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REGIONAL VARIABILITY IN THE SONG OF THE WILLOW FLYCATCHER

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Abstract.--A comparison of songs among different populations of Willow Flycatchers was used to test the taxonomic identity of several regional populations of purported *Empidonax traillii extimus* and *E. t. adastus*. Eight song groups sorted out by both geography and elevation. Low-elevation, southerly desert groups (low-elevation Arizona) had a unique vocal identity. More northern song groups, whether low-elevation (Colorado) or high-elevation (Colorado) were more closely aligned with the song group in Oregon (= *adastus*). High-elevation Arizona birds, while in the range of *E. t. extimus*, are more acoustically similar to more northern song groups (= *adastus*). The vocal background of northern New Mexico birds appears to be intermediate between that of *extimus* and *adastus*.

The Willow Flycatcher (*Empidonax traillii*) is a neotropical migratory passerine, breeding largely in the northern half of the United States and in southern Canada (A.O.U. 1983). Studies of various subspecies have identified the Willow Flycatcher as a highly stenotopic species in western riparian ecosystems (Sedgwick and Knopf 1992, Unitt 1987). Riparian ecosystems, in turn, are highly significant as nongame bird habitats both locally, regionally, and continentally. In addition, riparian habitats are degraded or declining in many locales due to water management practices, agricultural conversions, grazing, channelization, and recreational development.

In the western United States, the Willow Flycatcher is composed of a mosaic of healthy and threatened populations. It appears to be reproductively stable in many parts of the West, but has declined significantly in other areas, including Washington, Oregon, Arizona, California, and Nevada (BBS data, USFWS). Because of regional declines, the species has been designated a "sensitive species" in Region 1 (Washington, Idaho, Oregon, California, and Nevada) and Region 2 (Arizona, New Mexico, Oklahoma, Texas) of the U. S. Fish and Wildlife Service and was added to the U. S. Forest Service Region 5 Sensitive Species list in 1984. The Willow Flycatcher is state threatened in Missouri, and state endangered in California, New Mexico, and Arizona. Additionally, the Southwestern Willow Flycatcher (*E. t. extimus*) has been formally listed as a federally endangered subspecies (U.S. Fish and Wildlife Service 1995). Habitat loss (Hunter et al. 1988, Carothers 1977) and alteration (Harris et al. 1987, Knopf et al. 1988), and parasitism by the Brown-headed Cowbird (*Molothrus ater*) (Whitfield 1990, Harris 1991) pose the most severe threats to the Southwestern Willow Flycatcher and to other subspecies as well (Sedgwick and Knopf 1988, Holcomb 1972). The subspecies is heavily parasitized in California, and until cowbird trapping programs were initiated at Camp Pendelton and Kern River, those populations were in a rapid state of decline (Unitt 1987, Whitfield and Strong 1995).

The Willow Flycatcher is polytypic, with 4 subspecies currently recognized (Unitt 1987). However, morphological differences among the subspecies are minor; wing, tail, and bill proportions are similar, and even wing formula measures (primary 10 - primary 5) show few differences except between eastern (*E. t. traillii*) and the 3 western forms. Plumage color would appear to be the best criterion for differentiating the various subspecies, but is most useful in distinguishing *E. t. extimus* (paler and grayer on the back) from the other western forms. In the field, morphologic differences are not apparent, and differences in plumage color are much more difficult to discern than in the case of study skins. Thus, there is no reliable way for a field biologist to identify Southwestern Willow Flycatchers to subspecies based on plumage and morphology alone.

Advertising songs ("fitz-bew") of at least some individuals of *E. t. extimus* are detectably different, with experience, from those of the other forms (Sogge and Tibbitts 1992; S. Sferra, Arizona Game and Fish Dep., pers. comm.; pers. obs.); other vocalizations may differ, as well. Such differences may be true of all individuals of the subspecies, but this has not been demonstrated spectrographically. Additionally, differences in vocalizations near the periphery of a subspecies' range may blur, if hybridization among the different forms is occurring and intergradation is gradual. This study examines the consistency in song forms of the Southwestern Willow Flycatcher across its range and compares vocalizations between *E. t. extimus* and the geographically adjacent *E. t. adastus*.

Song has been widely used in the systematic study of bird species. In many birds, in fact, song is a better indicator of a species than any visual field mark, and the degree of variation in song among geographic populations may be used to infer taxonomic status. For example, song and call differences have led to the recognition of sympatric sibling species in several groups of birds: Podiciped grebes (Clark's [*Aechmophorus clarkii*] and Western [*A. occidentalis*]); *Empidonax* flycatchers (Willow and Alder [*E. alnorum*]); and song differences have been used in confirming the species distinctiveness of species (*Empidonax* flycatchers [Dusky (*E. oberholseri*), Hammond's (*E. hammondii*), and Gray (*E. wrightii*)], and *Aimophila* sparrows). In studies of owls, Marshall (1967, 1978) used the rule: "all taxa with the same song belong together" in studies of populations occurring in isolated regions. Others have suggested that if the songs of populations (subspecies) sort out along the same geographic lines as morphologically recognizable subspecies, this can be useful in determining whether populations are the same or different taxa. For example, regional songs correspond to subspecies in the Yellow Wagtail (*Motacilla flava*) (Czileki 1982) and Pine Grosbeak (*Pinicola enucleator*) (Adkisson 1981); i.e., the geography of the calls matches that of the morphology of the populations. This is not true in all cases (e.g., Corn Buntings [*Emberiza calandra*]) where there is no consistent pattern in geographic variation and song. But in certain instances, song and morphological differences among populations may covary and permit a functional or historical interpretation (Payne 1986).

The objectives of this study were to: (1) record songs of the Southwestern Willow Flycatcher, primarily in Arizona; (2) record songs of the geographically adjacent subspecies (*E. t. adastus*); (3) record songs of Willow Flycatchers in possible zones of intergradation between *E. t. extimus* and populations in northern New Mexico and southwestern Colorado; (4) develop a regional database of vocalizations; and, (5) describe the pattern of variation in advertising song of the various populations.

