bonferroni difference between groups. An equal sign (=) indicates no Bonferroni difference among groups.

^c Low frequency at -20db below maximum amplitude.

^d High frequency at -20db below maximum amplitude.

16-group CDA. The topology of the phenogram—similar song groups were joined at smaller distances and dissimilar groups were united at greater distances—suggested acoustic relationships of the 16 populations. A second UPGMA cluster analysis was performed on all 154 songs without assigning songs to geographical groups. Using the same reduced set of variables as was entered into the CDA, cluster analysis was used to hierarchically group individual songs sharing similarities in measured song characters. A phenogram was constructed from the matrix of between-song Euclidean distances, computed from the original, coordinate data (first standardized to $\bar{x} = 0$ and $SD = 1$). That provided a visual representation of the relationships of individual songs and an expression of the pattern of vocal similarity.

I evaluated the relationship between song type versus latitude and elevation in two ways. First, I regressed canonical scores of bird songs on latitude and elevation, and second, I used the Mantel test (Mantel 1967) to compare the matrix of song distances with a matrix of latitude and elevation dissimilarities. Distance matrices were derived from sepa-

rate, 16-group CDAs on the song variables and on the measures of latitude and elevation, respectively. The significance level of the Mantel statistic was determined by performing 5,000 Monte Carlo randomization simulations, followed by comparison of the test statistic with the randomization distribution (Manly 1991). All statistical procedures were conducted on the Statistical Analysis System, version 7 (SAS Institute, Inc. 1998) with the exception of the Mantel test, which was performed on the NetMul Web site with the ADE-4 multivariate analysis software package.

RESULTS

Univariate analysis.—Of 20 measures of duration or counts of notes, 12 differed ($P < 0.05$) and demonstrated Bonferroni differences across song groups (Table 2). In all cases, Bonferroni differences occurred between one or more of the southerly *extimus* song groups (E1–E5) and other populations. For total song du-

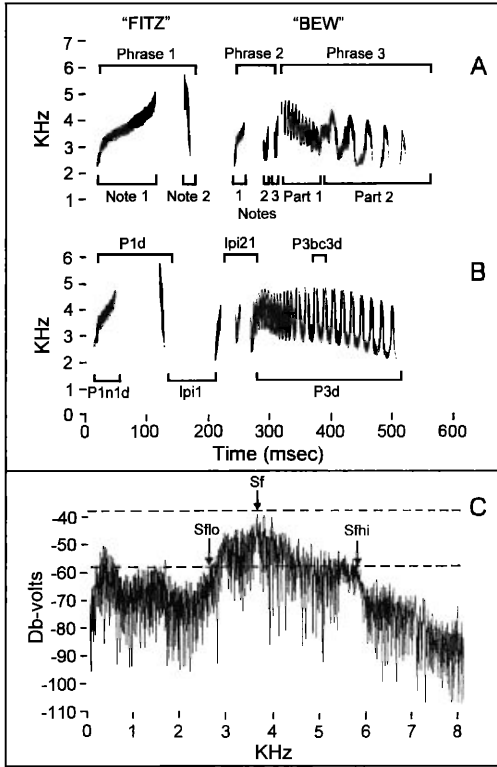


FIG. 2. A typical song of *E. t. extimus* (A) showing components and descriptive terminology of the "fitz-bew" song form of the Willow Flycatcher; note fewer, and more widely spaced frequency modulations (FMs) in phrase III, part 2. Typical song of *E. t. adastus* (B), showing some of the measures of duration taken from each song; note more numerous, and more closely spaced FMs in phrase III, part 2. Power spectrum (C) illustrating measures of frequency at maximum amplitude and at -20 db below maximum amplitude.

ration, for example, southerly groups E3 and E4 differed from groups A2 and U7 (high-elevation Arizona). The difference in the duration of the FMs in the second part of the phrase III (P3bc3d) was especially important in distinguishing among groups; that for southerly groups ranged from 26.6–32.1 ms compared to a range of only 15.6–16.3 ms for the more northerly song groups (see also Fig. 2). Song population U7, in the geographic range of *E. t. extimus*, was acoustically more similar to northerly *adastus* populations than to southerly *extimus* populations for every parameter where Bonferroni differences were expressed (Table 2).

