SONGS OF THE ALDER FLYCATCHER (*EMPIDONAX ALNORUM*) AND WILLOW FLYCATCHER (*EMPIDONAX TRAILLII*) ARE INNATE

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ABSTRACT.—I studied the song development of five Willow Flycatchers (*Empidonax traillii*) and four Alder Flycatchers (*Empidonax alnorum*) taken from nests at 7–10 days of age. Three Willow Flycatchers and four Alder Flycatchers were tutored with songs of the other species, and two Willow Flycatchers served as controls, hearing only conspecific songs. All nine subjects, both females (when administered exogenous testosterone) and males, and both experimentals and controls, produced remarkably normal songs; slight differences between songs of wild and experimental subjects could be attributed to motivational states rather than to the effects of acoustic isolation in the laboratory. I found no microgeographic variation of wild songs, no evidence of learning from a tutor tape, nor any similarity of song characters among kin. The vocal development of these suboscine flycatchers is strikingly different from that of typical oscines, where vocal learning is the rule. *Received 17 January 1983, accepted 1 September 1983.*

THE order Passeriformes consists of approximately 5,274 species (Bock and Farrand 1980). About 4,177 of these are songbirds or oscines, with centers of origin and adaptive radiation in the Holarctic. The other 1,097 or so are suboscines, with the largest groups centered in South and Central America. Until about five million years ago, when the Panamanian land bridge formed, these two suborders evolved independently on different land masses. A number of characters, including sperm and stapes structure but especially syrinx complexity, distinguish these two groups (e.g. Feduccia 1980).

Other data have suggested a difference in vocal development; while oscines imitate extensively, some or perhaps all suboscines may lack this ability. Among the oscines, vocal learning is the norm, and concrete or suggestive data are available for about 300 species (Kroodsma and Baylis 1982). Young birds must hear, often during a sensitive period early in life, the songs of adult conspecifics in order to learn and develop appropriate songs. The "subsong" or practice stage requires auditory feedback during a time when the young bird is attempting to match a motor output with that vocal pattern that had been memorized, often months before. When juvenile males learn songs and either remain nearby or migrate and then return to breed, song dialects and marked microgeographic variation often result. Song control centers in the songbird forebrain are involved in the learning process, and the entire task of sound production is known in some cases to be neurally lateralized, with the left side of the brain and the left hypoglossal nerve controlling the production of the majority of sounds in the typical, relatively complex, oscine song (for recent reviews on these topics see Konishi 1965, Nottebohm 1980, Marler and Peters 1982, Kroodsma 1982, Slater 1983). Because both oscine song and human speech are learned, many parallels exist between them (Marler 1970a).

On the other hand, two forms of indirect evidence suggest that vocal learning might be absent from the suboscines. First, there is an absence of marked geographic variation in advertising songs. Payne and Budde (1979) found no tendency for adjacent male Acadian Flycatchers (*Empidonax virescens*) to share similar song types. Lanyon (1978) found that body size and song frequency (in kHz) were positively correlated in *Myiarchus* flycatchers but that the overall form of the song was invariant over thousands of kilometers. Similarly, Stein (1963) and Johnson (1980) found that *Empidonax* songs varied little over distance. The second form of evidence is the apparent lack of oscine-like song control centers in the forebrain of an Eastern Kingbird (*Tyrannus tyrannus*, Tyrannidae), Hudson's Canastero (*Asthenes hudsoni*, Furnariidae), and a Sooty-fronted Spinetail (*Synallaxis frontalis,* Furnariidae) (Nottebohm 1980). Neither form of evidence is conclusive, however, for among oscines neighboring males do not always share similar song types (Kreutzer 1979, Bradley 1981, Hultsch and Todt 1981), entire learned songs may be relatively invariant over great distances (Nottebohm 1969), the same learned song components may occur throughout the entire geographic range of a species (Shiovitz and Thompson 1970), and suboscines, with very different syringes (Ames 1971), need not necessarily have the same neural organization as oscines in order to learn songs.

In order to make a more direct comparison of song development among representatives of these two passerine subgroups, I studied the Alder and Willow Flycatchers (*Empidonax alnorum* and *E. traillii,* respectively). Until 10 yr ago, when the American Ornithologists' Union (1973) formally recognized these two species, they were known as the *fee-bee-o* and the *fitz-bew* song populations of the former Traill's Flycatcher (*E. traillii;* see Stein 1963). These two forms are very closely related and are now sympatric over much of their geographic ranges in midwestern and northeastern North America. Though multivariate analyses of morphological characters may allow separation of these two species (J. C. Barlow unpubl. data), ornithologists in the field typically use the advertising song as the sole distinguishing character.

METHODS

Eight Willow Flycatchers were taken from three nests in Longmeadow, three were taken from one nest in Windsor, and six Alder Flycatchers were collected from two nests in Windsor, Massachusetts. The ages varied from 7 to 10 days when the birds were collected, and the song form of the male parent had been identified in all cases. I tutored eight Willow Flycatchers and all six Alder Flycatcher subjects with typical songs (see Figs. 1-6) of the other species. Three Willow Flycatchers served as controls and were tutored with conspecific song. Tutoring began immediately after birds were collected and continued through mid-September, when the birds ranged in age from 45 to 60 days. Birds were maintained on a daylength consistent with 42° north latitude.

The groups exposed to *fitz-bew* and *fee-bee-o* song types were tutored separately, so the 14 experimental (not the three control) subjects heard only heterospecific song in the laboratory. Vocalizations of all individuals were recorded until approximately day 35. Throughout the winter months, during which I heard no singing, the three treatment groups were housed separately. During the early spring, before the onset of singing, males were moved to individual sound isolation chambers until they were recorded in full song. Females, and some nonsinging males, were later implanted with a 15 mm section of silastic medical tubing packed with crystalline testosterone; these treated birds were then also isolated individually.

