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IDENTIFICATION OF INDIVIDUAL AND POPULATION-LEVEL VARIATION IN VOCALIZATIONS OF THE ENDANGERED SOUTHWESTERN WILLOW FLYCATCHER (*EMPIDONAX TRAILLII EXTIMUS*)

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Abstract.—An understanding of individuality in animal vocalizations can assist in tracking individuals spatially and temporally, and is particularly useful for species of conservation concern. We determined whether *fitz bew* vocalizations of the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) showed vocal individuality, assessed the differences in vocal individuality among three populations, and tested the ability of predictive vocalization models to reidentify individuals. *Fitz bew* vocalizations were recorded from two populations in Arizona (Roosevelt Lake and San Pedro River) and one in California (Kern River). Individuality was determined using discriminant function analysis (DFA) and trained artificial neural networks (ANN). Southwestern Willow Flycatchers showed individuality in the *fitz bew*, with the models correctly classifying 81–86% of the vocalizations. We also found population-level variations: vocal structure differed substantially between Roosevelt Lake and Kern River, but vocal structure in the San Pedro River population overlapped with that of the other two populations. These population differences could be related to dispersal patterns of adults or offspring, patterns of territory establishment, or habitat structure differences. The ANN vocalization models reidentified an average of 81% of the individuals and were able to identify novel individuals. On the basis of these results, we recommend that acoustic tracking should complement rather than replace current monitoring practices, given its logistical limitations. We provide a basic understanding of vocal parameters that can be used in the future to study different aspects related to vocal individuality (e.g., taxonomic, seasonal, yearly, and sex differences). *Received 18 June 2007, accepted 25 June 2008.*

Key words: *Empidonax traillii extimus*, mark–recapture, monitoring, neural networks, Willow Flycatcher, vocal individuality.

Identificación de Variación Individual y Poblacional en las Vocalizaciones del Ave Amenazada *Empidonax traillii extimus*

Resumen.—Entender el carácter individual de las vocalizaciones de los animales (individualidad vocal) puede ayudar al seguimiento de individuos en el espacio y el tiempo, y es particularmente útil en especies de interés en conservación. Determinamos si las vocalizaciones *fitz biu* del atrapamoscas amenazado *Empidonax traillii extimus* exhiben individualidad vocal, examinamos las diferencias en individualidad vocal entre tres poblaciones y pusimos a prueba la habilidad de modelos predictivos de vocalizaciones para reidentificar a los individuos. Se grabaron vocalizaciones *fitz biu* de dos poblaciones en Arizona (lago Roosevelt y río San Pedro) y una en California (río Kern). La individualidad fue determinada mediante análisis de funciones discriminantes y redes neurales artificiales entrenadas. El *fitz biu* de las aves exhibió individualidad: los modelos clasificaron correctamente el 81–86% de las vocalizaciones. También encontramos variaciones a nivel poblacional: la estructura vocal difirió sustancialmente entre la población del lago Roosevelt y la del río Kern, pero la estructura vocal de la del río San Pedro se superpuso con la de las otras dos poblaciones. Esas diferencias poblacionales podrían estar relacionadas con los patrones de dispersión de los adultos o de las crías, con los patrones de establecimiento de territorios, o con diferencias en la estructura del hábitat. Los modelos basados en redes neurales reidentificaron en promedio el 81% de los individuos y también pudimos identificar individuos nuevos. Con base en estos resultados y dadas sus dificultades logísticas, recomendamos que el seguimiento acústico debería complementar, en lugar de reemplazar, las prácticas de monitoreo actuales. Proveemos un entendimiento básico de los parámetros vocales que puede usarse en el futuro para estudiar diferentes aspectos relacionados con la individualidad vocal (e.g., diferencias taxonómicas, estacionales, anuales y entre sexos).

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The use of individual traits in signals, such as vocalizations, enhances communication during various types of animal interactions (e.g., territorial disputes, mate selection, parent–offspring recognition; Tibbetts and Dale 2007). Establishing the degree of individuality can help explain changes over time in the persistence of call types (Baker and Gammon 2006), variations in the intensity of the responses of territorial males toward neighbors in relation to strangers (Godard 1993), and changes in individual calls when males move into new territories in relation to the resident neighbors (Walcott et al. 2006). Vocal individuality could also aid in estimating processes of relevance in population biology (e.g., population dynamics, fecundity, and survivorship; Terry and McGregor 2002, Terry et al. 2005). Characterizing the degree of vocal variability within and between populations can help explain mechanisms of reproductive isolation that lead to micro- and macrogeographic variation in vocalizations (McGregor et al. 2000).

From an applied perspective, the study of vocal individuality can be employed as a noninvasive identification method (McGregor and Byle 1992, Parsons 2001, Delport et al. 2002, Hoodless et al. 2008), which could be particularly useful for species of conservation concern (Peake and McGregor 2001). An acoustic monitoring method could reduce injuries related to banding, track individuals in areas where banding and access are restricted, identify cryptic and more sensitive species, and assign individuals of uncertain origin to populations (McGregor et al. 2000). Vocal individuality has been used to census Bitterns (*Botaurus stellaris*; Gilbert et al. 1994) and Corncrakes (*Crex crex*; Peake et al. 1998) in the United Kingdom.

Our goal was to study vocal individuality in a passerine subspecies, the Southwestern Willow Flycatcher (Tyrannidae, *Empidonax traillii extimus*), which was listed as endangered in the United States in 1995 (U.S. Fish and Wildlife Service 1995). Recent surveys estimate between 900 and 1,200 breeding pairs in the United States (Durst et al. 2006). This is an interesting model species, because some of its vocalizations have been shown to differ geographically in relation to the other subspecies, *E. t. adastus* (Sedgwick 2001); however, little is known about the degree of vocal individuality at the subspecies level. Furthermore, the Southwestern Willow Flycatcher presents monitoring challenges because of its preference for dense riparian habitat, its multiple population clusters, its relatively short breeding season, and its migratory behavior (Kus et al. 2003). Currently, many populations of Southwestern Willow Flycatchers have individuals that are color-banded and monitored by local, state, and federal organizations, but some birds remain unmarked.

We assessed the degree of vocal individuality in this subspecies and developed and tested models to provide a basic understanding toward the potential acoustic tracking of individuals within and between populations. First, using discriminant function analysis (DFA) and artificial neural networks (ANN), we determined whether the Southwestern Willow Flycatcher showed vocal individuality. Second, we assessed differences in vocal individuality between populations. Third, we determined the ability of the ANN models to reidentify individuals acoustically by estimating (1) the proportion of individuals that could be successfully reidentified, (2) the number of vocalizations per bird necessary for reidentification, and (3) the success of models in recognizing novel individuals.

Methods

Study sites and sampling procedures.—Southwestern Willow Flycatcher vocalizations were recorded from three populations: Kern River (California; $n = 8$ individuals), San Pedro River (Arizona; $n = 29$ individuals), and Roosevelt Lake (Arizona; $n = 15$). The two Arizona populations were separated by 92 km. Kern River was separated from San Pedro River and Roosevelt Lake by 757 km and 690 km, respectively. We sampled in California in 2005 (30 May–1 August) and in Arizona in 2006 (16 May–29 June). We recorded 52 birds from the three populations. The population of Southwestern Willow Flycatchers at the San Pedro River was smaller ($n = 132$ territories) than that at Roosevelt Lake ($n = 163$ territories; English et al. 2006). The Kern River population was much smaller than the other two ($n = 20$ territories; Durst et al. 2006).