Nine measures of frequency differed ($P < 0.05$) and demonstrated Bonferroni differences across groups (Table 3). Again, Bonferroni differences were expressed as combinations of southerly populations of *E. t. extimus* (E1–E5) differing from the other groups. For all nine variables, the frequency at maximum amplitude was less for one or more southerly *extimus* song groups than for various subsets of the other 11 groups. For example, low frequency (Sflo) of the total song ($F = 5.18$, $df = 15$ and 138 , $P = 0.0001$) was lower for groups E1, E2, and E3 than for groups U5 and U7, and was lower for groups E1 and E3 than for groups A3, A4, U5, and U7 (Table 3). Again, the high-elevation Arizona population (U7) had a vocal identity more similar to that of northern song groups than to the southerly *extimus* populations.

Multivariate analysis.—Differences among song group means were striking; 11 of 20 variables were selected by the stepwise procedure for inclusion in the CDA, and four canonical discriminant functions (CDF) were significant ($P < 0.05$). CDF1 explained a major component (81%) of the between-group to pooled-within-group variation, being largely a measure of the length of FMs in the second part of the phrase III (P3bc3d) (correlation with CDF1 = 0.86).

Songs of birds from southerly *extimus* song groups (E1–E5) had high CDF1 scores and were situated to the right along CDF1 (Fig. 3), having long durations of FMs in the second part of phrase III. Songs of birds from the northerly *adastus* groups (A1–A4) had low CDF1 scores and were situated to the left along CDF1, having shorter durations of FMs in the second part of phrase III. Most of the birds of unknown taxonomy (U1–U7) were also situated to the left, falling within *adastus* song space. Songs of northern New Mexico population U6 were highly variable and centrally located along CDF1 (some lying to the right edge of the *adastus* cluster of points and some lying to the left edge of the *extimus* cluster). That is consistent with the extraordinarily high coefficient of variation for the northern New Mexico song group CDF1 mean ($CV = -2305\%$), pointing to acoustic heterogeneity in that region. Birds of Arizona song population U7, in the geographic range of *extimus*, grouped with the more northerly song populations, known to be *E. t. adastus*. Songs of individuals from the intermediate elevation population in western Colorado (U2)

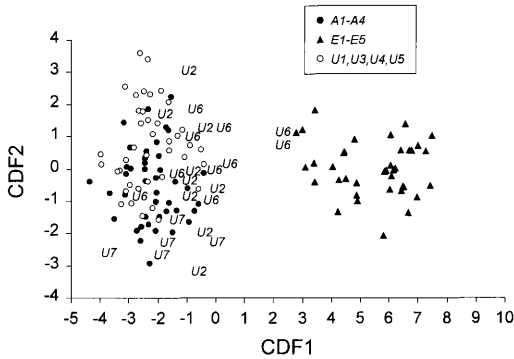


FIG. 3. Songs of *E. t. extimus* (triangles) and *E. t. adastus* (closed circles) are well separated in canonical song space. Songs of birds of unknown subspecies (open circles, representing populations U1, U3–U5), including those of a high-elevation Arizona population (U7) are situated within *adastus* song space. Songs of northern New Mexico (U6) and western Colorado (U2) birds lay near the edges of *adastus* song space, *extimus* song space, or both, suggesting intergradation.

were more closely aligned with northern, *adastus* song groups, but many songs fell near the right edge of *adastus* song space. Separation of song groups along CDF2, CDF3, and CDF4 was not as conspicuous as along CDF1, but those three canonical functions together summarized only 14% of the between-group variation in measured song characters.