Two Alder Flycatchers died during August and September of their first year; data on adult songs were available for the remaining four. Three Willow Flycatchers never sang and were not implanted with testosterone. One female and two males, even when given testosterone, never sang the typical adult songs of the species; they sang sporadically and unpredictably and uttered vocalizations more similar to other song-like vocalizations described by Stein (1963). Only the five Willow Flycatchers that sang vigorously are included in this study.

The fledgling flycatchers were recorded from 14 to about 35 days of age while separated visually, but not acoustically, from others in the treatment group. In the field, juvenile and adult flycatchers were recorded with a Nagra IS or Nagra IV and a Sennheiser MKH 106 microphone mounted in a 60-cm-diameter parabolic reflector or with Uher 4200 IC's and Sennheiser MKH 816 microphones. Sound spectrograms of selected vocalizations were prepared on a Kay Elemetrics Co. 7029A Sona-Graph (wide-band setting), and a more extensive series of spectrograms was prepared on the continuous spectrum analyzer (PAR Model 1412) at the Rockefeller University Field Research Center.

In order to assess the quality of the songs developed by the experimental subjects, I compared sonograms of their songs with those of their father (for most subjects) and other adult singing males in the wild population. Following Johnson (1980) and Payne and Budde (1979), I measured a number of parameters on the sonograms (see Figs. 1, 3, and Results) and then used several uni- and multivariate analyses from the BMDP statistical packages to aid in making comparisons. Principal components, cluster analyses, and stepwise discriminant function analyses were used in comparing songs of wild and laboratory birds. In addition, I calculated the correlation coefficients for each pair of birds using the 10-15 song characters for each bird; phenetic distances were then calculated using $D = 1 - r$, where r is the correlation coefficient for a given pair of birds (see also Payne and Budde 1979; Payne 1978 describes this method in more detail). Because the songs of experimental and control Willow Flycatchers did not differ, they were combined for many of these statistical tests.

RESULTS

Stein (1963) has presented a thorough analysis of the vocalizations of these two *Empidonax*

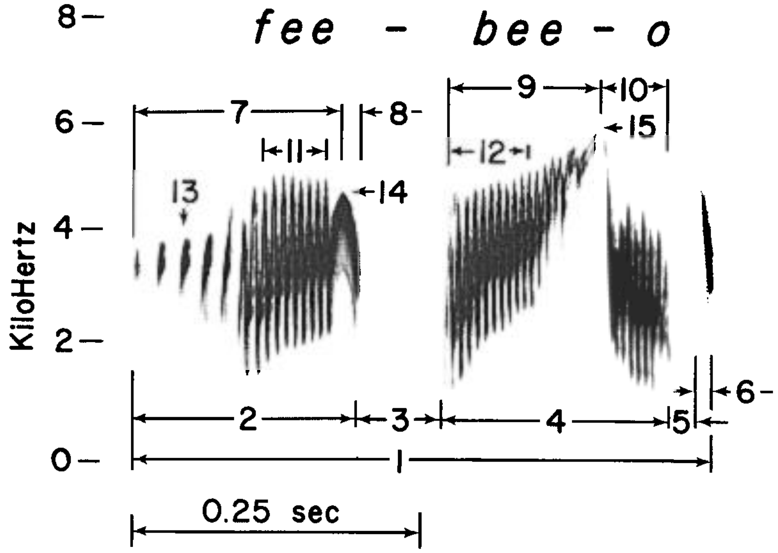

Fig. 1. The *fee-bee-o* song pattern of the Alder Flycatcher. The 15 parameters discussed in the text are illustrated. In all figures the abscissa is time and the ordinate kiloHertz.

species, and his numerous sonograms should be consulted for a more thorough catalogue than is displayed here (note, however, that Stein's and my sonograms are on a different scale). The characteristics of wild-type vocalizations discussed here are largely a summary of Stein's excellent survey.

THE ALDER FLYCATCHER

Wild-type song forms.—The song performance of the Alder Flycatcher is rather simple, with a single song form [the *fee-bee-o;* see Fig. 1 of Stein (1963) and Fig. 1 of this paper] being repeated as often as every 2 s. The *fee* consists of a few introductory notes, a frequency-modulated (fm) mid-portion, and a final loud chevron-like note. Except for the nearly inaudible note at the end of the song, the *bee-o* is a continuous sound on the spectrogram; after an initial rise, the mean frequency of the fm sound drops abruptly, producing the third syllable (*o*) in the *fee-bee-o* phonetic pattern.

Song parameters.—In Fig. 1 are illustrated the 15 song parameters that were measured on a representative sonogram for each of 15 wild and four laboratory subjects. They are: the duration of (1) the entire song, (2) the *fee,* (3) the interval between *fee* and *bee-o,* (4) the audible portion of *bee-o,* (5) the interval between the audible portion of the *bee-o* and the final note in the song, (6) the final note in the song, (7) the *fee* from the beginning to the highest frequency of the final bold frequency modulation (fm), (8) the *fee* from the highest frequency of the final bold fm to the end, (9) the *bee,* (10) the audible portion of the *o,* (11) the last seven complete fm's before the final bold fm in *fee* (measured to the highest frequency of the last fm), and (12) the first 10 complete fm's in *bee;* (13) the rate of repetition of the introductory notes in the *fee;* and (14) the highest frequency in the final note of *fee* and (15) the highest frequency at the abrupt break between *bee* and *o.*

This data set is redundant, for a number of parameters are correlated. For example, parameters 2 and 7 are highly correlated at $r = 0.96$, parameters 1 and 2 at $r = 0.79$, parameters 5 and 6 at $r = -0.73$, and parameters 3 and 4 at $r = 0.68$. All of these are significant at $P < 0.01$ ($n = 15$ wild birds). After selectively eliminating parameters, I retained only seven, which were not correlated with any others at the 0.05 level; they were 2, 4, 5, 8, 10, 11, and 15.