METHODS

Study areas.--Recordings of songs were secured in Arizona, Colorado, New Mexico, and Oregon. Most recordings were of birds from Arizona with additional recordings from other regions for comparative purposes. Recordings from Arizona were secured primarily from the following 4 regions: (1) San Pedro River (PZ Ranch and Cook's Lake); (2) Roosevelt Lake (Tonto Creek inflow and Salt River inflow); (3) east-central Arizona (Alpine and Greer); and, (4) west-central Arizona (Topock Marsh, Bill Williams River NWR, and Hunter's Hole). Recordings from Oregon were from Malheur NWR in southeastern Oregon and those from Colorado were from (a) high-elevation sites (> 2500 m) in north-central Colorado (Arapaho NWR) and on the West Slope of Colorado and (b) from low-elevation sites (< 1500 m) in southwestern Colorado (Escalante, Hart's Basin). Five additional males were recorded in northern and central New Mexico (Table 1). Whereas I recorded the advertising songs of 123 different males (75 from Arizona and 48 from the other states), only the best recordings were analyzed. This report is based on recordings of songs of 37 males from Arizona, 5 from New Mexico, 5 from Oregon, and 8 from low-elevation sites and 8 from high-elevation sites in Colorado (see Appendix 1 for complete list of song files).

Field recording.--Most vocalizations were recorded with a Sony TC-D5 PRO II cassette recorder and Kroodsma Pre-amp coupled with a Sennheiser ME20 omnidirectional microphone mounted in a 61-cm Roche graphite parabolic reflector.

Songs from New Mexico were recorded by James Travis with a Sony Pro-Walkman WM-D6C cassette recorder and Dan Gibson parabola-microphone setup and 2 songs from Arizona were recorded by Mark Sogge with a Sony TCM-5000 cassette recorder, coupled with a Sennheiser ME20 microphone mounted in a parabolic reflector. All but 2 Arizona recordings were secured between 21 May and 9 June 1995; the other 2 were secured in June 1992. All Colorado songs were recorded in June 1994 and the Oregon birds were recorded in July and August, 1995. Recordings of New Mexico birds were made in July 1979, June 1993, and May 1995. Whereas some migratory Willow Flycatchers occasionally sing during migration, this is relatively uncommon (Unitt 1987, J. Travis, pers. comm., pers. obs.) and birds heard singing repeatedly are likely on breeding territory. Females also occasionally sing the advertising song but such vocalizations are given only infrequently. Recordings were only secured from birds singing at high rates and which appeared to be territorial.

Sound analysis.--Digital sound acquisition, storage, and analysis were performed on a 486-66 MHZ microcomputer using Real Time Spectrogram (RTS) version 1.23 and SIGNAL version 3.0 programs and hardware (Beeman 1996). Sound acquisition was performed by the conversion of signals from analog to digital after passing through an anti-alias filter in order to prevent generation of spurious spectral material. Songs were stored as digitized waveforms in computer files using RTS (sample rate = 25 kHz). Measures of temporal parameters (msec) were determined using the digital screen cursor on spectrograms in RTS and measures of the distribution of sound energy among frequencies (Hz) were determined from power spectrums (frequency vs. amplitude displays) in SIGNAL. Hardcopy spectrograms were produced from SIGNAL (sample rate = 25 kHz, frequency range = 10 kHz, transform size = 128 points) and printed on a laserjet printer (600 dpi).

The song.--Willow Flycatchers sing two basic song types, rendered here as "fitz-bew" and a slightly more buzzy "fizz-bew" (after Stein 1963). Both types are usually part of the song repertoire of a given individual and neither type seems to predominate.

These two song types differ primarily in the first phrase ("fitz" vs. "fizz"), with the "fitz" consisting of 2 notes and the "fizz" consisting of one series of shorter, staccato, buzzy notes. This report is based only on recordings and analysis of the "fitz-bew" song type. "Fitz-bew" songs are composed of 3 phrases (Fig. 1). Phrase I is composed of 2 notes--the first ascending in frequency and averaging 40-75 msec in duration. The second note of phrase I is shorter in duration but often of higher peak frequency. Phrase II typically consists of 3 notes, all usually lower in frequency than phrase I notes and all of relatively short duration, typically lasting from 6-27 msec. Phrase III consists of 2 parts, the first made up of a series of 10-15 closely spaced notes, each lasting only 4-5 msec. The second part of phrase III consists of fewer notes (usually 5-10) of longer duration (15-35 msec).

Statistical analysis.--Spectrograms were grouped according to geography and elevation. This resulted in 8 groups for analysis (Table 1): (1) low-elevation (< 700 m), central Arizona (n = 13); (2) low-elevation (< 700 m), southeastern Arizona (n = 14); (3) low-elevation (< 200 m), west-central Arizona (n = 5); (4) high-elevation (> 2400 m), east-central Arizona (n = 5); (5) low to mid-elevation (1400 - 1860 m) northern and central New Mexico (n = 5); (6) low-elevation (< 1500 m), southwestern Colorado (n = 8); (7) high-elevation (> 2500 m), western and north-central Colorado (n = 8); and, (8) southeastern Oregon (n = 5).

Twenty measures of duration and 14 measures of frequency were taken from each song (Table 2). Acoustic features of duration included measures of song, phrase, note, and inter-note lengths, and parameters of frequency included measures of song, phrase, and note peak frequencies. I compared means of variables (one-way ANOVA) and used Bonferroni's multiple comparison test to determine specific differences among group means. I performed stepwise, canonical discriminant analyses on the subset of variables significantly different (P < 0.05) in the univariate ANOVAs. Significance levels for entry and elimination of variables in the stepwise procedures were set at the default (P = 0.15), with variables contributing most or least to the discriminatory power of the model (as measured by Wilks' Lambda) being entered or removed, respectively. Canonical discriminant analyses were then used to generate scores on canonical variables, plots of scores, and squared distances between class means (Mahalanobis distances) in discriminant "song" space. All statistical procedures were conducted on the Statistical Analysis System, Version 6.08 (SAS Institute, Inc. 1990).