The vocal repertoire of the Southwestern Willow Flycatcher typically consists of three vocalizations: the *fitz bew*, the *fizz bew*, and the *creet* (Sedgwick 2000). The *fitz bew* is the primary territorial signal and is more commonly heard than the *fizz bew.* The *creet* vocalization is mixed within bouts of the other two (Sedgwick 2000). We focused our study on the *fitz bew.* Females have been reported to sing, but not as frequently as males (Seutin 1987).

Birds were recorded between 0500 and 1200 hours. Singing males were located by sound and approached quietly to minimize disturbance. Mates were generally detected by sight (e.g., flying around a singing individual) or sound (e.g., *whitt* and *britt* calls). We are confident that all our recorded birds were males, given the following behavioral observations: recorded individuals sang continuously on the outer edge of perching trees, chased or fought with other individuals, flew, and perched near a nest or a quiet bird, which was likely a female.

We individually identified 18 birds by their colored leg bands. To ensure that songs from unbanded birds were assigned to the correct individuals, we used global positioning system (GPS) coordinates, mapped the presence of singing and nonsinging birds, and checked the location of each individual at least twice, particularly in the San Pedro River population. In the other two populations (Kern River and Roosevelt Lake), individual birds were monitored by the Southern Sierra Research Station and Arizona Game and Fish Department, which shared the information with us. We included in our data set only individuals whose presence and location were checked several times during the breeding season by these agencies. Although we cannot exclude the possibility that some individuals were recorded twice, we believe it was unlikely.

We recorded individuals using a K6-ME66 Sennheiser shotgun microphone with a foam windscreen and a PMD 670 Marantz Compact Flash digital recorder (16-bit sampling rate) on nonrainy days with light wind (wind speed < 0.3 m s^{-1}). We included in our analysis vocalizations recorded over a period of 30–90 min corresponding to two to three singing bouts separated by periods of 30–60 s in which the individuals were silent. To minimize disturbance and sound degradation, we did not record birds from <3 m or >14 m away. Only two birds were recorded at >10 m from the microphone; the results and classification factors did not differ with (81.18%, DFA) or without (81.35%, DFA) these individuals. Distances between the microphone and the singing bird were estimated visually after training. To avoid individual variation in

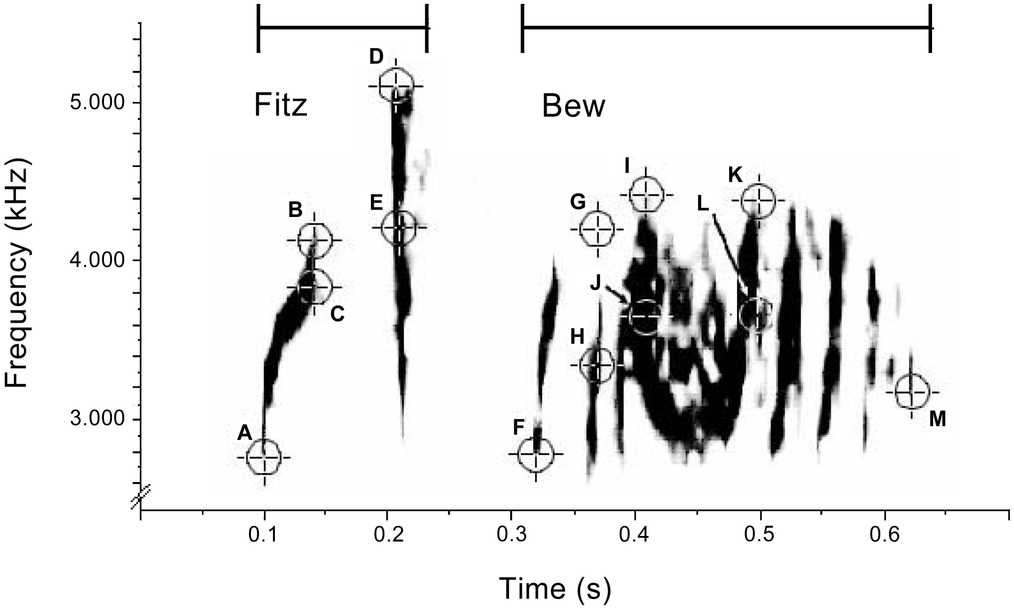

Fig. 1. Sonogram of the *fitz bew* call of Southwestern Willow Flycatcher showing locations of the predetermined fine-scale point-frequency (kHz) measurements and the duration measurements of each phrase. The five frequency variables measured for the *fitz* phrase are as follows: (A) beginning, (B) midway edge, (C) midway center, (D) peak edge, and (E) peak center. The following eight frequency variables were measured for the *bew* phrase: (F) beginning, (G) prepeak edge, (H) prepeak center, (I) peak edge, (J) peak center, (K) postpeak edge, (L) postpeak center, and (M) end. The two lines above the sonogram represent the duration of the *fitz* and *bew* phrases.

the responses to recorded songs, we did not use playback to elicit vocal responses (Terry et al. 2005).

During both seasons, we measured perching height (m) and ambient temperature (°C) during the recording sessions. In the 2006 season, we also measured ambient noise and vegetation cover. For each bird, 10 noise-level measurements (dB) were recorded with an 840029 Sper Scientific digital noise meter 60 s apart and averaged when the focal bird was not vocalizing. Percent vegetation cover (i.e., projection of bushes, trees, and saplings on the ground) was estimated visually within a 25-m-radius circular plot around the singing bird, following Prodon and Lebreton (1981).

Because the density of territorial males can influence singing behavior (Kroodsma 1979, Penteriani 2003), we calculated nearest-neighbor distance and the number of neighbor males within 100 and 250 m around the focal birds. We estimated the GPS coordinates in relation to the tree trunk where individual birds were observed most of the time. For birds that used more than one tree (generally, two), we used the middle distance between the trees to estimate the coordinates. Trees were flagged to facilitate resighting of previously recorded individuals. Nearest-neighbor distance was then calculated on the basis of distances between trees used by individuals.

We processed vocalizations with RAVEN, version 1.2.1 (Charif et al. 2004). We analyzed only vocalizations that were not interrupted by high-frequency noise (approximately >1,500 Hz) or other birds. In a preliminary stage, we analyzed sonograms using two methods. First, a coarse-scale method used the summary information recorded with the selection boxes from RAVEN, which calculated parameters averaged within the box (Nicholls and Goldizen 2006, Tripp and Otter 2006). Second, a fine-scale method measured frequency parameters at pre-established points along the sonograms of the *fitz* and *bew* phrases (Puglisi and Adamo 2004, Wiley 2005; Appendix 1 [online supplementary material; see Acknowledgments]). Using DFA, we established that the coarse method had a lower classification (75.75%) than the fine-scale method (86.27%); thus, we used the latter for all analyses.

We measured 15 vocal parameters related to the duration (s) and frequency (Hz) of the *fitz* and *bew* phrases (Fig. 1): duration of the *fitz* phrase, duration of the *bew* phrase, *fitz* start frequency, *fitz* peak edge and peak center frequencies, *fitz* midway edge and midway center frequencies, *bew* peak edge and center, *bew* prepeak edge and center, *bew* postpeak edge and center frequencies, and *bew* start and end frequencies. However, *bew* start and end frequencies were highly correlated ($r > 0.60$) with the *fitz* start frequency ($r = 0.71$, $P_{\text{Sidák}} < 0.05$ and $r = 0.62$, $P_{\text{Sidák}} < 0.05$, respectively), so we excluded them from the analysis. Of the remaining 13 parameters, some were still correlated to some degree ($r < 0.50$), which may lead to some redundancy in the analysis and the need to combine them for hypothesis testing. However, redundancy in vocal signals that are used to attract mates, such as the *fitz bew*, is expected to facilitate mate recognition (Johnstone 1996, Candolin 2003). Hence, we kept these 13 parameters (Fig. 1), because our ultimate intention was to build models to track individuals acoustically, which requires maximizing individual classification rates instead of identifying the parameters that are most sensitive to individual variation.