Vocal development of the fee-bee-o.—The nestling Alder Flycatchers produced a series of soft vocalizations, and immediately after fledging a louder call very similar to the adult *fee-bee-o* began to appear (Fig. 2A–D). Similar calls were

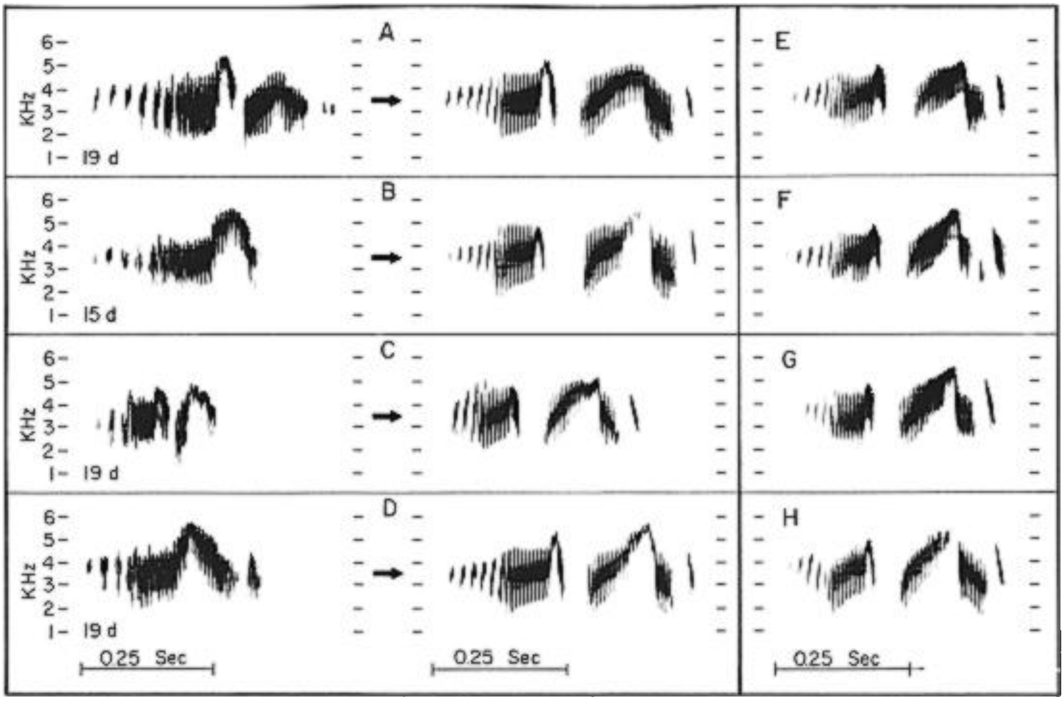

Fig. 2. Development of the *fee-bee-o* song form of the Alder Flycatcher. The vocalizations of four laboratory-reared birds (A–D) between 15 and 19 days of age (left column) foreshadowed their adult songs (middle column), which in turn are very similar to songs of wild males (E–H, right column). Birds A, C, and D are siblings, A–C are males, and D is a female (given testosterone as an adult).

recorded among newly fledged wild juveniles. During the first month or two of life, the calls did progress toward the adult song structure; the birds did not use these calls during the winter, and the final stable structure was produced only the following spring.

Qualitatively, the songs developed by the laboratory birds, which had been acoustically isolated from conspecific wild-type songs since 7–10 days of life, are remarkably similar to the songs of males in nature (Fig. 2 E–H). Each has all three song components (*fee*, *bee*, and *o*) in appropriate duration and with appropriate amplitude and frequency modulations throughout. There is variability among wild-type songs (e.g. the three-parted *bee-o* of Fig. 2F is atypical), and the songs of the laboratory-reared males appear to fall within the range of variability found among wild males.

The wild and laboratory birds differed significantly only in parameter 5, the duration of the silent interval preceding the final very brief note in the song (see Fig. 1, Table 1). The median intervals for the laboratory and wild birds were 0.019 and 0.012 s, respectively, and were significantly different ($P = 0.01$, 2-tailed Mann-Whitney *U*-test).

If songs are refined by vocal learning, greater variability in the laboratory data might be expected in the absence of model songs. I could detect no differences in variability between the data sets, however; three of the coefficients of variation (CV's hereafter) for the seven independent song parameters were actually larger among the wild birds (see Table 1).

To test whether a multivariate approach might detect a consistent difference between the laboratory and field data, I used the BMDP stepwise discriminant function program. Contrary to results that are typically obtained from oscine data, laboratory and wild birds could not be classified with complete accuracy (results were the same whether all 15 or only the 7 independent parameters were used). Eighty percent (12 of 15) of wild and 75% (3 of 4) of laboratory birds could be classified correctly (jackknifed classification). Two parameters, (5) the duration of the interval preceding the final

TABLE 1. Means, standard deviations, and coefficients of variation (%) for 15 *fee-bee-o* song parameters for 4 laboratory-reared and 15 wild Alder Flycatchers.