RESULTS

Univariate Analysis.– Of 34 acoustic features of song, 25 differed among the eight groups ($P < 0.05$). The nine features which did not differ (P1ini1, P1n2d, Ipi1, P2d, P2n2d, Ipi22, P2f, P2n1f, and P2n3f) will not be considered further. Of 20 measures of duration or counts of notes, 14 differed across the eight groups ($P < 0.05$; Table 3). In all cases, statistical significance was due in large part to differences between one or more of the three groups of low-elevation Arizona birds (groups 1, 2, and 3) and other groups. For song duration (Sd), for example, groups 1 and 3 differed from group 4 (high-elevation Arizona); for phrase I, note 1 duration (P1n1d), group 1 differed from groups 2 and 4, and groups 1, 3, and 6 (low-elevation Colorado birds) differed from group 4. In all cases but one, measures of duration of notes or phrases of one or more groups of low-elevation Arizona birds were greater than those of other groups. The difference in the length of the notes of the second part of the third phrase was especially important in distinguishing between groups (P3bc3d: $F_{(7, 55\ df)} = 62.16$, $P < 0.0001$; groups [1 = 2 = 3] > 5 > [4 = 6 = 7= 8]). Songs of low-elevation Arizona birds had fewer peaks in the second part of phrase III (P3bp: $F_{(7, 55\ df)} = 11.46$, $P < 0.0001$; groups [1 = 2] < [4 = 6 = 8], group 3 < [6 = 8]), and fewer notes in the first part of phrase III (P3an: $F_{(7, 55\ df)} = 4.06$, $P = 0.0012$; group 2 < 5).

Eleven measures of frequency differed among groups ($P < 0.05$) and 3 (P2f, P2n1f, and P2n3f) were not significant; an additional 3 features did not demonstrate Bonferroni differences across groups (P3f, P3af, and P3bf; Table 4); these 6 features will not be considered further. All measures of total song frequency (Sf, Sflo, and Sfhi), and of phrase I (P1f, P1n1f, and P1n2f) differed among groups and one feature each of phrase II (P2n2f) and phrase III (P3bc1f) differed among groups. Again, low-elevation Arizona birds (groups 1, 2, and 3) differed most from the other groups. For all 8 features, one or more groups of low-elevation Arizona birds had lower mean peak frequencies than various subsets of the other 5 groups (4 - 8). For example, total song peak frequency (Sf: $F_{(7, 55\ df)} = 4.10$, $P = 0.0011$; group 3 < [7 = 8]), phrase II, note 2 frequency (P2n2f: $F_{(7, 55\ df)} = 11.28$, $P < 0.0001$; groups [1 = 2 = 3] < [6 = 7 = 8] and groups [1 = 3] < [4 = 5 = 6 = 7 = 8]), and phrase III, second part, cycle 1 frequency (P3bc1f: $F_{(7, 55\ df)} = 4.66$, $P = 0.0004$; group 2 < [6 = 8]) were all lower for one or more groups of low-elevation Arizona birds than for various subsets of the other groups (Table 4).

Multivariate analysis.--Eight of 25 variables were selected for inclusion in the canonical discriminant analysis. Two discriminant functions (DF) were significant ($P < 0.0001$). DF1 was largely a measure of the duration of cycle 3, phrase III, part 2 (P3bc3d) and was also negatively correlated with phrase I peak frequency (P1f) (Table 5). Songs of birds from the three low-elevation Arizona sites were situated to the right along DF1, having high durations of cycles in the second part of phrase III (Fig. 2). Songs of New Mexico birds were centrally located along DF1 and those of the other groups were located at the left along DF1. Large differences among groups for the duration of notes of the second part of phrase III explain the separation along this dimension (x of Groups 1 -3 [msec]: 29.9 - 32.1; Group 5: 22.2; Groups 4, 6, 7, 8: 15.5 - 17.3) (Table 6). Similarly, songs of birds with low peak frequencies of phrase I (P1f) were situated to the right along DF1 (x of Groups 1 - 3: 3692 - 3808 Hz) whereas those with high peak frequencies of this feature were located to the left along DF1 (x of Groups 4 - 8: 3944 - 4579 Hz).

DF2 was most highly correlated with the duration of note 1, phrase I (P1n1d) and high frequency at -20db below maximum peak frequency (Sfhi) (Table 5). Songs of birds near the top of DF2 tended to have combinations of high values for P1n1d and Sfhi (e.g., *x* of Group 1: 76.7 msec, 4969 Hz, respectively) and those near the bottom of DF2 had lower values (e.g., *x* of Group 2: 54.4 msec, 4485 Hz) (Table 6).

Multivariate distances in song space (Mahalanobis distances) between song group means were generally greatest for low-elevation Arizona groups vs. other groups (Table 7, Fig. 2). Distances between low-elevation Arizona groups vs. the New Mexico group were intermediate and distances between the three Arizona groups themselves were relatively small. Surprisingly, distances between (a) low-elevation Arizona groups vs. the high-elevation Arizona group (M = 43.3 - 63.3) and (b) low-elevation Arizona groups vs. the low-elevation Colorado group (M = 38.7 - 52.6), were on the same order as distances between low-elevation Arizona groups vs the Oregon and high-elevation Colorado group, respectively (M = 39.3 - 56.9, and 38.7- 52.6, respectively). Most groups were significantly ($P < 0.05$) segregated from one another in multivariate song space with the following exceptions: (1) low-elevation Colorado songs were similar to Oregon and high-elevation Colorado songs; and, (2) Oregon songs were similar to high-elevation Colorado songs and high-elevation Arizona songs (Table 7).

DISCUSSION

Even though the overall form of the song of Willow Flycatchers is invariant over thousands of kilometers (Stein 1963), typical of other *Empidonax* flycatchers, as well (Johnson 1980), differences among regional populations were detected in this study. Acoustic features of the songs of low-elevation Arizona birds are unique, and differ from those of all other song groups examined. Songs of low-elevation Arizona birds were most segregated from those of the other groups in multivariate song space and differed based mostly on 4 features: the duration of notes in the second part of phrase III (P3bc3d), phrase I peak frequency (P1f), phrase I, note 1 duration (P1n1d), and total song high frequency at -20db below maximum peak frequency (Sfhi). Durations (total song, note, internote, or interphrase) were generally greater and peak frequencies were generally lower for low-elevation Arizona birds (Table 6). Songs of high-elevation Arizona birds were very unlike those of low-elevation Arizona birds ($P < 0.0001$), and were similar ($P = 0.14$) to those of Oregon birds. Mahalanobis distances were relatively small (but significantly different) between high-elevation Arizona birds and both groups of Colorado birds. Songs of New Mexico birds were intermediate, and statistically different ($P < 0.05$) from those of the other seven groups. Songs of low-elevation Colorado birds were similar to those of Oregon ($P = 0.51$) and high-elevation Colorado birds ($P = 0.39$).