Multivariate (Mahalanobis) distances between group means confirm the ordination of the 16 populations in song space (Fig. 3, Table 4). Northern *adastus* song groups (A1–A4) were close to other northern groups ($M = 3.59$, range = 1.50–6.46) and distances from southern, *extimus* (E1–E5) to other southern populations ($M = 9.93$, range = 5.13–16.72) were small, as well. Distances between song group means of *adastus* versus *extimus* populations ($M = 61.55$, range = 41.99–82.83) were much greater. Song group means of birds of uncertain taxonomic status (U1–U7) were more distant from southerly *extimus* populations ($M = 56.80$, range = 19.51–86.23) than from northerly, *adastus* populations ($M = 6.96$, range = 2.89–13.44), pointing to their closer vocal affinities with *adastus*. The acoustic background of two of those song groups of unknown taxonomic status stand apart from the others: northern New Mexico (U6) and western Colorado songs (U2) were not as vocally distinct, when compared to the five

extimus song groups, as were the remaining song groups of unknown taxonomy. The mean Mahalanobis distances of the two groups to *extimus* populations were notably small ($M = 33.73$, northern New Mexico birds; $M = 41.3$, western Colorado birds) compared to the other five groups of unknown taxonomy ($M = 60.07$ –74.17). Those smaller distances in song space suggest, for the northern New Mexico group, the presence of both *extimus* and *adastus* birds in the population, in addition to intergradation, and for the western Colorado birds, dilution of the *adastus* song type by birds with the vocal background of *extimus* (see also Fig. 3).

UPGMA cluster analyses revealed patterns of vocal relationships similar to those discovered from the univariate and canonical discriminant analyses. The dendrogram based on the 16 geographic song groups (Fig. 4) contains two distinct clusters, one linking *extimus* populations (E1–E5), and another joining the remaining song groups (A1–A4 and U1–U7). Within the two major clusters, song groups are separated by short branch lengths whereas the longest branch of the tree distinguishes the southerly from the more northerly populations.

The phenogram based on all 154 individual songs (not shown) was consistent with previous analyses. Two clusters distinguished (a) the songs of individuals of southerly *extimus* populations from (b) those of all other populations. Those two phenetic groups alone explained 40% of the variance in song characters. No songs of birds believed to be *extimus* united with songs of birds thought to be *adastus*. All of the songs originally characterized as being from birds of unknown taxonomy were imbedded in the *adastus*-like cluster, including those songs from the high-elevation Arizona and northern New Mexico populations. Some of the most distinctive songs of the *adastus*-like cluster, standing apart from other songs, were those of birds from northern New Mexico and western Colorado.

Latitude and elevation.—Linear, multiple regression of the CDF1 canonical scores for songs against latitude and elevation revealed that nearly 87% of the variation in song scores along CDF1 ($r^2_{\text{CDF1}|\text{elevation, latitude}} = 0.867$, $F = 474.7$, $df = 2$ and 145, $P < 0.0001$) is accounted for by latitude and elevation. The partial correlation coefficients of elevation ($r^2_{\text{CDF1 elevation}|\text{latitude}} = 0.680$, $F = 308.7$, $df = 1$ and 145, $P < 0.0001$) and lat-

TABLE 4. Mean, multivariate (Mahalanobis) distances in song space. Songs of birds of uncertain taxonomic status (U1-U7) were more distant from southerly *extimus* populations (E1-E5) than from northerly *adastus* populations (A1-A4) pointing to their closer vocal affinities with *adastus*. Distances of the northern New Mexico (U6) and western Colorado (U2) song groups to the *extimus* groups were notably small compared to the other five groups of unknown taxonomy, suggesting the presence of both subspecies (U6), in addition to intergradation between subspecies (U2, U6).

