

DEVELOPMENT AND USE OF TWO SONG FORMS BY THE EASTERN PHOEBE

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Vocal development among oscines typically involves some form of vocal imitation, with young birds learning the songs of adult conspecifics or heterospecifics during early life (e.g., Slater 1983). In the field, the consequences of this vocal learning are readily apparent in the form of local song traditions (Mundinger 1982) or interspecific mimicry (Baylis 1982). In the laboratory, juvenile oscines denied experience with conspecific song typically develop very abnormal songs or else learn the songs of other species (Kroodsma 1982).

Vocal development may be very different in the more "primitive" passerine suborder, the suboscines. In a study of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*), I could find no difference between the songs of wild birds and the songs of males or testosterone-treated females that were hand-reared in the laboratory from seven to ten days of age and denied access to conspecific song models (Kroodsma 1984). Vocal learning appears to play a negligible role in song development in these two *Empidonax* species. Such an interpretation is consistent with the relative absence of geographic vocal variation found in this genus (Stein 1963, Payne and Budde 1979, Johnson 1980).

Together with morphological characters such as sperm structure, stapes structure, and syrinx complexity (e.g., Feduccia 1980), the mode of vocal development may distinguish the oscines from the suboscines. However, more data on vocal ontogeny are needed from other suboscines before such a generalization can be accepted confidently. I therefore initiated a study of vocal development in the Eastern Phoebe (*Sayornis phoebe*), a species closely related to the *Empidonax* complex (W. E. Lanyon, unpubl. data). Here I report that male and female laboratory-reared phoebes not only develop the two song forms characteristic of the species (Smith 1977) but that they also use them in typical wild-type fashion.

METHODS

On 20 June 1981 I collected five Eastern Phoebe nestlings from a nest in Amherst, Massachusetts; the eyes of the nestlings were closed, and the birds fledged 10 days later, on 30 June. I estimated the nestlings were about five to six days old when collected. Birds were maintained on a daylength consistent with 42°N latitude.

In the laboratory these birds heard the songs of Willow Flycatchers and Marsh Wrens (*Cistothorus palustris*) over loudspeakers, but no songs of phoebes. The five birds were housed in separate cages but in the same room until early spring, when each bird was placed

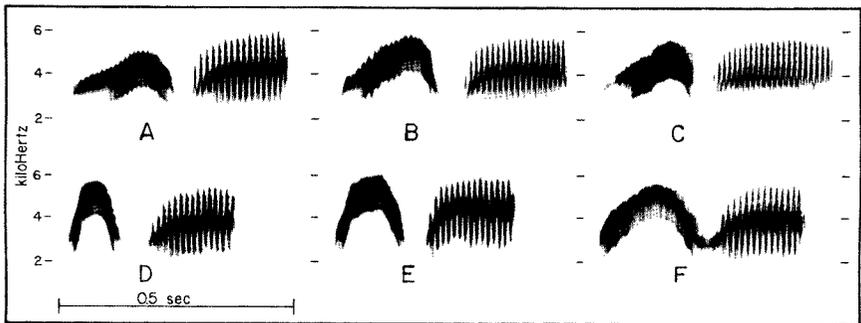


FIG. 1. The *fee-bee* song form of the Eastern Phoebe. Birds A and B are wild birds recorded in New York (LNS Catalogue Nos. 7913, 7917, respectively), and Bird C is from Massachusetts (Recording 5-308 in DEK library). Birds D, E, and F are hand-reared birds. Bird E is a female with a testosterone implant; D and F are males.

in a sound isolation chamber until it came into full song. The three males sang frequently. Smith (1977) has heard wild females sing, but I heard the two laboratory-reared females sing only after a 15-mm section of silastic medical tubing packed with crystalline testosterone was placed beneath the skin.

Several recordings were obtained from the Cornell Laboratory of Ornithology (Library of Natural Sounds [LNS] Cuts 7911-7919, 19782), and I recorded several adult phoebes in the vicinity of Amherst, Massachusetts. Field recording equipment consisted of a Nagra IS-DT or IV-S and either a Sennheiser 816 shotgun microphone or a Sennheiser 104 mounted in a 24 in. parabolic reflector. Tape speed was either $3\frac{3}{4}$ or $7\frac{1}{2}$ ips. Sound spectrograms were prepared on a Kay Elemetrics Co. 7029A Sona-Graph (wide-band setting).