Taxonomic relationships.–The study of bird songs may be useful in systematics at higher taxonomic levels (e.g., subspecific), especially in birds that do not learn their songs (Payne 1986). This is so because in species where the song is innate, songs are highly stereotyped and clues to genetic identity are not complicated by song-learning from different tutors at different times. The songs of all oscines studied so far are cultural imitations (Slater 1989) and are less likely to be good indicators of genotype, especially in zones of secondary contact. Among species that do not imitate their vocalizations from other individuals (e.g., suboscine flycatchers) vocal displays can provide good evidence of genetic background (Kroodsma et al. 1995). Hand-reared Willow Flycatchers raised in isolation sing like adults and the song of Willow Flycatchers is not learned. At less than a month of age, juveniles sing songs like those of the adult; their songs arise in nearly adult-like pattern without evident derivation from earlier sounds (Kroodsma 1982, 1984).

Thus, a comparison of songs among different populations of suboscines can provide a test of the taxonomic identity of isolated or remote populations. If populations are well defined by songs, we may expect less variation in acoustic characters within related subspecies than among subspecies. The question becomes: How similar must songs be for populations to be considered taxonomically equivalent, or how different to support a hypothesis of taxonomic distinctiveness? If songs of distinctive populations or subspecies sort out along the same geographic lines as morphologically recognizable subspecies, this can be used as an additional line of evidence and as a test of subspecific identity.

Morphologic evidence suggests that *E. t. extimus* is a valid subspecies, distinguishable from other populations of Willow Flycatchers by color and morphology (Unitt 1987). Plumage color and wing formula are the most discriminating morphological features whereas the overall size of *extimus* does not differ from that of the other subspecies. The taxonomic validity of *E. t. extimus* has been accepted by most authors (Phillips et al. 1964, Oberholser 1974, Hubbard 1987, Unitt 1987, Monson and Phillips 1981). If the currently accepted breeding range of *E. t. extimus* as outlined by Hubbard (1987) and Unitt (1987) is correct (s. California, Arizona, New Mexico, extreme s. Utah and Nevada, and possibly sw. Colorado), then all 4 Arizona song groups, the New Mexico group, and possibly the low-elevation Colorado group are of the *E. t. extimus* subspecies. Acoustic analysis data (this study) support the morphological evidence that low-elevation Arizona birds have a genetic identity unique from that of the more northerly subspecies (*E. t. adastus*). The songs of the high-elevation Arizona song group and the low-elevation Colorado song group do not sort out along the same geographic lines as determined by morphologic evidence. Songs of these groups are more similar to those of the more northerly *adastus* subspecies, including both high-elevation Colorado and Oregon song groups. Acoustic analysis further suggests that songs of northern and central New Mexico birds are intermediate between those of *adastus* and *extimus*, in line with Phillips (1948) suggestion that Willow Flycatchers breeding from northeastern Arizona east to the Rio Grande R. in New Mexico may be intergrades between *extimus* and *adastus*.

Thus, the 8 song groups sort out by both geography and elevation. Low-elevation, southerly desert groups (low-elevation Arizona) have a unique vocal identity. More northern song groups, whether low-elevation (Colorado) or high-elevation (Colorado) are more closely aligned with the song group in Oregon (= *adastus*). High-elevation Arizona birds, while in the range of *E. t. extimus*, are more acoustically similar to more northern song groups (= *adastus*). The vocal background of northern and central New Mexico birds appears to be intermediate between that of *extimus* and *adastus*. It should be noted that the samples from New Mexico were from the northern and central part of the state, and these birds may have a different vocal identity than birds from farther south in the state (Maynard 1994).

Whereas the subspecies of *E. traillii* lack striking plumage or external morphological differences, they nevertheless provide sufficient evidence of subspecies distinctiveness. Vocal differences are more obvious and provide an additional line of evidence of genetic evolution. Because songs of Willow Flycatchers are innate, differences among song groups are genetically based and suggest the existence of at least two independent evolutionary units (*extimus* and *adastus*). Intermediate song types in northern and central New Mexico suggest the occurrence of interbreeding. Additional studies of song differences, reproductive behavior, and genetics are needed to determine the degree of divergence between song types, and to assess the extent and consequences of hybridization.

Management Implications.--The concept of subspecies is often an elastic one. At higher taxonomic levels, differences among populations--whether morphologic, behavioral, acoustic, or genetic--often become smaller and more difficult to discern. If hybridization among populations is extensive, differences become even more blurred, resulting in a gradual intergradation across groups. Whereas the U.S. Fish and Wildlife Service currently has described suitable habitat parameters for *E. t. extimus* in southwestern Colorado, and has identified critical habitat along numerous drainages in northern New Mexico, and along some high-elevation drainages in east-central Arizona, birds in these areas do not share the vocal identity of birds in more southern desert regions of Arizona, which have been assigned with greater confidence to *E. t. extimus*. Nevertheless, because the Endangered Species Act (Section 3[15]) defines species as " ... any subspecies of ... wildlife ..., and any distinct population segment of any vertebrate species ... ", these populations of questionable genetic identity still deserve protection under the Endangered Species Act.

A knowledge of the acoustic features which differ between *extimus* and the adjacent *adastus* subspecies can aid the field biologist in distinguishing between subspecies. Songs of *extimus* are detectably different with practice to the field biologist with a good ear. *Extimus* songs sound slower, slightly lower in pitch, and are given with what has been decribed as a "southern drawl". This difference in sound is largely due to the duration of the cycles (longer, drawn out) in the second part of Phrase III (P3bc3d) and the number (fewer) of peaks in the second part of phrase 3 (P3bp). The slightly lower pitch of the *extimus* song is largely due to lower peak frequencies of several variables including total song (Sf, Sflo, and Sfhi), Phrase I ("fitz": P1f, P1n1f, and P1n2f), note 2 of Phrase II (P2n2f), and the cycles in the second part of Phrase III (P3bc1f) (see Tables 3 and 4). An acoustic analysis package capable of producing (and measuring) sonograms would allow identification to subspecies in most cases.

Future research is needed to validate the results of this study. Larger sample sizes from high-elevation Arizona birds and from those along the lower Colorado River would add to the validity of this study. In addition, recordings from low-elevation areas where recording was not possible earlier (e.g., Verde Valley) are needed. Additional recording in New Mexico would clarify the zone of intergradation between *extimus* and *adastus* and aid in delineation of range boundaries.

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Table 1. Willow Flycatcher song groups.