Song parameter[a]	Wild[b]	Laboratory-reared[b]
1	0.919 (0.070, 7.6)	0.984 (0.110, 11.2)
2	0.412 (0.053, 12.8)	0.427 (0.082, 19.3)
3	0.091 (0.015, 16.5)	0.104 (0.029, 28.2)
4	0.341 (0.025, 7.4)	0.375 (0.039, 10.3)
5	0.023 (0.010, 42.7)	0.038 (0.006, 16.5)
6	0.050 (0.011, 22.5)	0.039 (0.009, 23.2)
7	0.380 (0.059, 15.6)	0.386 (0.085, 22.1)
8	0.035 (0.006, 16.8)	0.040 (0.007, 18.3)
9	0.243 (0.037, 15.2)	0.255 (0.024, 9.3)
10	0.106 (0.021, 19.8)	0.116 (0.014, 12.2)
11	0.104 (0.009, 8.4)	0.102 (0.005, 4.5)
12	0.127 (0.006, 5.0)	0.133 (0.007, 5.0)
13	25.221 (2.109, 8.4)	25.315 (1.479, 5.8)
14	5.091 (0.203, 4.0)	5.032 (0.332, 6.6)
15	5.755 (0.347, 6.0)	5.352 (0.608, 11.4)

[a] Song parameters 1-12 are measures of duration in seconds. Parameter 13 is the number of notes/s. Parameters 14 and 15 are kHz.

[b] Data are given as means (standard deviation, coefficient of variation).

note of the song and (10) the duration of the audible portion of the *o*, were, in that order, most effective in discriminating between the laboratory and wild birds (see Fig. 1). Durations in each case were greater in the laboratory subjects. Interestingly, these two parameters were also highly variable among wild males, ranking first and third, respectively, in the CV's among all 15 parameters (see Table 1); also, in 15 consecutive songs from one wild individual, parameters 5 and 10 were highly variable (ranking first and fourth among the 15 parameters, with CV's of 11.2 and 5.4%, respectively). The data set is not large, but the data do suggest that the three laboratory-reared males and one female produced songs that were remarkably similar to the wild-type songs in local populations.

THE WILLOW FLYCATCHER

Wild-type song forms.—The singing behavior of the Willow Flycatcher is more complex. Instead of a single song form, the Willow uses three distinct vocalizations during a singing session. As with the Alder Flycatcher, these sounds have been given numerous phonetic interpretations. Here, I will use *fitz-bew* (Figs. 3, 5), *fizz-bew* (Fig. 6), and *creet* (Fig. 4) (see also Figs. 2-4 of Stein 1963). The *fitz* consists of two elements, an upslur and a downslur (see Fig. 3), while the *fizz* consists of a series of very brief, rapidly delivered elements, which rise in frequency (Fig. 6). The *bew* portion of each of these song forms consists of two or three brief introductory notes and an fm portion that is modulated first rapidly but then abruptly at a slower rate. As illustrated in Figs. 5 and 6, the *bew* portion of the two song forms in the same bird is not identical. The *bew* in *fitz-bew* usually contains three rather than only two introductory notes, and the fm portion is usually slightly different, though not in any consistent manner. The *creet*, the third song form of the Willow Flycatcher, is simpler and begins with a series of brief sounds, gradually rising in both frequency and intensity (Fig. 4.)

Song parameters.—Because the *creet* was not as loud as the other two song forms, good recordings were more difficult to obtain. In addition, it is a simpler vocalization, and therefore no detailed measurements were made.

The 10 parameters of *fitz-bew* song forms that were measured for each of the 23 wild and 5 laboratory subjects are illustrated in Fig. 3. Those parameters are: the duration of (1) the entire song, (2) the *fitz* at 4 kHz, (3) the interval between the *fitz* and *bew*, (4) the *bew*, (5) the introductory notes to the *bew*, (6) the fm portion of the *bew*, (7) the first 7 fm's of the *bew*, and (8) the last 5 fm's of the *bew*; and the (9) minimum and (10) maximum frequency of the last complete fm in *bew*.

Again, the data set is redundant, for parameters 1 and 6 are correlated at $r = 0.87$, 1 and 10 at $r = -0.59$ (both significant at $P < 0.01$, $n = 23$ wild birds), and parameters 1 and 3, 8 and 9, and 2 and 9 are significantly correlated at $P < 0.05$. After selectively deleting parameters, I retained six that were not significantly correlated with any others at $P \leqq 0.05$; they were parameters 2-5, 7, and 8.

The 10 parameters of *fizz-bew* song forms measured for 22 field and 5 laboratory subjects are nearly identical to those of the *fitz-bew* and therefore not illustrated separately. Parameters 1 and 4-9 are the same as for *fitz-bew*. The remaining parameters are (2) the duration of the *fizz*, (3) the duration of the interval between *fizz* and *bew*, and (10) the minimum frequency of the last (usually second) introductory note of the *bew*.

Several parameters were again highly cor-

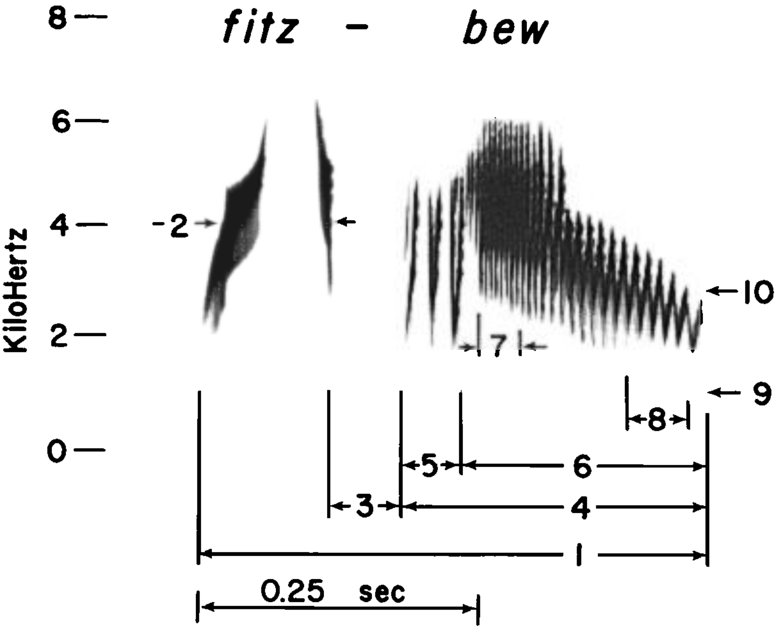

Fig. 3. The *fitz-bew* song form of the Willow Flycatcher. The 10 parameters discussed in the text are illustrated.