| From group | Squared distance to group | | | | | | | | | | | | | | | |
|------------|---------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------|-----|--|
| | A1 | A2 | A3 | A4 | U1 | U2 | U3 | U4 | U5 | U6 | U7 | E1 | E2 | E3 | E4 | |
| A1 | 0.0 | | | | | | | | | | | | | | | |
| A2 | 1.74 | 0.0 | | | | | | | | | | | | | | |
| A3 | 5.42 | 6.46 | 0.0 | | | | | | | | | | | | | |
| A4 | 1.50 | 3.27 | 3.12 | 0.0 | | | | | | | | | | | | |
| U1 | 3.90 | 6.99 | 2.89 | 3.82 | 0.0 | | | | | | | | | | | |
| U2 | 5.12 | 7.40 | 9.29 | 5.11 | 9.30 | 0.0 | | | | | | | | | | |
| U3 | 10.32 | 13.43 | 6.34 | 5.88 | 8.08 | 10.81 | 0.0 | | | | | | | | | |
| U4 | 4.35 | 7.05 | 3.42 | 2.80 | 3.98 | 6.33 | 2.92 | 0.0 | | | | | | | | |
| U5 | 6.65 | 6.31 | 8.32 | 6.21 | 10.68 | 8.86 | 11.21 | 6.27 | 0.0 | | | | | | | |
| U6 | 5.75 | 7.84 | 11.95 | 5.95 | 11.11 | 4.24 | 9.36 | 8.08 | 14.88 | 0.0 | | | | | | |
| U7 | 7.20 | 10.65 | 9.71 | 10.05 | 6.07 | 12.07 | 19.20 | 13.10 | 13.02 | 16.52 | 0.0 | | | | | |
| E1 | 41.99 | 47.09 | 51.01 | 42.97 | 48.06 | 28.80 | 43.43 | 46.84 | 60.67 | 19.51 | 49.57 | 0.0 | | | | |
| E2 | 44.34 | 50.66 | 55.81 | 49.58 | 49.13 | 30.18 | 56.30 | 53.26 | 62.61 | 28.20 | 42.49 | 7.73 | 0.0 | | | |
| E3 | 68.72 | 75.82 | 82.83 | 72.88 | 79.02 | 49.41 | 73.65 | 74.62 | 86.23 | 41.22 | 76.34 | 8.54 | 11.03 | 0.0 | | |
| E4 | 66.40 | 75.21 | 76.79 | 70.83 | 74.54 | 50.20 | 71.94 | 71.57 | 80.95 | 44.54 | 69.43 | 16.72 | 15.16 | 5.13 | 0.0 | |
| E5 | 59.26 | 65.38 | 70.58 | 62.81 | 66.27 | 47.90 | 64.72 | 68.43 | 80.40 | 35.21 | 62.52 | 6.74 | 12.38 | 6.68 | 9.2 | |

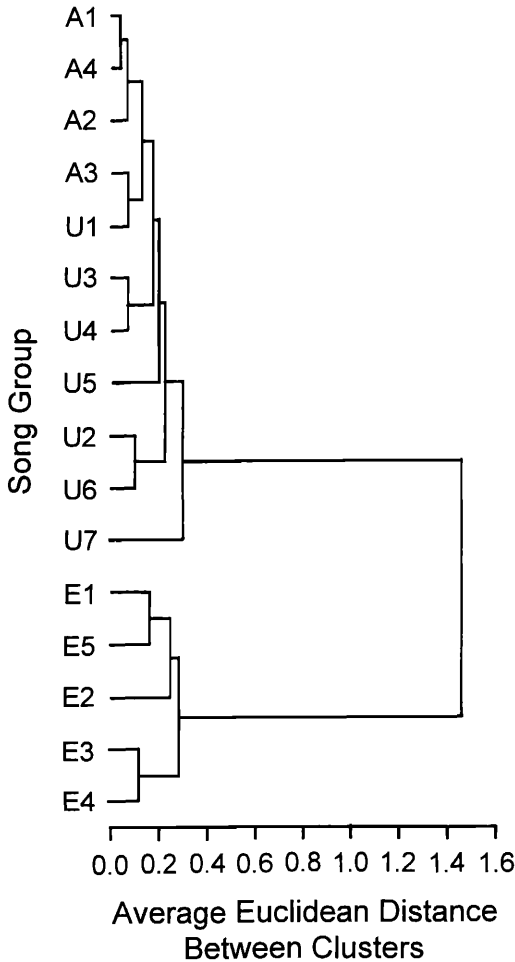


FIG. 4. Two distinct clusters link *E. t. extimus* populations (E1–E5) and the remaining song groups. All birds of unknown subspecies (U1–U7) clustered with birds of the *E. t. adastus* song type (A1–A4). Phenogram is from a UPGMA cluster analysis of 16 Willow Flycatcher populations based on Mahalanobis distances between song groups. The cophenetic correlation coefficient ($r_{cc} = 0.919$) indicates good agreement between the original data matrix and the phenogram.