We present results in the following order: (a) descriptive information on individual vocalizations, (b) variation in singing rates in relation to neighbor distance and number of territorial males, (c) variation in vocal variability at two different times during the breeding season, (d) vocal individuality, (e) effects of ambient noise and recording distance on vocal variability, (f) variation in vocalizations at the population level, and (g) reidentification analysis.

Statistical analysis.—We first explain the statistical analyses related to individual variation in vocalizations (d, f, g), because of their similar analytical procedures. We then explain the other statistical analyses (b, c, e).

Discriminant function analysis and artificial neural networks.—We used both DFA and ANNs in the vocal-individuality and population-level variation analyses, because their classification functions employ different algorithms. Discriminant function analysis has been more generally used (e.g., Peake et al. 1998, Bard et al. 2002, Mays et al. 2006), but recent studies have recognized the greater application of ANNs (Deecke et al. 1999, Terry and McGregor 2002, Nickerson et al. 2006). Discriminant function analysis generates a linear combination of variables to maximize the probability of correctly assigning vocalizations to individuals (McGarigal et al. 2000, Quinn and Keough 2002). Artificial neural networks model data to establish membership to a particular individual and the extent of discrimination among individuals (Lek et al. 1996, Reby et al. 1997). We used a probabilistic neural network (PNN), a type of ANN model, because of its better classification accuracy in a previous study on vocal individuality (Terry and McGregor 2002). Artificial neural networks can also recognize novel data not used in the training data set and can assign these data to a new classification group (e.g., "unknown" category; Terry et al. 2005). Therefore, our reidentification analyses were based only on ANNs.

We followed similar procedures in running ANN models. We programmed the ANN to create 1,500 best-fit classification models and to select 20 models with the lowest error. From these 20 models, we selected one PNN on the basis of its having the highest training and selection performances (StatSoft 2007). Selection performance is the ability to classify the vocalization to an individual with an associated level of confidence (Terry and McGregor 2002, StatSoft 2007). Models with high training and selection performance levels are expected to classify the vocalizations to the correct individual with a higher degree of confidence. We determined the percentage of correctly classified vocalizations and the average and range of the confidence levels for each individual (StatSoft 2007). We calculated the sensitivity of the vocal parameters and their relevance to increase the PNN model training and selection performance rates (StatSoft 2007).

For the vocal individuality analysis, we used only birds recorded in the two Arizona populations because of the larger sample size in relation to the birds recorded in California and because we added ambient-noise-level variables to our sampling protocol in the 2006 season in Arizona. However, for the population-level variation analysis, we used all three populations.

Our reidentification analysis involved three steps that addressed key questions for developing the basic understanding needed to track individuals acoustically with ANNs. We used only Arizona birds because of the larger sample sizes. In the first step, our question was what proportion of individuals could be correctly reidentified using ANNs. We ran ANNs 10 times using a reduced randomly chosen data set per run, each data set consisting of 20% of the 440 *fitz bew* vocalizations ($n = 88$ vocalizations) recorded from the two Arizona populations. The 10 data sets included an average of 28.6 ± 1.2 (range: 26–30) of the 32 individuals with an average of 14.2 ± 6.5 (range: 13–44) vocalizations per individual. These 10 data sets were then run against the trained PNN model developed in the vocal individuality analysis. The identities of the birds were altered so that they would be unknown to the trained neural network models. Successful reidentification was defined as correctly classifying 80% or more of the vocalizations (see Terry and McGregor 2002). We then averaged the percent correct classification for each run.

In the second step, our question was how many vocalizations were needed to classify a given individual with a high level of confidence with ANNs. We performed a reidentification analysis on all individuals that had ≥15 randomly chosen vocalizations ($n = 14$ birds) to maximize the number of individuals included in the analysis. We performed reidentification ANN runs with data sets containing 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, and 15 *fitz bew* vocalizations per individual. We conducted five ANN runs in each of the data sets containing 3, 4, 5, 6, 7, 8, 9, 10, 11, and 12 vocalizations per individual. However, sample-size limitations allowed us to perform only three ANN runs in the 13 vocalizations per individual data set, two ANN runs in the 14 vocalizations per individual data set, and a single ANN run in the 15 vocalizations per individual data set. Each data set was run against the PNN model created and trained during the individuality analysis. We then calculated the average correct classification and coefficient of variation for each run.

In the third step, our question was whether new birds not recorded in the database could be identified as such by the ANNs. We selected 14 individuals with ≥15 vocalizations. We created 10 novel-bird data sets, each consisting of two randomly selected birds (representing ~10% of the 14 birds, following Terry and McGregor 2002). The identities of the birds were different among data sets. The remaining 12 birds per data set were incorporated into 10 known-individual data sets. We created a new ANN for each data set and trained it using the known-individual data set. We then ran the novel-individual data set against the known-individual data set. We calculated the average of the training and selection performances and errors for all the 10 trained models.

Other statistical analyses.—We used Pearson product moment correlations to assess the relationship between (1) singing rates, frequency, and duration parameters and (2) neighbor distance and number of territorial males.

We assessed whether individuals' vocalizations were consistent over time with a repeated-measures analysis of variance (ANOVA). We studied six birds that were recorded twice from the San Pedro River population in Arizona ($n = 127$ total *fitz bew* vocalizations, mean = 21.2 ± 11.6, range: 12–44 *fitz bew* vocalizations individual^{-1}). These birds were recorded with an interval of 14–21 days between the two sessions. For each vocal parameter, we averaged the values of all vocalizations per recording session and per individual. We tested each of the 13 frequency and duration variables individually and used recording session as the repeated-measures factor. However, we caution that this analysis should be considered preliminary because of the low sample size.

Vocal variability in Southwestern Willow Flycatchers can be affected by other factors besides individuality, such as noise levels and recording distance. First, we used general linear models (GLMs) to determine whether ambient noise varied among the recorded individuals. Ambient noise was introduced in the model as the dependent factor and individual bird identity as a categorical random factor. Second, we ran GLMs to establish which frequency and duration parameters were affected by recording distance at the population level after controlling for the effects of time of day, temperature, and perching height. Third, we used GLMs to determine which frequency and duration parameters were affected by the potential confounding effects of ambient noise and recording distance. Bird identity was included as a random factor in the models. Establishing statistically the relative contributions of confounding factors in relation to individuality is essential for estimating the degree of confidence in using vocalizations to track individuals in areas with different microhabitats.

Because of the high number of probability estimations in our analyses, we applied a correction to avoid the effect of increasing the probability of type I error. We first identified groups of related tests (following Chandler 1995) and then performed Sidák correction over each of the groups (Wright 1992). The groups of tests, along with the number of $p_{\text{Sidák}}$ estimates for each group, are as follows: variation in singing rates in relation to neighbor distance and number of territorial males (28 estimates), variation in vocal variability at two different times during the breeding season (13 estimates), individuality in vocalizations (14 estimates), effects of ambient noise and recording distance on vocal variability (44 estimates), and population-level differences (14 estimates). P values (p_i) were first ordered so that $p_1 < p_2 < \ldots < p_n$, and then each p_i was sequentially adjusted to $p_{i(\text{Sidák})} = 1 - (1 - p_i)^{(n-i+1)}$, with n being the number of p values in each group of tests (Wright 1992).