related with each other (4 and 6, $r = 0.95$; 1 and 4, $r = 0.81$; 8 and 9, $r = -0.71$; 2 and 3, $r = -0.64$; 2 and 7, $r = -0.47$; 7 and 10, $r = 0.47$—the first four are significant at 0.01, the last two at 0.05, with $n = 22$ wild males). I retained five independent parameters, 1, 2, 5, 8, and 9, for more thorough study.

Vocal development of the creet.—The calls of juvenile birds often change at fledging, and the most noticeable change in the Willow Flycatcher is the immediate appearance of a vocalization resembling the adult *creet* (Fig. 4). These calls, recorded during the third week of life (16–20 days), occur in both males and intact females, though adult females in the laboratory use this sound only when administered testosterone. Some variation in *creet* microstructure is evident in the sonograms of wild birds, and the vocalizations of the laboratory-reared birds appear to fall within this range. There is no evidence suggesting that the sexes are different, that siblings develop *creets* more similar to each other than to non-related birds, that offspring develop *creets* especially similar to their fathers, or that tutoring of a male or a female improved the quality of the *creet*.

Vocal development of the fitz-bew.—All 5 laboratory-reared Willow Flycatchers, both the 2 controls and 3 experimentals, produced *fitz-bews* very similar in structure to the song forms of wild males (Fig. 5). The *fitz* consists of two notes, the introduction to the *bew* consists of three distinguishable notes, and the pattern of frequency modulation in the *bew* is very normal.

Of the 10 parameters that I measured (see Fig. 3, Table 2), the laboratory and wild birds differed signficantly only in parameter 3, the duration of the interval between the *fitz* and *bew* ($P = 0.01$, two-tailed Mann-Whitney U-test). The duration for only 1 of the 5 laboratory birds fell outside the range of the wild birds, and the median durations were 0.073 s for laboratory and 0.087 s for wild birds. The data for the laboratory birds were no more variable than were those for the wild birds; of the 6 independent parameters (2–5, 7, 8), CV's for 3 were greater in the field than in the laboratory data (see Table 2).

The BMDP stepwise discriminant function program was able to classify correctly (using jackknifed classification) 86.4% (19 of 22) of the wild and 80% (4 of 5) of the laboratory birds (analysis is based on all 10 parameters). Two parameters, (9) the minimum frequency of the last complete fm in *bew* and (3) the interval between *fitz* and *bew*, were, in that order, most