Group	*n*	Type	Specific Location
1	13	Low elevation, central Arizona (< 700 m)	Roosevelt Lake: Tonto Cr. inflow, Salt R. inflow
2	14	Low elevation, southeastern Arizona (< 700 m)	Lower San Pedro River: PZ Ranch, Cook's L.
3	5	Low Elevation, west-central Arizona (< 200 m)	Topock Marsh, Bill Williams NWR, Hunter's Hole
4	5	High elevation, east-central Arizona (> 2400 m)	Alpine, Greer
5	5	northern and central New Mexico	Bosque del Apache NWR, Orilla Verde, Taos Junction, Espanola
6	8	Low elevation, southwestern Colorado (< 1500 m)	Escalante, Hart's Basin, Red Mesa
7	8	High elevation, north-central and western Colorado (> 2500 m)	Arapaho NWR, Ruby Anthracite Cr., Flattops Wilderness, Rio Grande R.
8	5	Mid-elevation, southeastern Oregon	Malheur NWR

Table 2. Physical variables of Willow Flycatcher songs.

Measures of duration (msec) or number of notes	
Total Song	
Sd:	Total song length
Phrase I	
P1d:	Phrase I duration
P1n1d:	Duration of first note of phrase I
P1ini1:	Duration of interval between first and second note of phrase I
P1n2d:	Duration of second note of phrase I
Ipi1:	Duration of interval between phrase I and phrase II
Phrase II	
P2d:	Phrase II duration
P2n1d:	Duration of first note of phrase II
P2ini1:	Duration of interval between first and second note of phrase II
P2n2d:	Duration of second note of phrase II
P2ini2:	Duration of interval between second and third note of phrase II
P2n3d:	Duration of third note of phrase II
Ipi21:	Duration of interval between phrase II and phrase III from end of first note
Ipi22:	Duration of interval between phrase II and phrase III from end of second note
Phrase III	
P3d:	Phrase III duration
P3an:	Number of notes in first part of phrase III
P3bp:	Number of peaks in second part of phrase III
P3ad:	Duration of first part of phrase III
P3bd:	Duration of second part of phrase III
P3bc3d:	Duration of cycle of note 3 of second part of phrase III
Measures of Frequency (kHz)	
Total Song	
Sf:	Average peak frequency of total song
Sflo:	Minimum peak frequency of total song at -20db below Sf
Sfhi:	Maximum peak frequency of total song at -20db below Sf
Phrase I	
P1f:	Average peak frequency of phrase I
P1n1f:	Average peak frequency of first note of phrase I
P1n2f:	Average peak frequency of second note of phrase I
Phrase II	
P2f:	Average peak frequency of phrase II
P2n1f:	Average peak frequency of first note of phrase II
P2n2f:	Average peak frequency of second note of phrase II
P2n3f:	Average peak frequency of third note of phrase II
Phrase III	
P3f:	Average peak frequency of phrase III
P3af:	Average peak frequency of first part of phrase III
P3bf:	Average peak frequency of second part of phrase III
P3bc1f:	Average peak frequency of cycle 1 of second part of phrase III

Table 3. Univariate differences: acoustic features of duration (msec) of songs of Willow Flycatchers.

Variable[1]	$F_{(7, 55\ df)}$	P	Bonferroni difference between groups[2]
Sd	4.35	0.0007	(1 = 3) > 4
Phrase I			
P1d	2.51	0.0260	nd[3]
P1n1d	5.66	0.0001	(1 = 3 = 6) > 4; 1 > (2 = 4)
P1ini1	1.17	ns	nd
P1n2d	2.02	ns	nd
Ipi1	1.00	ns	nd
Phrase II			
P2d	2.10	ns	nd
P2n1d	4.18	0.0009	2 > 8
P2ini1	2.31	0.0392	3 > 4
P2n2d	1.16	ns	nd
P2ini2	8.44	0.0001	3 < (4 = 6 = 7 = 8); (1 = 2 = 3) < (6 = 7 = 8)
P2n3d	3.88	0.0017	(1 = 2 = 3) > 4
Ipi21	2.74	0.0164	3 > (4 = 8)
Ipi22	1.33	ns	nd
Phrase III			
P3d	2.55	0.0241	nd
P3an	4.06	0.0012	2 < 5
P3bp	11.46	0.0001	(1 = 2) < (4 = 6 = 8); 3 < (6 = 8)
P3ad	3.72	0.0023	nd
P3bd	3.41	0.0042	3 > 7
P3bc3d	62.16	0.0001	(1 = 2 = 3) > 5 > (4 = 6 = 7 = 8)

[1] See Table 2 for description of variables.
[2] Groups 1 - 3 = low elevation Arizona birds; group 4 = high elevation Arizona; group 5 = New Mexico; group 6 = low elevation Colorado; group 7 = high elevation Colorado; group 8 = Oregon.
[3] = No differernce between groups

Table 4. Univariate differences: acoustic features of frequency (kHz) of songs of Willow Flycatchers.

Variable[1]	$F_{(7, 55\ df)}$	P	Bonferroni difference between groups[2]
Sf	4.10	0.0011	3 < (7 = 8)
Sflo	5.43	0.0001	(2 = 3) < (4 = 7); 3 < (4 = 6 = 7 = 8)
Sfhi	6.14	0.0001	(2 = 3) < (4 = 5 = 7)
Phrase I			
P1f	6.24	0.0001	(1 = 2 = 3) < 7; 3 < (6 = 7)
P1n1f	5.26	0.0001	3 < (5 = 6 = 7)
P1n2f	2.57	0.0228	3 < (1 = 5 = 6 = 7)
Phrase II			
P2f	1.99	ns	nd[3]
P2n1f	0.92	ns	nd
P2n2f	11.28	0.0001	(1 = 2 = 3) < (6 = 7 = 8); (1 = 3) < (4 = 5 = 6 = 7 = 8);
P2n3f	1.75	ns	nd
Phrase III			
P3f	2.37	0.0346	nd
P3af	3.18	0.0067	nd
P3bf	2.80	0.0144	nd
P3bc1f	4.66	0.0004	2 < (6 = 8)

[1] See Table 2 for description of variables.
[2] Groups 1 - 3 = low elevation Arizona birds; group 4 = high elevation Arizona; group 5 = New Mexico; group 6 = low elevation Colorado; group 7 = high elevation Colorado; group 8 = Oregon.
[3] = No differernce between groups.

Table 5. Summary of discriminant analysis of song features of eight groups[1] of Willow Flycatchers.