Results are presented as means ± SD throughout. We checked for normality in all variables and found no deviation that would require transformation. All statistical analyses were performed using STATISTICA, version 7.1 (Statsoft, Tulsa, Oklahoma; StatSoft 2007).

RESULTS

Descriptive information on individual vocalizations.—We measured an average of 10.2 ± 7.6 (range: 3–44) *fitz bew* calls per recorded bird. (Descriptive statistics of the vocalizations of each bird are available on request.) On the basis of a preliminary DFA, we concluded that including seven or more *fitz bew* calls per individual reduced the variability of classification rates in relation to the number of vocalizations per individual, allowing us to maximize the number of individuals in the database. Therefore, of the 44 birds recorded in Arizona, we included in the analyses 32 individuals (San Pedro River: n = 23 birds, n = 319 vocalizations; Roosevelt Lake: n = 9 birds, n = 121 vocalizations). In addition, in some analyses (see above), we included individuals from California (Kern River: n = 8 birds, n = 103 vocalizations).

Variation in singing rates in relation to neighbor distance and number of territorial males.—We found that singing rates (number of songs min^{-1}) and frequency and duration parameters were not significantly associated with nearest neighbor distance or with the number of territorial males (Pearson product moment correlations, r varied from 0.02 to 0.32, $P_{\text{Sidák}} > 0.05$).

TABLE 1. Variables that were used in the discriminant function analysis (DFA) model for classifying individual Southwestern Willow Flycatchers. "Tolerance" is the amount of redundancy in a variable and shows how correlated a particular variable is to all the others in a DFA model; thus, variables with a low tolerance variable are less redundant and provide more discriminatory power in the model. All significant $P_{\text{Sidák}}$ values are in bold. DF = 31 and 396.

Fitz bew vocalization parameter	F	$P_{\text{Sidák}}$	Tolerance
Fitz start frequency	18.51	**<0.001**	0.90
Fitz peak edge frequency	13.87	**<0.001**	0.88
Fitz peak center frequency	9.27	**<0.001**	0.88
Fitz midway edge frequency	4.50	**<0.001**	0.89
Fitz midway center frequency	7.96	**<0.001**	0.90
Bew peak edge frequency	15.46	**<0.001**	0.72
Bew peak center frequency	9.53	**<0.001**	0.85
Bew prepeak edge frequency	1.49	0.49	0.88
Bew prepeak center frequency	8.98	**<0.001**	0.90
Bew postpeak edge frequency	5.51	**<0.001**	0.76
Bew postpeak center frequency	2.88	**<0.001**	0.88
Duration of the *fitz* phrase	27.64	**<0.001**	0.91
Duration of the *bew* phrase	16.24	**<0.001**	0.96

Variation in vocal variability at two different times during the breeding season.—We determined the change in frequency and duration parameters in the vocalizations of six individuals in two different recording events during the breeding season. We found that only 1 out of 13 parameters changed significantly: *bew* postpeak center frequency (F = 185.85, df = 1 and 5, $P_{\text{Sidák}} < 0.01$). All other parameters showed no significant variation between recording sessions (F = 0.02–8.60, df = 1 and 5, $P_{\text{Sidák}} > 0.05$). Nevertheless, these results should be considered preliminary because of the low number of individuals sampled.

Individuality in vocalizations.—The DFA identified 12 of the 13 frequency and duration parameters as being significant in the model (F = 12.39, df = 403 and 4,803, $P_{\text{Sidák}} < 0.001$; Table 1). Of these 12 significant parameters, the two that had the lowest tolerance (e.g., high discriminatory power) were the *bew* peak and postpeak edge frequencies. The DFA correctly classified 86.4% of the 440 *fitz bew* vocalizations to the correct individual (correct classification rates per individual ranged between 54.5% and 100%; Appendix 2 [online supplementary material; see Acknowledgments]). Fourteen individuals (43.8%) had between 90% and 100% correct classification, with nine individuals (28.1%) having all their vocalizations correctly classified (online Appendix 2). Classification functions for each individual are available on request.

The retained PNN model had a training performance of 1.00 and a selection performance of 0.72, and the training and selection errors were 0.03 and 0.12, respectively. The model had 220 hidden neurons and 10 input neurons. The PNN model classified 80.7% of the 440 *fitz bew* vocalizations as belonging to the correct individual with a mean confidence level of 0.79 ± 0.09 (range: 0.21–1.00; Appendix 3 [online supplementary material; see Acknowledgments]). The PNN correctly classified all vocalizations of four individuals, representing 12.5% of the birds, with a mean confidence level of 0.78 ± 0.06 (range: 0.22–1.00; online Appendix 3). The

Table 2. General linear model results of the effects of distance, ambient noise, and bird identity on *fitz bew* frequency and duration parameters in Southwestern Willow Flycatchers (distance and ambient noise, df = 1 and 428; bird identity, df = 31 and 428). All significant $P_{\text{Sidák}}$ values and associated η^2 values (proportion of variability explained) are in bold.

Fitz bew vocalization parameter	Source of variability	*F*	$P_{\text{Sidák}}$	η^2
Fitz start frequency	Recording distance	9.20	0.05	0.02
	Ambient noise	3.61	0.80	0.01
	Bird identity	28.20	**<0.001**	0.68
Fitz peak edge frequency	Recording distance	0.41	1.00	0.00
	Ambient noise	0.05	1.00	0.00
	Bird identity	27.51	**<0.001**	0.68
Fitz peak center frequency	Recording distance	1.87	1.00	0.00
	Ambient noise	0.00	1.00	0.00
	Bird identity	11.32	**<0.001**	0.46
Fitz midway edge frequency	Recording distance	25.81	**<0.001**	0.06
	Ambient noise	6.52	0.22	0.02
	Bird identity	13.34	**<0.001**	0.50
Fitz midway center frequency	Recording distance	1.64	1.00	0.00
	Ambient noise	19.43	**<0.001**	0.05
	Bird identity	10.29	**<0.001**	0.44
Bew peak edge frequency	Recording distance	5.22	<0.43	0.01
	Ambient noise	0.70	1.00	0.00
	Bird identity	27.10	**<0.001**	0.67
Bew peak center frequency	Recording distance	1.10	1.00	0.00
	Ambient noise	5.26	0.40	0.01
	Bird identity	8.88	**<0.001**	0.40
Bew prepeak edge frequency	Recording distance	1.16	1.00	0.00
	Ambient noise	2.97	0.92	0.01
	Bird identity	5.28	**<0.001**	0.29
Bew prepeak center frequency	Recording distance	0.28	1.00	0.00
	Ambient noise	6.59	0.20	0.02
	Bird identity	10.25	**<0.001**	0.44
Bew postpeak edge frequency	Recording distance	12.34	**<0.01**	0.03
	Ambient noise	12.31	**<0.01**	0.03
	Bird identity	9.77	**<0.001**	0.43
Bew postpeak center frequency	Recording distance	0.66	1.00	0.00
	Ambient noise	2.56	0.97	0.01
	Bird identity	4.28	**<0.001**	0.25
Duration of the *fitz* phrase	Recording distance	0.04	1.00	0.00
	Ambient noise	4.65	0.55	0.01
	Bird identity	27.78	**<0.001**	0.68
Duration of the *bew* phrase	Recording distance	0.37	0.57	0.00
	Ambient noise	0.47	1.00	0.00
	Bird identity	20.65	**<0.001**	0.61

sensitivity analysis ranked nine variables that were used in classifying vocalizations and left out four (*bew* prepeak center frequency, duration of *fitz*, and peak edge frequency of *fitz*). The three variables with the highest sensitivity were *fitz* peak edge frequency, *bew* prepeak center frequency, and duration of the *fitz* phrase. Combining the DFA and ANN results, we found evidence supporting individuality in the Southwestern Willow Flycatcher vocalizations.