RESULTS

Song forms of wild and laboratory-reared adults.—As described by Smith (1969, 1977), each adult phoebe regularly sings two different song forms (Figs. 1, 2). The one used most frequently sounds like *fee-bee*, and gives the bird its name. The second song form begins in the same way, but the bird seems to stutter on the second half of the song; Smith renders this song *fee-b-be-bee*, though the *bee*'s of the two song forms are quite different.

The *fee-bee* songs of different individuals are usually distinguishable after fine scrutiny of sonagrams. For example, the songs of Birds A, B, and C in Fig. 1 have frequency modulations in the *bee* at the rate of 10 per 0.128, 0.120, and 0.117 sec, respectively, and the rate is highly stereotyped within a male (e.g., 10 consecutive songs from Bird C gave a mean of 0.117 sec, SE = 0.00007 sec, CV = 1.91%).

The five hand-reared birds, including three males and two females, all developed very typical *fee-bee* songs (Fig. 1). I measured the overall duration of the song, the duration of the *bee* portion, the number and rate

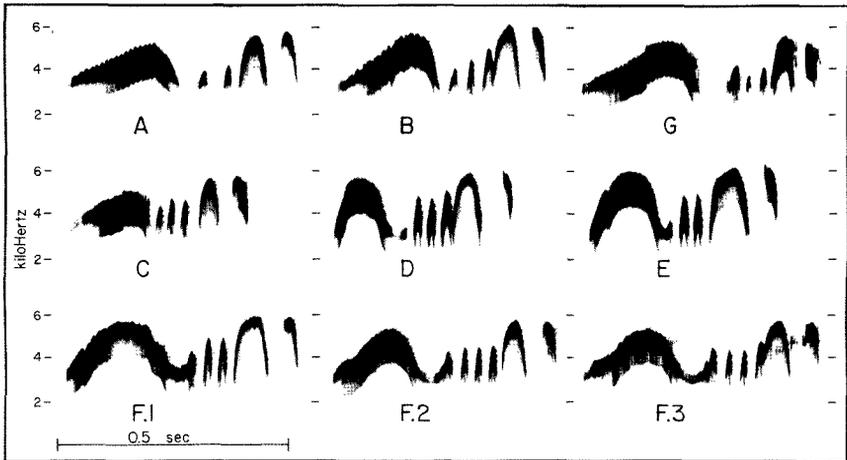


FIG. 2. The *fee-b-bee* song form of the Eastern Phoebe. See Fig. 1 legend for identification of Birds A–F; Bird G is an adult male from North Carolina (LNS Cat. No. 7915). Three song forms (F.1, F.2, F.3) are displayed for Bird F.

of frequency modulations in the *bee*, and the maximum frequency of both the *fee* and the *bee*; I could find no significant differences when these parameters were compared to measured parameters in the songs of five wild individuals.

The *fee-b-bee* songs appear more variable among males. The *b-bee* portion consists of varying numbers of notes with different temporal organizations (Fig. 2), yet each male sings a highly stereotyped form of this song. It is possible that there is geographic variation in these parameters, yet four males from Ithaca, New York (LNS Cat. Nos. 7913 [Bird A], 7917 [Bird B], 7911, and 7914) displayed nearly the full spectrum of variation seen in wild birds. Furthermore, during song development, Bird F (Fig. 2) also sang several variations, indicating that each individual is capable of producing several renditions of this song. Apparently most wild males settle on one particular variation, but I had not recorded Bird F long enough in the laboratory to obtain that stereotypy. As with the *fee-bee* song, I could find no consistent differences between the songs of laboratory-reared birds and wild birds.

Singing behavior of adult males.—Smith (1969, 1977) noted that the proportion of the two song forms during a given performance varied with the rate of singing. In order to assess this feature in both the wild and laboratory-reared males, I determined the proportion of *fee-bee* songs during 1-min samples from dawn singing sessions.