itude ($r^2_{CDF1 \text{ latitude|elevation}} = 0.642$, $F = 260.1$, $df = 1$ and 145 , $P < 0.0001$) were similar, indicating that both variables contribute to the linear prediction of song scores. Plots (not shown) of latitude and elevation versus CDF1 scores exhibit *adastus*-like songs at high latitude and elevation, and *extimus*-like songs at low latitude and elevation. Birds with the vocal identity of *extimus* occur as far north as 37°N if at low elevation (song group E2), and those acoustically

similar to *adastus* occur as far south as 33.7°N if at high elevation (song group U7). The results of the Mantel test further demonstrate the relationship among song type, latitude, and elevation. The correlation of the matrix of song distances with the matrix of elevational and latitudinal dissimilarities yielded $r = 0.539$, $P = 0.0004$, indicating that the pattern of distances in song space is a function of latitude and elevation.

DISCUSSION

Pattern of variation.—Even though the overall form of the song of Willow Flycatchers varies little over thousands of kilometers (Stein 1963), typical of other *Empidonax* as well (Johnson 1980), regional populations have statistically unique vocal identities. Acoustic features of southerly low-elevation populations include longer durations (total song, note, FM, internote, or interphrase) and lower frequencies at maximum amplitude. Songs of those southerly populations were segregated in multivariate song space from those of northerly song groups, which sang shorter songs with maximum amplitude occurring at higher frequencies. Birds of uncertain taxonomic identity (U1–U7), occurring at latitudes intermediate between those of song groups known to be *extimus* or *adastus*, were more similar vocally to birds of the *adastus* song type (A1–A4). Songs of high-elevation Arizona birds (U7), geographically closer to *extimus* than to *adastus* song populations, were more similar acoustically to northerly *adastus* populations. Northern New Mexico birds (U6) had the most variable vocal background: some individuals sang songs acoustically similar to the *adastus* song type and some sang songs resembling the *extimus* song type. The tree-linkage diagrams supported the vocal distinctness of the *adastus* and *extimus* song groups and confirmed the structure of vocal differentiation revealed by the CDA. The topologies of dendrograms portrayed songs of birds known to be *extimus* uniting with other *extimus*, and birds known to be *adastus* clustering with other *adastus*. Songs of all birds of uncertain taxonomy (U1–U7) were imbedded within the *adastus* cluster, including the geographically isolated, high-elevation population of eastern Arizona (U7).

Both the regression of song scores on latitude and elevation, and the Mantel test of correlation between song distances and latitudinal and elevational dissimilarities supported the hypothesis of latitudinal and elevational partitioning in song: the 16 song groups sort out by both latitude and elevation. Vocal analysis distinguishes (a) latitudinally distant populations (E1–E5 from A1–A4), and (b) latitudinally proximate but elevationally different populations (U7 from E1 and E4; E2 from U3 and U4), while (c) revealing the vocal alliance of latitudinally distant but elevationally variable populations (U7 to A1–A4 and U1–U6; see Table 1, Fig. 1). The combined influence of latitude and elevation on the distribution of vocal types explains the acoustic similarity of song types as distant latitudinally as Oregon (A1) and east-central Arizona (U7); the occurrence of *extimus* song types (E2) farther north (37°N) than some *adastus* song types; the occurrence of *adastus* song types (U7) farther south (33.7°N) than some *extimus* song types; and the geographical proximity of some *adastus* (U7) and *extimus* (E4) populations (Fig. 1). A similar pattern of distribution, where a more northerly taxon extends farther south if at high elevation such that it overlaps by latitude with the more southerly taxon, is exhibited by the Brewer's (*Spizella breweri*) and Timberline (*S. b. taverneri*) sparrows (Klicka et al. 1999, J. Barlow pers. comm.).