Ambient noise and recording distance effects.—Ambient noise levels were significantly different among recorded birds ($F = 51.84$, df = 39 and 427, $P_{\text{Sidák}} < 0.001$, range: 20.9–53.3 dB). We did not find significant differences in recording distance among populations ($F = 2.26$, df = 2 and 34, $P_{\text{Sidák}} = 0.98$), after controlling for the effects of time of day ($F = 0.09$, df = 1 and 34, $P_{\text{Sidák}} = 1.00$), temperature ($F = 0.15$, df = 1 and 34, $P_{\text{Sidák}} = 1.00$), and perching height ($F = 48.24$, df = 1 and 34, $P_{\text{Sidák}} < 0.001$).

We then analyzed each frequency and duration parameter to determine the relative roles of ambient noise, recording distance, and bird identity (Table 2). We found that two frequency parameters, *fitz* midway center and *bew* postpeak edge, were significantly affected by ambient noise levels, which explained 3% and 5% of their variability, respectively (Table 2). Two frequency parameters, *fitz* midway edge and *bew* postpeak edge, were significantly affected by recording distance, which explained 3% and 6% of their variability, respectively (Table 2). All 13 frequency and duration parameters were significantly affected by bird identity, which explained from 25% to 68% of the variability (Table 2). The proportion of variability attributed to ambient noise or recording distance was always less than that associated with bird identity (Table 2).

Population-level variation.—The DFA found vocalizations to be significantly different among populations ($F = 39.36$, df = 26

Table 3. Variables used in the discriminant function analysis model for classifying vocalizations of Southwestern Willow Flycatcher at the population level. Significant $P_{\text{Sidák}}$ values are in bold. DF = 2 and 528.

Fitz bew vocalization parameter	F	$P_{\text{Sidák}}$	Tolerance
Fitz start frequency	74.08	**<0.001**	0.85
Fitz peak edge frequency	0.11	1.00	0.59
Fitz peak center frequency	0.40	1.00	0.73
Fitz midway edge frequency	13.43	**<0.001**	0.69
Fitz midway center frequency	3.63	0.24	0.85
Bew peak edge frequency	50.98	**<0.001**	0.48
Bew peak center frequency	58.92	**<0.001**	0.92
Bew prepeak edge frequency	0.48	1.00	0.67
Bew prepeak center frequency	0.66	1.00	0.88
Bew postpeak edge frequency	28.27	**<0.001**	0.58
Bew postpeak center frequency	6.01	**<0.05**	0.85
Duration of the *fitz* phrase	4.24	0.13	0.86
Duration of the *bew* phrase	11.94	**<0.001**	0.92

and 1,056, $P_{\text{Sidák}} < 0.001$). Seven of the 13 studied vocal parameters were significant in the model (Table 3), including duration of *bew*, *fitz* start frequency, *fitz* midway edge frequency, *bew* peak edge frequency, *bew* peak center frequency, *bew* postpeak edge frequency, and *bew* postpeak center frequency. The two parameters with the lowest tolerance in the DFA model were the peak edge and postpeak frequencies of the *bew* phrase (Table 3). Overall, the DFA correctly classified 78.0% of the 522 vocalizations to the correct population: Kern River (81 of 103 vocalizations, 78.6%), Roosevelt Lake (84 of 121 vocalizations, 69.4%), and San Pedro River (276 of 319 vocalizations, 86.5%). The plot of the first and second canonical axis scores shows that there is little overlap between Roosevelt Lake (Arizona) and Kern River (California) (Fig. 2). However, the San Pedro River (Arizona) population overlaps substantially with the other two populations (Fig. 2). Furthermore, the variability in vocalization structure (e.g., parameter space or ellipse area in Fig. 2) was more limited at Roosevelt Lake than at Kern River and San Pedro River.

The retained ANN model for the population-level analysis had a training performance and error of 1.00 and 0.10, respectively. The selection performance was 0.93, and the selection error was 0.21. The model had 273 hidden neurons and 13 input neurons. The ANN correctly classified 95.3% of the 522 vocalizations to the correct population: Kern River (97 of 103 vocalizations, 94.2%; confidence level = 0.88 ± 0.11, range: 0.00–1.00), Roosevelt Lake (114 of 121 vocalizations, 94.2%; confidence level = 0.87 ± 0.11, range: 0.52–1.00), or San Pedro River (311 of 319 vocalizations, 97.5%; confidence level = 0.87 ± 0.14, range: 0.47–1.00). The sensitivity analysis ranked all 13 frequency and duration variables that were used in classifying vocalizations. The three variables with the highest sensitivity were *bew* prepeak center frequency, *fitz* beginning frequency, and *bew* postpeak center frequency.

Reidentification analysis.—In the first step, we determined the proportion of individuals that could be reidentified and found that the 10 ANN runs averaged a correct classification percentage

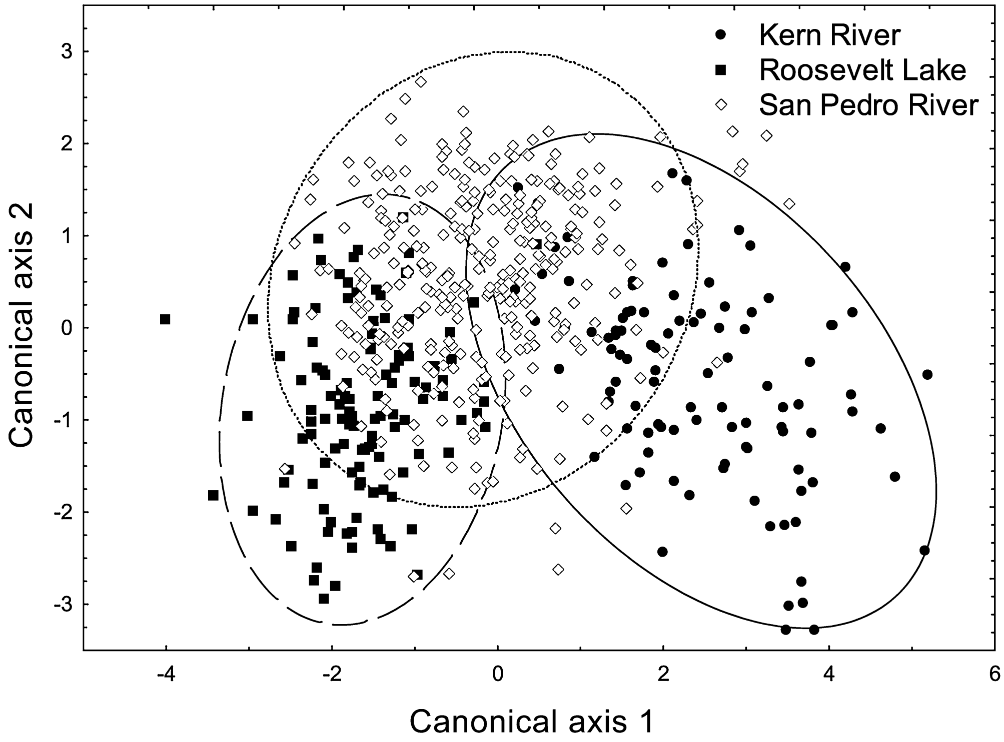

Fig. 2. Scatterplot of the DFA discriminant functions (canonical axis scores) with 95% confidence ellipses showing the discrimination of the three study populations of Southwestern Willow Flycatcher. Only two canonical axis scores were computed, and they represented all 13 frequency and duration variables.