In all five males, two from the laboratory and three from the wild, the

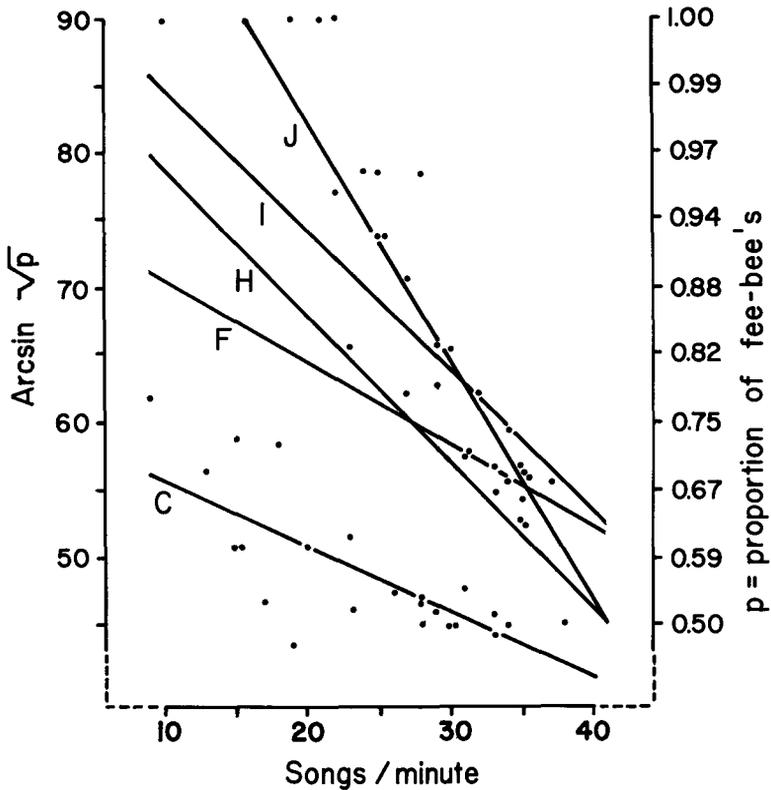


FIG. 3. The relationship between the rate of singing in songs per min and the proportion of *fee-bee* songs in a singing performance. The proportion and its angular transformation ($\arcsin \sqrt{p}$) are both given on the abscissa; calculations are performed with the transformed values. Birds F and H are hand-reared laboratory males; Birds C, I, and J are wild males recorded in the Amherst area between 19 May and 1 June 1984 (DEK Recordings 5-308, 5-307, and 5-306, respectively). Songs of Birds C and F are displayed in Figs. 1 and 2. The regression coefficients, slope, and number of 1-min sample periods, respectively, are as follows: C (-0.76, -0.50, 23), F (-0.72, -0.59, 30), H (-0.84, -1.08, 30), I (-0.88, -1.04, 18), J (-0.90, -1.80, 30). To illustrate the variation in the data, I have displayed the data points for Birds C and J; all data points above line H are for Bird J, all data points below for Bird C. All five regression analyses are highly significant at $P < 0.001$.

rate of singing and the proportion of *fee-bee* songs in the performance were inversely related ($P < 0.001$, Fig. 3). Males clearly differed from one another. When Bird J, for example, sang fewer than 25 songs per min, nine out of ten 1-min sample periods consisted of more than 90% *fee-bee*'s. Bird C, on the other hand, never sang more than 80% *fee-bee*'s,

even though his rate of singing dropped as low as 10 songs per min. The singing of the two laboratory males was comparable to that of the three wild males.

One other intriguing feature of Eastern Phoebe singing behavior involves the temporal relationship of the two song forms during a singing performance (see Table 1). During early morning singing, there is a relatively short pause between the delivery of a *fee-bee* and a *fee-b-be-bee* song form (median value from beginning of first song to the beginning of the second song for five males = 1.65 sec; sample sizes for each male are given in Table 1), a slightly longer pause between successive *fee-bee*'s (1.81 sec), and the longest pause between the *fee-b-be-bee* and the next *fee-bee* (2.06 sec); successive *fee-b-be-bee*'s rarely occur. Except for Bird C, where a small sample for *fee-bee* to *fee-bee* transitions probably does not represent the actual distribution, this pattern held for all birds, and the laboratory and wild birds did not differ in their behavior. Furthermore, not only is the time from the *fee-bee* to the *fee-b-be-bee* much briefer, but it is also much less variable, as indicated by the coefficients of variation (CV). For the four males with sufficient sample sizes ($N > 20$ for all three transitions), the median CV for each of the three transitions was 9.1, 22.6, and 23.0, respectively.