Congruence of taxonomies and subspecies limits.—Although there is consensus that the Willow Flycatcher is polytypic, "few species have had such a confused nomenclatural history with so many differences of opinion among systematists as to the validity of several proposed races as the Willow or Traill's Flycatcher" (Behle 1985). Just how confusing and contentious the issue of subspecific identification of Willow Flycatcher subspecies is was emphasized in a recent paper by Yong and Finch (1997), and a subsequent critique (Hubbard 1999) and response (Yong and Finch 1999). Three factors have clouded Willow Flycatcher subspecific taxonomy: (a) throughout its range, morphological differences are minimal and plumage patterns are both subtle and complex; (b) it is closely similar to the Alder Flycatcher; and (c) there are relatively few breeding-season specimen records, especially in parts of the western and southwestern United States. The taxonomic revision of the Traill's Flycatcher, recognizing

the Willow and Alder Flycatchers as separate species, alleviated much of the nomenclatural ambiguity, but disagreement continues as to the number and distributional limits of races of the Willow Flycatcher. Two of the most recent examinations of the races of Willow Flycatcher (Unitt 1987, Browning 1993) could not provide unequivocal subspecific differentiation. Unitt (1987) was unable to separate the subspecies on the basis of size (bill length and width, wing chord, and tail length), but wing formula distinguished the eastern subspecies (*traillii*) from the three western subspecies (*extimus*, *adastus*, and *brewsteri*). The three western subspecies were mostly separable from one another on the basis of subtle plumage variation. Browning (1993) also relied on plumage differences to distinguish the subspecies, but found "no taxonomically important differences in size" among races. Even more recently, Unitt (1999), employing both morphologic measurements and colorimetry was able to mostly distinguish eastern from western Willow Flycatchers and *extimus* from combined *adastus*–*brewsteri* groups using discriminant analysis.

Poorly defined range boundaries are a corollary of the unresolved taxonomy of the races. Burleigh (1972), for example, reported the occurrence of *E. t. extimus* as far north as southern Idaho. Twomey (1942) and Snyder (1953) identified specimens from northeastern Utah as *E. t. extimus*, and as intergrades, respectively, whereas Behle (1985) regards birds in extreme northern Utah as pure forms of *E. t. adastus*, with *E. t. extimus* occurring only in extreme southern Utah. Intergradation may (Behle 1985) or may not (Browning 1993) occur in central Utah. The northern extent of pure forms of *E. t. extimus* in New Mexico and its occurrence in Colorado also remain unresolved on the basis of morphological taxonomy.

Despite the confused nomenclatural history of the races of the Willow Flycatcher, the geographical distribution of *adastus* and *extimus* inferred from vocal evidence is largely concordant with that provided by morphology. Both character suites suggest separate evolutionary histories for *adastus* and *extimus*, especially in the extreme north and south of their distributions, respectively. Even in northern New Mexico, there is congruence between the two data sets. Vocal analysis reveals acoustic heterogeneity in that region, which is in line with Phil-

lips (1948): "... breeding birds from northeastern Arizona, southwestern Colorado, and much of New Mexico (particularly from Springerville, Arizona, east to the Rio Grande) show great individual variation, and are thus intermediate."

Morphological evidence is either lacking or is at variance with acoustic evidence in several regions at intermediate latitudes. In east-central Arizona, birds of the high-elevation population (U7), thought to be in the range of *extimus*, sing songs acoustically similar to more northern populations (*E. t. adastus*), and do not sort out along the same geographic lines as determined by morphological evidence. Unitt (1999) identified three high-elevation Arizona specimens as *extimus*, but was able to confirm only two as *extimus* using discriminant analysis. In Utah, vocal evidence does not support intergradation along a north-south line, as birds at all sites from 37 to 39°N (except for E2 in the extreme southwest) were vocally similar to more northerly *adastus* populations. And in Colorado, *E. t. extimus* apparently does not occur, because even the southernmost populations are acoustically similar to more northerly *adastus* populations. The vocal identity of a low-elevation population in western Colorado (U2), however, stands apart from that of other *adastus* populations and has a vocal signature more resembling that of *extimus* than other Colorado populations (see Fig. 3), suggesting moderate introgression of *extimus* genes into the *adastus* gene pool. Intermixing may also occur in eastern Utah, from which no vocal samples were obtained, but where Willow Flycatchers may occur in small numbers.