Table 4. Reidentification results of 10 trials using data sets of 20% randomly selected *fitz bew* vocalizations from the data set of birds from the Arizona populations of Southwestern Willow Flycatcher, using the trained artificial neural network model. This analysis used the trained probabilistic neural network model from the individuality analysis.

Trial number	Mean percent correct classification per trial ± SD	Number of birds in recapture trial	Average number of *fitz bew* calls bird^{-1} trial^{-1}
Trial 1	75.88 ± 27.0	29	3.03
Trial 2	88.92 ± 17.6	30	15.50
Trial 3	80.17 ± 25.5	26	3.38
Trial 4	83.30 ± 23.0	28	1.96
Trial 5	78.80 ± 31.1	28	3.03
Trial 6	89.37 ± 16.9	29	3.03
Trial 7	73.13 ± 39.8	29	2.97
Trial 8	78.08 ± 35.1	30	2.93
Trial 9	82.01 ± 27.7	29	3.03
Trial 10	84.69 ± 29.7	28	3.14

of 81.4 ± 27.3% (range: 73.1–89.4%) of the vocalizations to the correct individuals (Table 4). Overall, the 10 ANN runs reidentified successfully an average of 19.9 of the 28.6 birds included in the database with ≥80% correct classification.

In the second step, the classification percentage did not vary considerably (1.4% variation) with the number of *fitz bew* vocalizations per individual (Table 5). However, the coefficient of variation of the classification decreased ~11% with an increase in the number of *fitz bew* vocalizations individual^{-1} (Table 5). These results indicate that gathering 15 vocalizations individual^{-1} would increase the precision of the ANN to classify Southwestern Willow Flycatcher *fitz bew* calls.

In the third step, the 10 trained PNN models using the known-individual data sets had an average training performance and error of 1.00 ± 0.00 and 0.04 ± 0.04, respectively. The selection performance and error were 0.80 ± 0.07 and 0.17 ± 0.02, respectively. The model had 222 hidden neurons and 11 input neurons. The model was able to successfully identify the two birds in each of the data sets that were novel individuals by attributing 100% of both birds' vocalizations to the "unknown" category.

Table 5. Summary of the reidentification analysis trials to determine how many vocalizations per bird are necessary to produce a more precise and accurate reidentification result. This analysis used the probabilistic neural network model from the individuality analysis.

Number of *fitz bew* vocalizations per individual	Mean percent correctly reidentified ± SD	Coefficient of variation
3	87.15 ± 19.89	0.23
4	86.19 ± 17.31	0.20
5	84.76 ± 16.18	0.19
6	85.03 ± 14.65	0.17
7	85.44 ± 13.68	0.16
8	84.99 ± 12.90	0.15
9	85.21 ± 12.67	0.15
10	85.86 ± 11.61	0.14
11	86.17 ± 11.50	0.13
12	86.61 ± 10.59	0.12
13	86.14 ± 11.48	0.13
14	85.97 ± 10.74	0.12
15	85.71 ± 10.41	0.12

DISCUSSION

Geographic differences in the vocal structure of the *fitz bew* have been shown to occur between two Willow Flycatcher subspecies, *E. t. extimus* and *E. t. adastus* (Sedgwick 2001). Our results show new levels of vocal individuality within one subspecies (*E. t. extimus*) at the individual and population levels. We found that (1) Southwestern Willow Flycatchers have vocal individuality based on the frequency and duration of their *fitz bews*; (2) vocalizations from individuals belonging to different populations could be distinguished, particularly between Roosevelt Lake (Arizona) and Kern River (California); and (3) artificial neural networks and discriminant function models could reidentify vocalizations from different individuals with high accuracy and precision, and ANNs were successful at identifying new birds.

Our DFA classification rates are comparable to those individuality analyses found in passerine species (Steere's Liocichla [*Liocichla steerii*], 86%, Mays et al. 2006; Rufous Bristlebird [*Dasyornis broadbenti*], 87%, Rogers and Paton 2005) and also in a nonpasserine (Western Screech-Owl [*Megascops kennicottii*], 87.3%, Tripp and Otter 2006). Our ANN classification rates were lower than those found in Corncrake (96.5%, Terry and McGregor 2002), the only other bird species, to our knowledge, for which an ANN has been used to assess individuality. The discrepancy in ANN classification rates could be related to the fact that we included more variable numbers of vocalizations per individual than Terry and McGregor (2002) did. Interestingly, despite the higher versatility of ANNs in dealing with nonlinear data, we found the performance of DFA to be as good as that of ANNs or, in some cases, slightly better (but see Parsons and Jones 2000). This unexpected result could be influenced by linear relationships between vocal parameters in this species, which would be better captured by DFA, or by the high variability in the data set in terms of the number of vocalizations per individual. The training performance of ANNs could also be lower when within-individual variability is increased, such as when a data point (e.g., vocalization) is not characteristic of a particular individual (Sarle 2002).

We found that the frequencies just before, after, and at the peaks of the *bew* phrase contributed the most to vocal individuality in Southwestern Willow Flycatchers. Acadian Flycatchers (*E. virescens*) also had the greatest individual variability in the frequency peaks of their songs (Wiley 2005). These peaks represent the frequency where the most energy is discharged by a vocalizing animal, which allows the vocalization to be heard farther away (Blumstein and Turner 2005, Wiley 2005, Boncoraglio and Saino 2007). Having individually based traits in the long-range portion of the songs may allow male Southwestern Willow Flycatchers to attract females or keep rivals at bay (Naguib and Wiley 2001).

The variability in Willow Flycatcher vocalizations has been proposed to be innate and not affected by learning (Kroodsma 1984, Sedgwick 2001). At least three factors that deserve further consideration can explain vocal individuality in our subspecies: genetic variability of innate songs, morphological differences in vocal anatomy, and enhanced discrimination of neighbors.

Genetic variability is likely to cause vocal patterns associated with the dispersion patterns of territorial males and their offspring and the distances separating populations (see below). Individual variation in male morphology may covary with syrinx size, which could affect vocal parameters, as found in other bird species (see Shy 1983, Handford and Lougheed 1991, Podos et al. 2004). Finally, individuality in Southwestern Willow Flycatcher vocalizations may facilitate nearest-neighbor discrimination and save energy by avoiding unnecessary conflicts with familiar individuals. Nearest-neighbor discrimination has been reported in two phylogenetically related species with individually distinctive vocalizations: the Alder Flycatcher (*E. alnorum*; Lovell and Lein 2004, 2005) and the Acadian Flycatcher (Wiley 2005).

At least two processes can account for the variation in vocal structure in relation to environmental cues: vegetation structure can affect the transmission of vocalizations through sound degradation (Marten and Marler 1977, Dabelsteen et al. 1993), and noise levels can alter the frequency at which individuals vocalize (reviewed in Wood and Yezerinac 2006). Despite the potential low degree of song learning in Southwestern Willow Flycatcher, ambient noise and recording distance influenced the upper frequencies of the *bew* and the middle and upper frequencies of the *fitz* phrase, which correspond to frequencies between 3,500 and 4,300 Hz (Fig. 1). However, the maximum bias that resulted from these confounding factors was ~6% (based on the maximum amount of variability explained). Consequently, individual differences have higher relevance in explaining vocal variability (≤68%) in this subspecies.