The rate of singing increases as the proportion of *fee-b-be-bee* songs increases. However, because of the characteristic temporal relationships of the song forms, the sequence from *fee-bee* to *fee-b-be-bee* to *fee-bee* (3.22, 4.24, 3.71, and 3.69 sec for Birds F, H, I, and J, respectively) actually takes about as long as it does to go from *fee-bee* to *fee-bee* to *fee-bee* (3.38, 4.34, 3.62, and 3.40 sec for Birds F, H, I, and J, respectively). Thus, the relationship between the rate of singing and proportion of the two song types in the performance is not simply explained by the relative time for transitions between different song types. Neither does the duration of the two song forms explain this relationship. In two males (F and H) the duration of the *fee-bee* was greater than the *fee-b-be-bee* while it was just the reverse for Bird J; the two song forms were the same length for the fourth bird (I).

DISCUSSION

The song forms and singing behavior of five Eastern Phoebes, hand-reared in the laboratory and isolated from conspecific songs from about five or six days of age, appear very similar to the songs and behavior of wild males. The sonagrams are indistinguishable from wild-type songs, and the hand-reared birds during early morning singing produced not only the typical inverse relationship between the rate of singing and proportion of *fee-bee*'s but also the typical temporal distribution of the two song forms.

TABLE 1
TEMPORAL ORGANIZATION OF SINGING BEHAVIOR IN TWO LABORATORY (F, H) AND THREE WILD (C, I, J) ADULT MALE EASTERN PHOEBES

Bird	Song transition \bar{x} (sec) \pm SE			Duration of songs* /fee-bee/fee-b-bee
	fee-bee to fee-b-bee	fee-bee to fee-bee	fee-b-bee to fee-bee	
F	1.39 \pm 0.03 (N = 22, CV = 9.2)	1.69 \pm 0.05 (N = 29, CV = 16.7)	1.83 \pm 0.06 (N = 22, CV = 15.7)	0.43/0.49
H	1.71 \pm 0.03 (N = 62, CV = 12.0)	2.17 \pm 0.07 (N = 144, CV = 37.2)	2.53 \pm 0.14 (N = 65, CV = 45.1)	0.48/0.52
C	1.86 \pm 0.09 (N = 89, CV = 47.5)	3.45 \pm 0.46 (N = 7, CV = 35.2)	2.43 \pm 0.14 (N = 89, CV = 52.6)	0.49/0.39
I	1.65 \pm 0.02 (N = 25, CV = 6.4)	1.81 \pm 0.08 (N = 25, CV = 23.4)	2.06 \pm 0.05 (N = 25, CV = 12.6)	0.50/0.50
J	1.53 \pm 0.03 (N = 25, CV = 9.0)	1.70 \pm 0.07 (N = 25, CV = 21.7)	2.16 \pm 0.13 (N = 25, CV = 30.2)	0.50/0.42

* Average of two to 10 songs for each male.

The apparent lack of vocal imitation during ontogeny is similar to that found in the Alder and Willow flycatchers (Kroodsma 1984), and all three flycatcher species contrast sharply with vocal development typical in oscines. Songbirds reared in isolation from conspecific song would typically develop either highly abnormal song or learn songs of heterospecifics (e.g., Lanyon 1957, 1979; Marler 1970; Ewert 1979).

Songbirds actually have two "critical periods" during song development (Nottebohm 1969, Marler and Peters 1982). During the first phase, songs of other adults are memorized; during the second phase, the young bird attempts to match its motor output with this model stored in the brain. In some species these two phases overlap, but in others they may not. The three flycatcher species that I have studied lack the first critical period, for young birds do not have to imitate songs of other adults in order to produce normal songs. Thus, the song "template" (Marler 1976) is not refined by vocal learning.

It is unclear whether these flycatchers have a developmental phase analogous to the second learning phase of songbirds. Fledgling flycatchers use calls that are rudimentary forms of the adult songs, and it is possible that the motor output is gradually perfected by comparing the vocal output with an innate song template. Determining whether or not these flycatchers are *learning* to match the motor output of the syrinx with an inherited song template will require experimental work with deafened suboscines (Konishi and Nottebohm 1969, Nottebohm 1975).