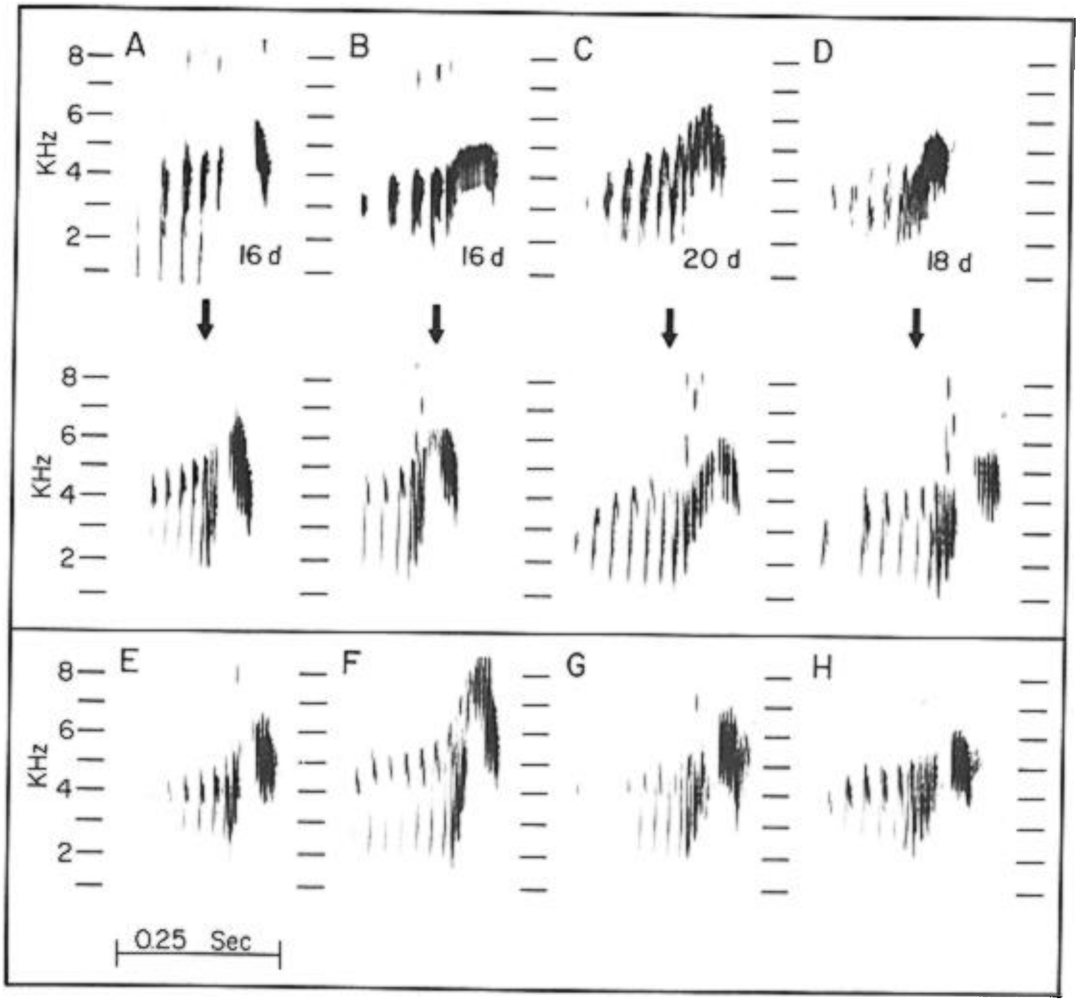

Fig. 4. Development of the *creet* in the Willow Flycatcher. The fledgling calls of four laboratory-reared birds (A–D) between 16 and 20 days of age resembled their adult *creets* (middle row). Birds E–H are adult males recorded in the wild. Bird E is the father of the sibling females A and B (each given testosterone as adults). Birds C and D are males; H is the father of D. Bird C was tutored with conspecific songs, while birds A, B, and D heard only the adult Alder Flycatcher *fee-bee-o* in the laboratory.

effective in discriminating laboratory and wild birds. Among all 10 parameters, these 2 ranked fifth and first in variability among the wild males (CV's = 13.4 and 18.0, respectively). These same two parameters were most variable in 15 consecutive *fitz-bews* recorded from a single wild individual (CV's were 4.9 and 3.6%, respectively, for variables 9 and 3, and CV's for the other 8 parameters were 1.9% or less).

Using principal components analysis, and the phenetic distances, I could detect no greater similarity than expected by chance either in the songs of relatives (siblings and fathers) or in the songs of the training tape and those developed by the tutored male and female in the laboratory. Furthermore, as might be expected if no learning is occurring in the field, neighboring wild males had songs no more similar to each other than they did to birds 50–200 km distant (using phenetic distance $D = 1 - r$, Mann-Whitney U-test, 1-tailed, $P = 0.4$).

Vocal development of the fizz-bew.—The *fizz-bew* also seemed to develop quite normally in all five laboratory-reared subjects (Fig. 6). The *fizz* rises appropriately in frequency, the introduction to the *bew* consists of only two notes, and

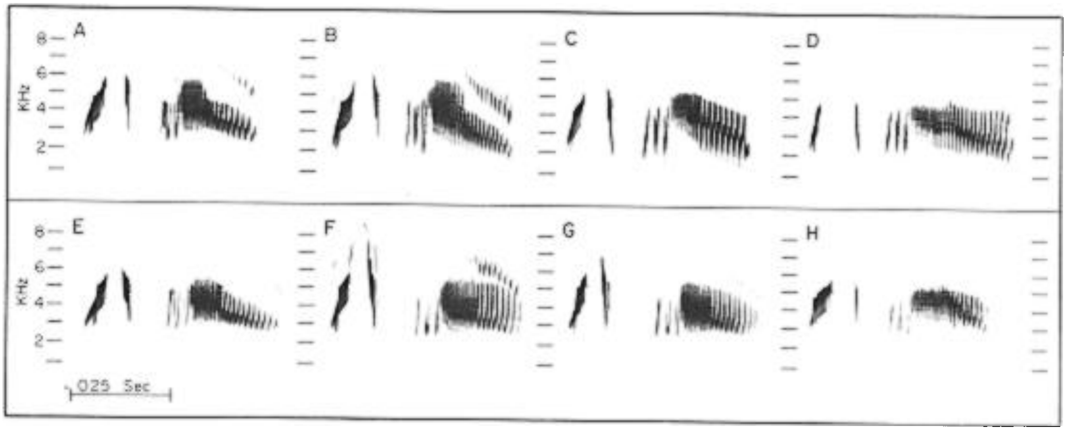

Fig. 5. The *fitz-bew* of laboratory-reared Willow Flycatchers (A–D) is similar to that of wild males (E–H). See legend of Fig. 4 for sexes and relationships among the birds.

the fm portion of the *bew* has the same overall pattern in laboratory subjects of both sexes as in wild males.

Of the 10 measured parameters (see Table 3), only one differed significantly between the lab and wild birds. That was parameter 8, the duration of the last five fm's of the *bew* portion of the song ($P = 0.05$, 2-tailed Mann-Whitney *U*-test). In this measure, three laboratory birds fell just outside the range of the wild birds, and the median durations for laboratory and wild birds were 0.058 and 0.066 s, respectively.

Again, the laboratory data appeared no more variable than the field data (Table 3). Among the 5 parameters that were not highly correlated with other parameters, only 7 from a total of 25 measurements for the 5 laboratory birds fell outside the range of the data from the wild males; the most extreme value was 11% outside the range, and the median departure was only 1.9%. CV's were comparable for the two data sets.

Using all 10 parameters, the BMDP stepwise discriminant function program classified correctly only 66.7% (14 of 21) of the wild and 60% (3 of 5) of the laboratory birds. Parameters 8 and 3, the duration of the last five fm's of the *bew* and the interval between *fizz* and *bew*, were the most effective discriminators in the analysis, and these two parameters ranked fourth and first in variability among the wild males. Parameter 3 was also the most variable parameter in 15 consecutive *fizz-bews* from one wild individual Willow Flycatcher. Overall, then, two laboratory birds produced songs indistinguishable from the wild males (Figs. 6A, C—only Bird C had been tutored with conspecific songs), and a third of wild songs were misclassified by discriminant function analysis. As with the *fitz-bew* data, songs of relatives, songs of the tutor tape and the exposed birds in the laboratory, and songs of neighboring males in the wild were no more similar to each other than expected by chance.