I propose a more complex distribution of *E. t. adastus* and *E. t. extimus* than currently accepted. Simply put, the populations are geographically constrained on the basis of both latitude and elevation resulting in a patchy, yet largely allopatric distribution. A rough division of the subspecies occurs at about 37°N latitude, or the Colorado-New Mexico border. Populations of the *adastus* song type can occur farther south (U7), and populations of the *extimus* song type can occur farther north (E2), depending on elevation. In low-elevation regions of eastern Utah and western Colorado, in particular, undiscovered populations of *extimus* may occur.

Maintenance and consequences of variation in song.—The distributions of *extimus* and *adastus* appear to be limited by climate, mediated by latitude and elevation, as each song type gravitates toward slightly different temperature and precipitation regimes. *Extimus* is desert-adapted, occurring in the hot, arid regions of the Southwest; *adastus* occurs at cooler, more humid latitudes and elevations. It is tempting to invoke Holdridge's (1967) scheme of plant formations based on climate as a driving force in the distribution of *extimus* and *adastus*: latitudinal and elevational gradients of temperature, precipitation, and humidity define plant formations and these, in turn, constrain the distributions of *extimus* and *adastus*. The effects of climate are somewhat ameliorated, however, because the occurrence and persistence of riparian plant communities, to which *adastus* and *extimus* are restricted in the western United States, depend less on precipitation and more on river flows. The biological effect of climate on riparian vegetation is diminished and we find that riparian plant communities vary less across elevational or latitudinal gradients than upland vegetation. Habitat preferences of *extimus* and *adastus* bear that out because the plant communities that those two subspecies inhabit share more similarities than differences. There are some differences, however, and it is not difficult to imagine differential selection pressures in the two environments those races inhabit. *Adastus* breeds at higher latitudes and elevations where willows (*Salix* spp.) are the dominant, and frequently the only, nesting shrub. *Extimus* is seemingly more catholic in its habitat preferences, breeding in riparian zones often dominated by tamarisk (*Tamarix* sp.), boxelder maple (*Acer negundo*), seepwillow (*Baccharis quitinosa*), and willow (Sedgwick 2000).

It seems likely that the *adastus* and *extimus* song types arose as the result of fragmentation of an ancestral population into isolates, perhaps during a Pleistocene glaciation. The lineage leading to the *extimus* song type may have been isolated in an arid-land refugium, separate from the pre-*adastus* song type. Those two fragmented groups then differentiated in isolation into today's *adastus* and *extimus* song types (sensu Hubbard 1973). Today, they are essentially either latitudinally or elevationally allopatric but do come into contact in a few areas

that are intermediate in latitude or elevation. Differences in song are likely maintained by one or more of several mechanisms. (1) Most likely, is that allopatry— isolation by distance and elevation—may discourage exchange of individuals and constrain gene flow among populations. (2) Habitat and environmental preferences may limit the exchange of individuals and act as a barrier to gene flow as each song type gravitates to its preferred environment. (3) Because environmental differences and song differences covary, natural selection may favor one song type over the other for local adaptation to different environments. Birds that wander beyond their normal environmental limits may be at a competitive disadvantage, thereby opposing the influence of gene flow. (4) Song may function as a reproductive isolating mechanism if females select consorts on the basis of vocal identity. Mating may thus be assortative as females mate selectively with males of the same vocal background, discouraging gene migration. (5) Biased juvenile dispersal may reduce the exchange of birds between populations, thus reducing gene migration. The congruence of vocal and genetic differentiation of mated pairs in regions of secondary contact would lend support to the mechanism of assortative mating, as would a comparison of songs of mated pairs (sensu Baptista and Morton 1982). A comparison of survival or nest success (fitness) of song types within and outside of their normal, environmental limits would test whether or not song differences, or features evolving in concert with song, confer adaptation to different environments, pointing to natural selection as the mechanism maintaining geographic variation.

The *adustus* and *extimus* song types appear to be in an early stage of evolutionary divergence. They are largely allopatric, being geographically separated by latitude and elevational barriers. Vocal evidence from northern New Mexico and western Colorado, suggesting limited intermixing and hybridization, points to a lack of reproductive isolation in areas of contact. Unique vocal identities and slightly different ecological preferences suggest, however, that those subspecies are evolving independently of one another and clearly warrant, at least, subspecific status.

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