	DF1	DF2
Canonical correlation	0.9632	0.6949
Wilks' Lambda	0.0125	0.1733
Eigenvalue	12.8277	0.9338
Significance (*P*)	0.0001	0.0001
Variables entered[2]	Pooled within correlation with function	
P1n1d	0.1175	0.6632
Ipi21	0.1001	0.1581
P3an	-0.1481	0.2935
P3ad	-0.1417	0.3924
P3bc3d	0.7846	0.0607
Sfhi	-0.1751	0.5759
P1f	-0.2146	0.3301
P1n2f	-0.0610	0.3835

[1] See Table 1 for description of groups.

[2] See Table 2 for description of variables.

Table 6. Means of acoustic features of the advertising song of eight groups[1] of Willow Flycatchers.

	1AZLO (*n* = 13)		2AZLO (*n* = 14)		3AZLO (*n* = 5)		4AZHI (*n* = 5)		5NMEX (*n* = 5)		6COLO (*n* = 8)		7COHI (*n* = 8)		8OREG (*n* = 5)	
Variable[2]	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE
Duration (msec)																
Sd	553.23	12.10	524.79	12.11	556.60	13.17	467.20	26.12	532.40	22.09	523.13	14.14	483.38	7.26	489.20	11.36
P1d	146.76	3.39	127.23	7.36	144.80	2.67	122.60	5.06	145.40	6.79	134.13	2.87	130.25	4.12	136.40	5.74
P1n1d	76.69	4.44	54.36	3.47	67.80	2.56	43.60	3.23	63.00	2.92	66.50	2.04	56.75	5.59	55.60	5.80
P1ini1	56.15	2.88	56.83	4.87	64.00	4.64	64.20	6.95	62.60	3.59	51.88	3.32	52.13	4.43	63.20	3.48
P1n2d	13.15	0.78	18.83	2.33	12.00	0.95	14.80	2.48	19.00	2.51	15.63	1.22	21.63	3.54	17.20	3.80
Ipi1	102.15	6.30	102.41	7.04	100.20	4.18	90.00	13.63	98.40	8.21	100.88	4.76	93.50	3.92	79.20	6.45
P2d	182.77	6.99	185.25	7.97	186.00	6.04	158.40	13.96	177.40	11.49	175.88	5.96	168.63	4.02	149.60	7.93
P2n1d	22.69	1.09	27.43	2.60	20.40	2.46	18.00	0.63	18.40	1.12	18.25	1.03	18.38	1.29	16.00	1.26
P2ini1	23.92	0.98	21.15	3.08	30.00	2.37	15.60	0.93	28.60	3.72	22.38	3.82	19.13	2.01	18.20	1.56
P2n2d	15.92	1.11	15.85	1.01	14.40	0.98	14.60	0.75	12.00	0.71	14.25	1.97	14.63	1.15	12.20	1.07
P2ini2	8.62	0.49	8.75	0.90	8.40	1.29	14.00	1.26	9.80	1.32	14.75	0.84	14.88	1.83	15.40	0.93
P2n3d	10.08	0.42	10.57	0.40	10.60	0.68	6.60	0.87	10.00	0.89	8.75	0.56	8.25	1.25	7.80	0.20
Ipi21	60.69	1.27	58.21	2.53	67.00	3.03	51.80	0.66	61.80	2.61	58.13	1.60	57.63	1.39	55.60	2.62
Ipi22	21.15	0.71	20.85	1.40	22.80	3.40	21.20	0.20	21.20	0.97	24.38	0.50	23.88	1.09	24.40	1.75
P3d	221.00	6.94	205.21	9.38	227.40	15.96	184.00	9.17	202.40	5.66	213.25	8.72	182.88	5.24	203.00	9.14
P3an	11.23	0.36	9.93	0.47	12.00	0.32	12.00	0.55	13.00	0.00	12.88	0.83	12.63	0.86	12.60	0.24
P3bp	5.54	0.24	5.57	0.36	6.20	0.66	8.00	0.31	6.80	0.49	8.88	0.35	7.63	0.46	8.80	0.66
P3ad	59.46	2.04	51.00	2.50	60.00	2.49	62.00	2.93	66.00	1.61	67.13	4.99	67.50	4.38	62.60	1.57
P3bd	154.77	6.65	144.93	9.81	159.60	14.23	119.20	8.89	131.20	5.24	141.50	4.57	109.75	5.07	134.00	8.92
P3bc3d	32.08	0.60	29.86	0.76	31.40	1.69	16.40	1.33	22.20	1.96	17.25	0.86	15.50	0.50	16.20	0.73

Table 6. (continued).

Variable	1AZLO (n = 13)		2AZLO (n = 14)		3AZLO (n = 5)		4AZHI (n = 5)		5NMEX (n = 5)		6COLO (n = 8)		7COHI (n = 8)		8OREG (n = 5)	
	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE
Frequency (Hz)																
Sf	3307	46	3277	100	3179	173	3479	145	3407	126	3576	82	3755	77	3737	124
Sflo	2336	48	2172	32	2066	66	2558	86	2345	174	2448	88	2538	76	2509	69
Sfhi	4969	92	4485	121	4428	170	5231	291	5229	93	5099	103	5283	90	4903	141
P1f	3808	118	3754	89	3692	133	3944	236	4313	129	4396	106	4579	151	4129	166
P1n1f	3530	55	3530	91	3384	41	3614	162	3989	144	3968	86	4015	151	3815	64
P1n2f	4810	65	4517	255	3703	228	4489	244	4848	118	4843	187	4961	160	4523	275
P2f	3184	133	3205	158	2794	144	3315	220	3585	45	3570	121	3410	126	3470	186
P2n1f	3376	21	3397	107	3228	87	3294	180	3475	31	3519	76	3553	124	3410	128
P2n2f	2606	76	2769	89	2641	48	3303	238	3322	143	3602	145	3407	127	3453	176
P2n3f	2762	39	2803	90	2749	268	3033	163	3221	193	2903	135	2617	113	2811	157
P3f	3408	53	3250	121	3162	134	3384	175	3366	117	3639	96	3605	107	3709	170
P3af	3268	74	3358	80	3361	120	3674	122	3493	152	3713	129	3659	92	3637	78
P3bf	3407	38	3005	121	3029	141	3300	212	3392	100	3399	197	3611	148	3617	215
P3bc1f	2970	39	2769	87	2788	35	3102	63	3096	155	3217	119	3162	54	3223	56

[1] Groups: 1AZLO = low elevation, central Arizona; 2AZLO = low elevation, southeastern Arizona; 3AZLO = low elevation, west-central Arizona; 4AZHI = high elevation, east central Arizona; 5NMEX = New Mexico; 6COLO = low elevation, Colorado; 7COHI = high elevation, Colorado; 8OREG = southeastern Oregon.