Artificial neural networks have been used before to detect vocal variability among populations of Corncrakes separated by distances similar to those between our populations (30–900 km; Terry and McGregor 2002). Southwestern Willow Flycatchers at Kern River and Roosevelt Lake were distinct from each other in vocal structure. However, vocalization structure at San Pedro River overlapped considerably with the other two populations (Fig. 2). There are several non-mutually exclusive factors that may account for population differences. First, differences in body size between populations could affect vocal parameters through variations in the size of the vocal tract and syrinx. We did not capture individuals to assess this possibility because of their endangered status. Second, the geographic distance between populations may explain the similarity between the San Pedro River and Roosevelt Lake populations; however, it cannot explain the similarity found between the San Pedro River and Kern River populations, because they are even farther apart (~680 km). Third, our data set may have included some migrant individuals, particularly in the San Pedro population, where monitoring of individuals was slightly more limited than in the other populations. However, we gathered our largest sample sizes in San Pedro, which could, in turn, have increased the variability in vocal structure.

Fourth, population-level variations may be influenced by habitat structure, which varies qualitatively between Kern River and Roosevelt Lake. The Kern River is dominated by both willow (*Salix* spp.) and Fremont Cottonwood (*Populus fremontii*; M. Whitfield pers. comm.), whereas our recording sites at Roosevelt Lake contained primarily saltcedar (*Tamarix* spp.; English et al. 2006). Interestingly, recording sites within the San Pedro River area contained patches of habitats similar to those found in both Kern River and Roosevelt Lake. We therefore suggest that there is a certain degree of overlap in habitat structure between populations that may be similar to the overlap found in vocal differences (Fig. 2). If so, vocalizations may vary because animals adjust their vocal parameters to the surrounding environment (e.g., Slabbekoorn 2004), but we cannot unequivocally support this. Alternatively, we speculate that vocalizations may reflect variations in habitat selection after migration, whereby individuals that were fledged at both Kern River and Roosevelt Lake may establish breeding territories in the San Pedro River population because both types of natal habitats are available there. Previous surveys have detected Southwestern Willow Flycatchers moving from Roosevelt Lake to San Pedro River between breeding seasons (e.g., English et al. 2006), but further research on the postnatal dispersal patterns of this subspecies is necessary.

Our results provide a basic understanding of the individual patterns in *fitz bew* vocalizations that can be used to enrich current individual-tracking and species-monitoring efforts. Spatial and temporal tracking of individuals using vocalizations have been successful in Corncrakes (Terry and McGregor 2002). Given the classification performance of our models, we suggest that two statistical techniques can be used for Southwestern Willow Flycatcher: DFA for discriminating between known individuals and ANNs for identifying new individuals in the population. Using DFA may facilitate tracking of individuals, because it is easier to use, and classification functions can be directly derived to calculate scores, which can assign vocalizations to individual birds. Those vocalizations with low scores could be run against an ANN to check for new individuals.

However, acoustic tracking can be challenging, because it requires the special training of personnel to reduce noise, maintain a certain recording distance, and ensure a given number of vocalizations per individual. Noise variations could be minimized by recording animals on days with very low wind speeds, though the noise generated by other species is probably unavoidable. Recording distance effects could be reduced at 2–3 m from the focal bird without causing too much disturbance; however, reaching this distance may not be possible in habitats with dense, shrubby vegetation. We recommend gathering 15 vocalizations per individual, though recording 11 vocalizations would maintain the low levels of variability in classification levels. However, even 11 vocalizations could be difficult to obtain from an individual, given variations in recording conditions (e.g., vegetation structure, noise, etc.). Furthermore, in a population with several unbanded individuals, the probabilities of rerecording the same unknown individual need to be estimated before implementing this technique. Given all these shortcomings, we suggest that acoustic tracking should complement rather than replace current monitoring practices—for instance, in areas in which banding is not practical or when human resources are limited.

Individuality in Southwestern Willow Flycatchers opens up interesting research venues besides individual tracking. Vocal individuality can help solve some taxonomic questions in areas where subspecies overlap and help us to understand differences in song structure between males and females, differences between seasons and years, and variation in the song structure of individuals changing territory location within a population. More importantly, vocal individuality could assist in the estimation of population-level parameters (recruitment, dispersal) necessary to monitor the status of this endangered subspecies.

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Literature Cited

Baker, M. C., and D. E. Gammon. 2006. Persistence and change of vocal signals in natural populations of chickadees: Annual sampling of the gargle call over eight seasons. Behaviour 143:1473–1509.

Bard, S. C., M. Hau, M. Wikelski, and J. C. Wingfield. 2002. Vocal distinctiveness and response to conspecific playback in the Spotted Antbird, a Neotropical suboscine. Condor 104:387–394.

Blumstein, D. T., and A. C. Turner. 2005. Can the acoustic adaptation hypothesis predict the structure of Australian birdsong? Acta Ethologica 15:35–44.

Boncoraglio, G., and N. Saino. 2007. Habitat structure and the evolution of bird song: A meta-analysis of the evidence for the acoustic adaptation hypothesis. Functional Ecology 21:134–142.

Candolin, U. 2003. The use of multiple cues in mate choice. Biological Reviews 78:575–595.

Chandler, C. R. 1995. Practical considerations in the use of simultaneous inference for multiple tests. Animal Behaviour 49:524–527.

Charif, R. A., C. W. Clark, and K. M. Fristrup. 2004. Raven 1.2 User's Manual. Cornell Lab of Ornithology, Ithaca, New York.

Dabelsteen, T., O. N. Larsen, and S. B. Pedersen. 1993. Habitat-induced degradation of sound signals: Quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal to noise ratio in blackbird song. Journal of the Acoustical Society of America 93:2206–2220.

Deecke, V. B., J. K. B. Ford, and P. Spong. 1999. Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (*Orcinus orca*) dialects. Journal of the Acoustical Society of America 105:2499–2507.

Delport, W., A. C. Kemp, and J. W. H. Ferguson. 2002. Vocal identification of individual African Wood Owls *Strix woodfordii*: A technique to monitor long-term adult turnover and residency. Ibis 144:30–39.

Durst, S. L., M. K. Sogge, H. C. English, S. O. Williams, B. E. Kus, and S. J. Sferra. 2006. Southwestern Willow Flycatcher breeding site and territory summary—2005. U.S. Geological Survey Southwest Biological Science Center, Flagstaff, Arizona.

English, H. C., A. E. Graber, S. D. Stump, H. E. Telle, and L. A. Ellis. 2006. Southwestern Willow Flycatcher 2005 survey and nest monitoring report. Arizona Game and Fish Department, Phoenix.

Gilbert, G., P. K. McGregor, and G. Tyler. 1994. Vocal individuality as a census tool: Practical considerations illustrated by a study of two rare species. Journal of Field Ornithology 6:335–348.

Godard, R. 1993. Tit for tat among neighboring Hooded Warblers. Behavioral Ecology and Sociobiology 33:45–50.

Handford, P., and S. C. Lougheed. 1991. Variation in duration and frequency characters in the song of the Rufous-collared Sparrow, *Zonotrichia capensis,* with respect to habitat, trill dialects and body size. Condor 93:644–658.