Early forms of the fizz- *or* fitz-bew.—The first fledgling calls of the Willow Flycatcher are undoubtedly homologous with *creets* (Fig. 4), but shortly thereafter each individual utters a two-parted call, which is undoubtedly the first trace of the *fizz-* or *fitz-bew* (Fig. 7). The *fizz* or *fitz*

TABLE 2. Means, standard deviations, and coefficients of variation (%) for 10 *fitz-bew* song parameters for 5 laboratory-reared and 23 wild Willow Flycatchers.

Song parameter[a]	Wild[b]	Laboratory-reared[b]
1	0.953 (0.075, 7.9)	0.949 (0.052, 5.5)
2	0.209 (0.020, 9.3)	0.212 (0.016, 7.8)
3	0.181 (0.033, 18.0)	0.137 (0.016, 11.4)
4	0.513 (0.088, 17.1)	0.560 (0.056, 9.9)
5	0.121 (0.011, 8.6)	0.120 (0.011, 9.2)
6	0.408 (0.060, 14.7)	0.439 (0.053, 12.1)
7	0.070 (0.004, 5.4)	0.073 (0.005, 7.3)
8	0.131 (0.009, 6.7)	0.138 (0.014, 10.3)
9	1.6 (0.2, 13.4)	1.2 (0.2, 19.4)
10	4.3 (0.7, 16.5)	3.5 (0.6, 16.3)

[a] Parameters 1–8 are durations in seconds and parameters 9 and 10 are in kHz.

[b] Data are given as means (standard deviations, coefficient of variation).

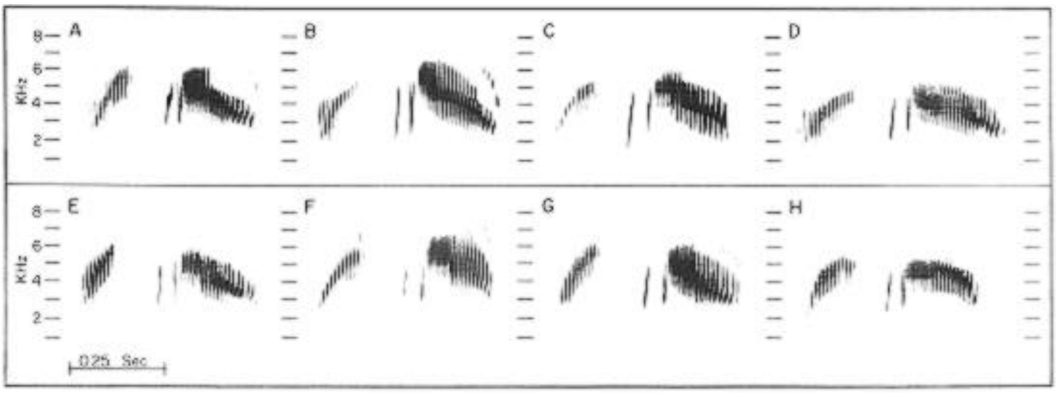

Fig. 6. The *fizz-bew* of laboratory-reared Willow Flycatchers (A–D) is similar to that of wild males (E–H). See legend of Fig. 4 for sexes and relationships among the birds.

actually appears to be a *creet* (compare Fig. 7A–D with the top row in Fig. 4), while the *bew* portion seems to be little more than white noise, with perhaps a glimpse of some added detail or intensity at the beginning (especially in Fig. 7A, C). The quality of this call never matched the clarity of detail found in the well-defined fm's of the Alder Flycatcher *fee-bee-o* given at the same age (see especially Fig. 2A). The timing of development, together with the similarity in the structure of the early *creets* (Fig. 4 top) and *fee* (Fig. 2, left column) of the *fee-bee-o,* suggests that the *creet* and the *fee* are homologous sounds and that elaboration of these two sounds may have been involved in the process of speciation.

DISCUSSION

The song development in these two suboscines is strikingly different from that of all oscines studied to date (compare Lanyon 1957, 1979; Marler 1970b, Ewert 1979). Typical oscines would have produced very abnormal songs, or may even have learned the heterospecific songs, and the statistical analyses that I used here would have been unnecessary—mere inspection of the sonograms or listening to the birds would have sufficed. Rearing the birds from the egg or maintaining them in complete acoustic isolation from all, and especially *Empidonax,* sounds would very likely not have produced results significantly different from those reported here. These flycatchers were collected before 10 days, an age before which the similarly altricial songbirds show no evidence of vocal imitation (e.g. Thielcke-Poltz and Thielcke 1960, Marler 1970b, Kroodsma 1978). Some nonpasserines can learn to recognize parental sounds while still in the egg; this is not vocal imitation, however, only recognition, and this has been documented only in *precocial* species (e.g. Tschanz 1968). It is therefore highly unlikely that these altricial flycatchers could have learned to imitate the adult song before 7–10 days.

In contrast to typical oscines, the nestling Alder and Willow flycatchers, even though tutored with heterospecific songs from 7–10 days of age, produced remarkably good conspecific, wild-type songs. In neither the *fee-bee-o* of the Alder nor the *fizz-bew* or *fitz-bew* of the Willow Flycatcher was discriminant function analysis

TABLE 3. Means, standard deviations, and coefficients of variation (%) for 10 *fizz-bew* song parameters for 5 laboratory-reared and 23 wild Willow Flycatchers.