[2] See Table 2 for description of variables.

Tab! 7. Multivariate song (Mahalanobis) distances between eight groups[1] of Willow Flycatchers.

From Group	Squared distance to Group (P): 1AZLO		2AZLO		3AZLO		4AZHI		5NMEX		6COLO		7COHI	
1AZLO	0.0													
2AZLO	6.85	(0.0001)	0.0											
3AZLO	10.79	(0.0006)	9.75	(0.0013)	0.0									
4AZHI	59.32	(0.0001)	43.35	(0.0001)	63.30	(0.0001)	0.0							
5NMEX	24.77	(0.0001)	19.13	(0.0001)	24.97	(0.0001)	14.41	(0.0012)	0.0					
6COLO	50.03	(0.0001)	38.65	(0.0001)	52.61	(0.0001)	8.52	(0.0110)	7.22	(0.0276)	0.0			
7COHI	66.13	(0.0001)	52.58	(0.0001)	70.81	(0.0001)	6.82	(0.0366)	13.78	(0.0003)	2.49	(0.3893)	0.0	
8OREG	56.86	(0.0001)	39.29	(0.0001)	53.68	(0.0001)	6.03	(0.1373)	9.88	(0.0156)	2.74	(0.5088)	5.72	(0.0787)

[1] Groups: 1AZLO = low elevation, central Arizona; 2AZLO = low elevation, southeastern Arizona; 3AZLO = low elevation, west-central Arizona; 4AZHI = high elevation, east central Arizona; 5NMEX = New Mexico; 6COLO = low elevation, Colorado; 7COHI = high elevation, Colorado; 8OREG = southeastern Oregon.

Appendix 1. Willow Flycatcher song files of 123 different males; 63 of the highest quality songs (underlined) were used in the analysis.

Song Group											
Low elevation central Arizona		Low elevation southeastern Arizona		Low elevation west-central Arizona	High elevation east-central Arizona		New Mexico	Low elevation Colorado	High elevation Colorado	Oregon	Miscellaneous Arizona
Tonto Cr. Inflow	Salt R. Inflow	Cook's Lake	PZ Ranch	Topock Marsh, Bill Williams NWR, Hunter's Hole	Alpine	Greer	Espanola, Orilla Verde, Taos Jxn, Bosque del Apache	Escalante, Hart's Basin	Arapaho NWR, West Slope	Malheur NWR	Tuzigoot, Cardenas Marsh
18A_A2	18B_E1	18B_F2	14_AO1	9A_J2	9A_I1	19_AA3	NMEXA_R1	1A_P1	4A_A12	15_AU6	10_AI1
18A_B1	20_BG2	18B-G2	14_AP1	9A_K1	10_AD1	10_AE2	WNMX_S2	7A_Q1	4A_B1	15_AV1	10_AJ1
18A_C1	20_BH3	18B_H2	14_AQ4	9B_L1		10_AF1	WFTA_F1	3B_Q1	4A_C5	15_AW1	10_AK1
18A_D1	20_BI1	9B_M1	14_AR1	14_AL1		10_AG5	WFTA_G2	1A_R1	4B_D2	15_AX1	WFAZ_AI2
20_BB2	20_BJ1	9B_N2	14_AS1	14_AM2		10_AH2	WFTA_H1	IB_S5	4B_E1	15_AY3	WFAZ_AJ1
20_BC3	20_BK5	9B_O1	14_AT1	14_AN1		19A_Z2	WFTA_I1	1B_T1	3A_K2	15_AZ1	WFAZ_AK3
20_BD1	20_BL2	19A_T1	15_AU6			AZ_AH1	WFTA_J3	1B_U1	3A_N2	15_BA1	
20_BE2	20_BM2	19A_U1	15_AV1			AZ_AG1		7A_V5	3A_O1	25_CA1	
20_BF1	23_BN2	19A_V1	23_BR1					21A_X3	3B_P1	25_CB2	
	23_BO1	19A_W1	23_BS1					21A_Y1		25_CC1	
	23_BP2	19A_X1	23_BT2					21A_Z3		25_CD1	
	23_BQ1	19A_Y2	23_BU2					21_AA2		25_CE2	
		19A_Z2	23_BV1					21_AB3		25_CF2	
		10_AB2	23_BW1					21_AC4		25_CG1	
		10_AC3	23_BX1					21_AD2		25_CH1	
			24_BY1					21_AF3		MN_W3	
			24_BZ1								