Hoodless, A. N., J. G. Inglis, J.-P. Doucet, and N. J. Aebischer. 2008. Vocal individuality in the roding calls of Woodcock *Scolopax rusticola* and their use to validate a survey method. Ibis 150:80–89.

Johnstone, R. A. 1996. Multiple displays in animal communication: 'Backup signals' and 'multiple messages.' Philosophical Transactions of the Royal Society of London, Series B 351:329–338.

Kroodsma, D. E. 1979. Vocal dueling among male Marsh Wrens: Evidence for ritualized expressions of dominance/subordinance. Auk 96:506–515.

Kroodsma, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24.

Kus, B. E., P. P. Beck, and J. M. Wells. 2003. Southwestern Willow Flycatcher populations in California: Distribution, abundance, and potential for conservation. Pages 12–21 *in* Ecology and Conservation of the Willow Flycatcher (M. K. Sogge, B. E. Kus, S. J. Sferra, and M. J. Whitfield, Eds.). Studies in Avian Biology, no. 26.

Lek, S., M. Delacoste, P. Baran, I. Dimopoulos, J. Lauga, and S. Aulagnier. 1996. Application of neural networks to modelling nonlinear relationships in ecology. Ecological Modelling 90: 39–52.

Lovell, S. F., and M. R. Lein. 2004. Neighbor–stranger discrimination by song in a suboscine bird, the Alder Flycatcher, *Empidonax alnorum*. Behavioral Ecology 15:799–804.

Lovell, S. F., and M. R. Lein. 2005. Individual recognition of neighbors by song in a suboscine bird, the Alder Flycatcher *Empidonax alnorum*. Behavior Ecology and Sociobiology 57:623–630.

Marten, K., and P. Marler. 1977. Sound transmission and its significance for animal vocalization 1. Temperate habitats. Behavioral Ecology and Sociobiology 2:271–290.

Mays, H. L., Jr., C.-T. Yao, and H.-W. Yuan. 2006. Antiphonal duetting in Steere's Liocichla (*Liocichla steerii*): Male song individuality and correlation between habitat and duetting behavior. Ecological Research 21:311–314.

McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate Statistics for Wildlife and Ecology Research. Springer, New York.

McGregor, P. K., and P. Byle. 1992. Individually distinctive bittern booms: Potential as a census tool. Bioacoustics 4:93–109.

McGregor, P. K., T. M. Peake, and G. Gilbert. 2000. Communication behaviour and conservation: The application of sound science: Pages 261–280 *in* Behaviour and Conservation (L. M. Gosling and W. J. Sutherland, Eds.). Cambridge University Press, Cambridge, United Kingdom.

Naguib, M., and R. H. Wiley. 2001. Estimating the distance to a source of sound: Mechanisms and adaptations for long-range communication. Animal Behaviour 62:825–837.

Nicholls, J. A., and A. W. Goldizen. 2006. Habitat type and density influence vocal signal design in Satin Bowerbirds. Journal of Animal Ecology 75:549–558.

Nickerson, C. M., L. L. Bloomfield, M. R. W. Dawson, and C. B. Sturdy. 2006. Artificial neural network discrimination of Black-capped Chickadee (*Poecile atricapillus*) call notes. Journal of the Acoustical Society of America 120:1111–1117.

Parsons, S. 2001. Identification of New Zealand bats (*Chalinolobus tuberculatus* and *Mystacina tuberculata*) in flight from analysis of echolocation calls by artificial neural networks. Journal of the Zoological Society of London 253:447–456.

Parsons, S., and G. Jones. 2000. Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. Journal of Experimental Biology 203:2641–2656.

Peake, T. M., and P. K. McGregor. 2001. Corncrake *Crex crex* census estimates: A conservation application of vocal individuality. Animal Biodiversity and Conservation 24:81–90.

Peake, T. M., P. K. McGregor, K. W. Smith, G. Tyler, G. Gilbert, and R. E. Green. 1998. Individuality in Corncrake *Crex crex* vocalizations. Ibis 140:120–127.

Penteriani, V. 2003. Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality. Ibis 145:E127–E135.

Podos, J., J. A. Southall, and M. R. Rossi-Santos. 2004. Vocal mechanics in Darwin's finches: Correlation of beak gape and song frequency. Journal of Experimental Biology 207:607–619.

Prodon, R., and J.-D. Lebreton. 1981. Breeding avifauna of a Mediterranean succession: The holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. Oikos 37:21–38.

Puglisi, L., and C. Adamo. 2004. Discrimination of individual voices in male Great Bitterns (*Botaurus stellaris*) in Italy. Auk 121:541–547.

Quinn, G. P., and M. J. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, United Kingdom.

Reby, D., S. Lek, I. Dimopoulos, J. Joachim, J. Lauga, and S. Aulagnier. 1997. Artificial neural networks as a classification method in the behavioural sciences. Behavioural Processes 40:35–43.

Rogers, D. J., and D. C. Paton. 2005. Acoustic identification of individual Rufous Bristlebirds, a threatened species with complex song repertoires. Emu 105:203–210.

Sarle, W. S., Ed. 2002. Neural Network FAQ, part 2 of 7: Learning. [Online.] Available at ftp://ftp.sas.com/pub/neural/FAQ.html.

Sedgwick, J. A. 2000. Willow Flycatcher (*Empidonax traillii*). *In* The Birds of North America, no. 533 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Sedgwick, J. A. 2001. Geographic variation in the song of Willow Flycatchers: Differentiation between *Empidonax traillii adastus* and *E. t. extimus*. Auk 118:366–379.

Seutin, G. 1987. Female song in Willow Flycatchers (*Empidonax traillii*). Auk 104:329–330.

Shy, E. 1983. The relation of geographical variation in song to habitat characteristics and body size in North American tanagers (Thraupinae: Piranga). Behavioral Ecology and Sociobiology 12:71–76.

Slabbekoorn, H. 2004. Habitat-dependent ambient noise: Consistent spectral profiles in two African forest types. Journal of the Acoustical Society of America 116:3727–3733.

StatSoft. 2007. Electronic Statistics Textbook. [Online.] Available at http://www.StatSoft.com/textbook/stathome.html.

Terry, A. M. R., and P. K. McGregor. 2002. Census and monitoring based on individually identifiable vocalizations: The role of neural networks. Animal Conservation 5:103–111.

Terry, A. M. R., T. M. Peake, and P. K. McGregor. 2005. The role of vocal individuality in conservation. Frontiers in Zoology 2. [Online.] Available at www.frontiersinzoology.com/content/2/1/10.

Tibbetts, E. A., and J. Dale. 2007. Individual recognition: It is good to be different. Trends in Ecology and Evolution 22:529–537.

Tripp, T. M., and K. A. Otter. 2006. Vocal individuality as a potential long-term monitoring tool for Western Screech-Owls *Megascops kennicottii*. Canadian Journal of Zoology 84:744–753.

U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. Federal Register 60:10694 (27 February 1995).

Walcott, C., J. N. Mager, and W. Piper. 2006. Changing territories, changing tunes: Male loons, *Gavia immer*, change their vocalizations when they change territories. Animal Behaviour 71:673–683.

Wiley, R. H. 2005. Individuality in the songs of Acadian Flycatchers and recognition of neighbours. Animal Behaviour 70:237–247.

Wood, W. E., and S. M. Yezerinac. 2006. Song Sparrow (*Melospiza melodia*) song varies with urban noise. Auk 123:650–659.

Wright, S. P. 1992. Adjusted *P*-values for simultaneous inference. Biometrics 48:1005–1013.

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