Song parameter[a]	Wild[a]	Laboratory-reared[a]
1	0.969 (0.073, 7.5)	1.005 (0.087, 8.6)
2	0.268 (0.039, 14.2)	0.293 (0.056, 19.0)
3	0.198 (0.058, 29.3)	0.162 (0.012, 7.5)
4	0.505 (0.047, 9.2)	0.551 (0.048, 8.6)
5	0.125 (0.013, 10.3)	0.118 (0.008, 6.9)
6	0.375 (0.048, 12.7)	0.424 (0.051, 11.9)
7	0.073 (0.007, 8.4)	0.073 (0.003, 4.8)
8	0.116 (0.012, 9.9)	0.127 (0.012, 9.5)
9	1.9 (0.3, 15.8)	1.7 (0.2, 11.2)
10	2.1 (0.2, 11.5)	2.0 (0.2, 11.7)

[a] See explanatory notes for Table 2.

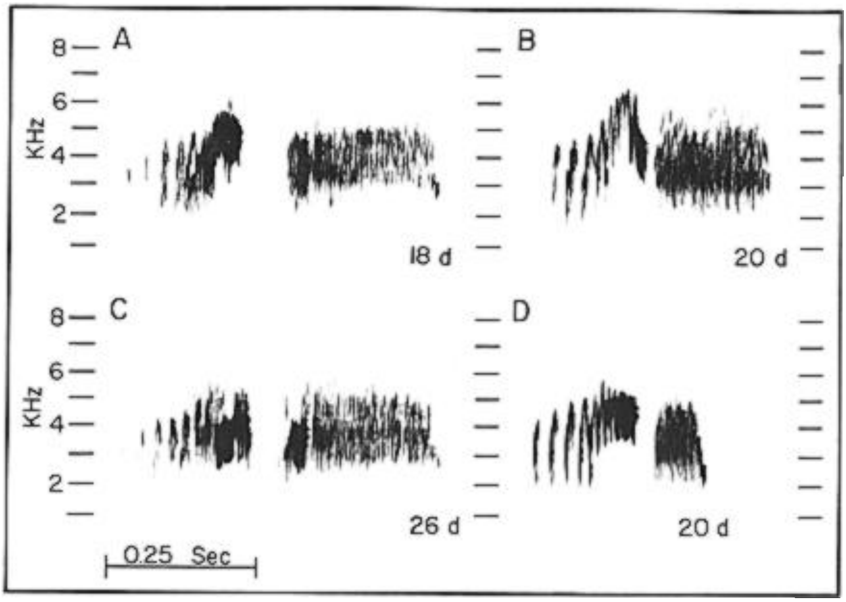

Fig. 7. The earliest calls of laboratory-reared Willow Flycatchers that resemble the adult form of the *fizz-bew* or the *fitz-bew*. Birds A and B are the same as males D and C, respectively, in Figures 4–6. Birds C and D are females whose vocalizations have not been illustrated before.

able to classify unequivocally the songs of wild and laboratory-reared birds. Partial success in discriminating the two data sets was achieved using those parameters that varied most both among wild males and within consecutive songs from a single wild male. Parameters such as the intervals between song components (parameter 5 for *fee-bee-o*, 3 for *fitz-bew* or *fizz-bew*) were effective discriminators, but they undoubtedly vary with motivational levels within a bird. The fact that the effective discriminators were also highly variable among wild males suggests that the discriminant function analyses were recognizing laboratory-reared and wild birds less than they were two sets of birds under very different motivational states. I believe that these motivational differences, perhaps together with a difference in ages of the two groups (all laboratory birds were 1 yr old; based on typical survival rates in north temperate passerines, roughly half of the wild birds would be older and could conceivably have refined the song with age), account more for the slight differences between the songs of the laboratory-reared and wild birds than do the acoustic isolation and lack of opportunity for the laboratory birds to learn conspecific songs. Supporting this is the fact that the two control Willow Flycatchers, which were tutored with conspecific song, developed no more "normal" songs than those tutored with Alder Flycatcher *fee-bee-o*'s.

I have obtained similar results from Eastern Phoebes (*Sayornis phoebe*), where 5 laboratory-reared birds (2 females with testosterone and 3 males) all produced very typical wild-type songs (Kroodsma unpubl. data). The extent to which these three species of flycatchers are representative of all suboscines, however, must await further studies. The order Passeriformes appears to be a monophyletic group (Raikow 1982), and all indications are that the suboscines [including the Eurylami, Pitti, Furnarii, and Tyrannomorpha as listed by Cracraft (1981)] and the oscines (including the lyrebirds and scrub-birds) are also monophyletic assemblages (Cracraft 1981, C. G. Sibley unpubl. data, R. J. Raikow unpubl. data).

Vocal learning, to varying degrees, is so ubiquitous among all oscines studied to date that it is tempting to conclude that the three tyrannid flycatchers discussed here are also typical of the entire family Tyrannidae, if not all suboscines. Supporting a generalization beyond the Tyrannidae are unpublished data from E. S. Morton, who has hand-reared a Barred

Antshrike (*Thamnophilus doliatus*, Formicariidae) from 7 days of age; its fledgling calls were similar to the adult song, and by ear the adult song of this experimental bird was identical to those of males in nature. These data are very similar to those that I report here for the flycatchers.

The evolution of vocal learning in the Passeriformes does pose an interesting problem. If vocal learning does not occur among suboscines, the data would suggest that imitation developed among the oscines after the oscine-suboscine split millions of years ago. On the other hand, if vocal learning can be found among nontyrannid suboscines, the interpretation could be either that vocal learning has evolved independently in those suboscines or that (some) tyrannid flycatchers independently lost that vocal learning. Deciding which of these or other scenarios is correct must await studies of other suboscines, including pittas, ovenbirds, antbirds, cotingas, and additional flycatchers.

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