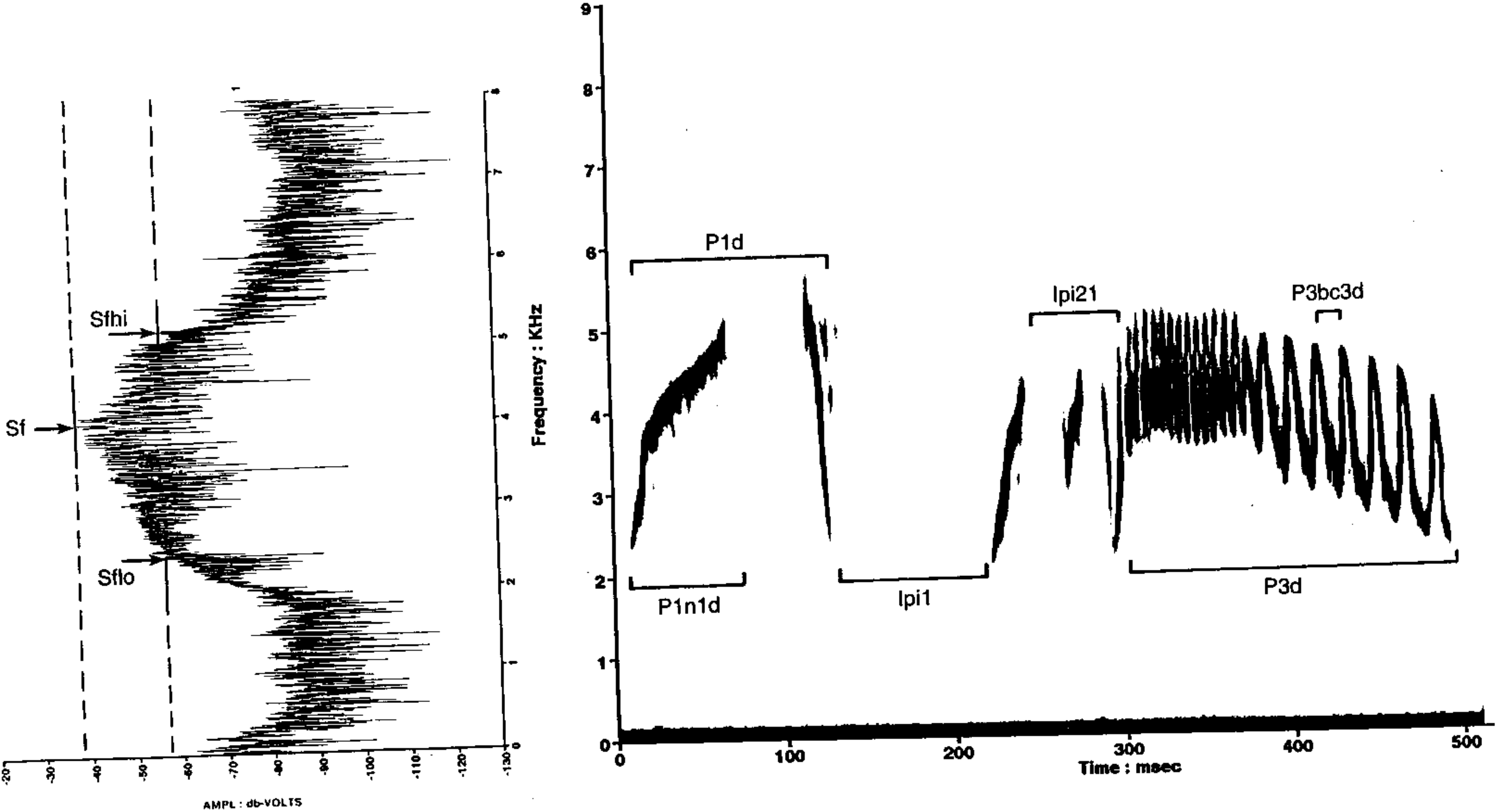

Figure 1. Power spectrum (left) and spectrogram (right) of a song of *Empidonax traillii* showing some of the measures of duration and frequency. See table 2 for descriptions of variables.

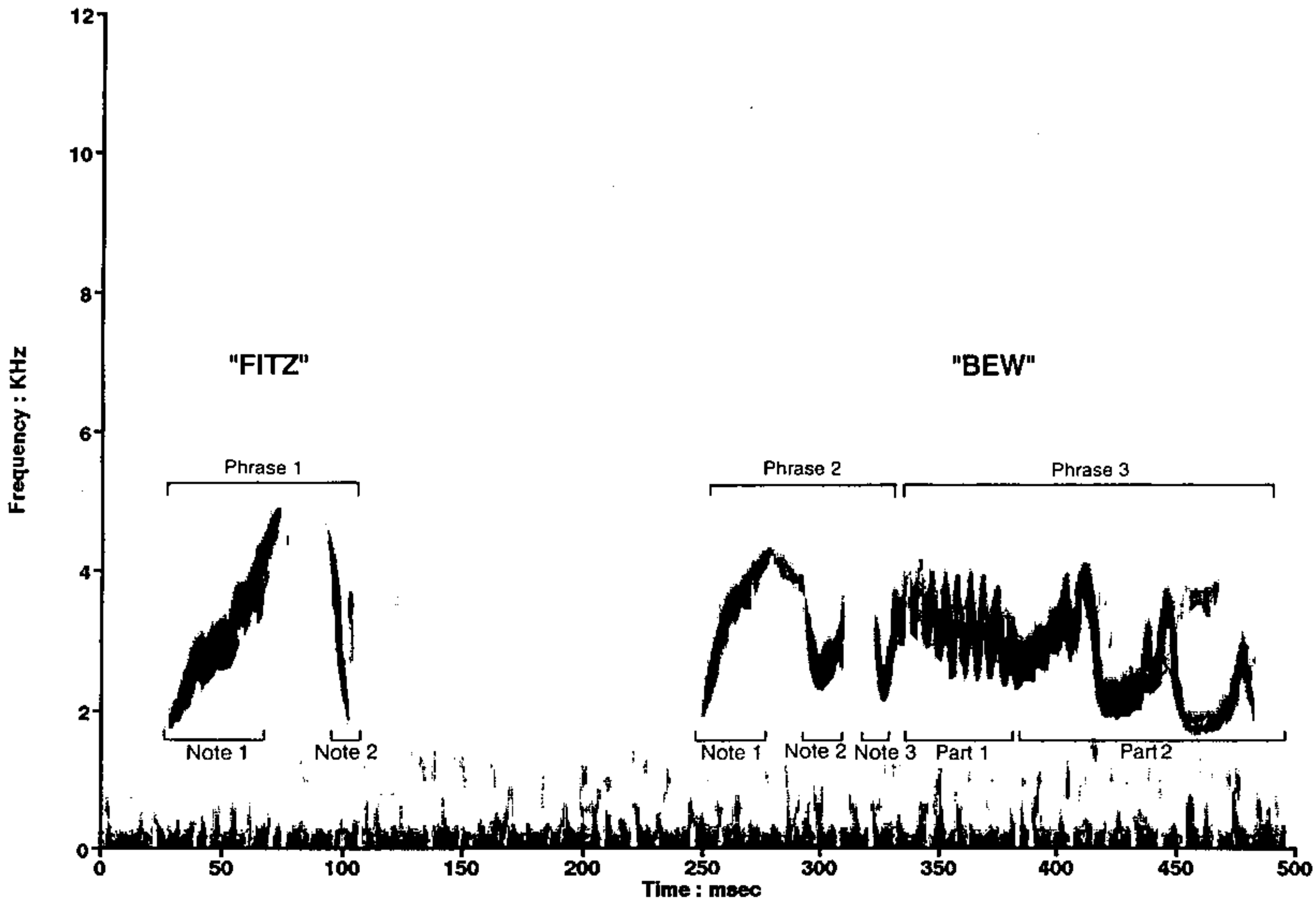

Fig. 4. Spectrogram and descriptive terminology of a Willow Flycatcher song.