The variation in the *fee-b-be-bee* song form produced by Bird F does suggest the possibility of one form of environmental influence on vocal development. This male appears capable of producing a variety of these song forms, but it is possible that the one favored is that which matches the singing of other adults in the vicinity. This might be tested by looking for "neighborhood effects" (i.e., dialects) in the field or by rearing non-related males together in the laboratory to determine whether they converge on similar song forms. Thus, a subtle form of vocal learning could influence the details of the final song form, but learning from other phoebes is not necessary for the development of wild-type song forms and behavior.

The data reported here further support the possibility of a distinct difference in vocal development between the suboscines and the oscines. I have now examined three flycatcher species from the Tyrannidae, and have found that vocal development proceeds normally in nestlings isolated from conspecific song. There are, of course, another 1094 suboscines (Bock and Farrand 1980), including pittas, ovenbirds, antbirds, cotingas, as well as other tyrannid flycatchers, some of which have more compli-

cated songs and singing behaviors than the Eastern Phoebe, Alder Flycatcher, and Willow Flycatcher. Careful study of vocal development in some of these species would be especially welcome in attempting to sketch the evolution of vocal learning in the order Passeriformes.

SUMMARY

Five Eastern Phoebe (*Sayornis phoebe*) nestlings were collected at five to six days of age and reared in the laboratory. The three males and two females heard heterospecific but no conspecific song, yet each developed the two wild-type Eastern Phoebe song forms (*fee-bee*, Fig. 1; *fee-b-be-bee*, Fig. 2) and used the two song forms normally during early morning singing performances (Fig. 3, Table 1). These data are consistent with the hypothesis that vocal development among the suboscines requires no imitation of conspecifics. This is in sharp contrast to the oscines, the more "advanced" passerine suborder, where vocal learning is the rule.

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LITERATURE CITED

- BAYLIS, J. R. 1982. Avian vocal mimicry: its function and evolution. Pp. 51–83 in *Acoustic communication in birds*, Vol. 2 (D. E. Kroodsma and E. H. Miller, eds.). Academic Press, New York, New York.
- BOCK, W. J. AND J. FARRAND, JR. 1980. The number of species and genera of recent birds: a contribution to comparative systematics. *Amer. Mus. Novitates* No. 2703.
- EWERT, D. N. 1979. Development of song in a Rufous-sided Towhee raised in acoustic isolation. *Condor* 81:313–316.
- FEDUCCIA, A. 1980. *The age of birds*. Harvard Univ. Press, Cambridge, Massachusetts.
- JOHNSON, N. K. 1980. Character variation and evolution of sibling species in the *Empidonax difficilis-flavescens* complex (Aves: Tyrannidae). *Univ. California Publ. Zool.* 112:1–153.
- KONISHI, M. AND F. NOTTEBOHM. 1969. Experimental studies in the ontogeny of avian vocalizations. Pp. 29–48 in *Bird vocalizations* (R. A. Hinde, ed.). Cambridge Univ. Press, Cambridge, England.
- KROODSMA, D. E. 1982. Learning and the ontogeny of sound signals in birds. Pp. 1–23 in *Acoustic communication in birds*, Vol. 2 (D. E. Kroodsma and E. H. Miller, eds.). Academic Press, New York, New York.
- . 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. *Auk* 101:13–24.
- LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. *Publ. Nuttall Ornithol. Club* No. 1.
- . 1979. Development of song in the Wood Thrush (*Hylocichla mustelina*), with

- notes on a technique for hand-rearing passerine birds from the egg. Amer. Mus. Novitates No. 2666.
- MARLER, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. J. Comp. Physiol. Psychol. Monogr. 71:1-25.
- . 1976. Sensory templates in species-specific behavior. Pp. 314-329 in *Simpler networks and behavior* (J. Fentress, ed.). Sinauer, Sunderland, Massachusetts.
- AND S. PETERS. 1982. Long-term storage of birdsongs prior to production. *Anim. Behav.* 30:479-482.
- MUNDINGER, P. C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. Pp. 147-208 in *Acoustic communication in birds, Vol. 2* (D. E. Kroodsma and E. H. Miller, eds.). Academic Press, New York, New York.
- NOTTEBOHM, F. 1969. The "critical period" for song learning. *Ibis* 111:386-387.
- . 1975. Vocal behavior in birds. Pp. 287-332 in *Avian biology, Vol. 5* (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.
- PAYNE, R. B. AND P. BUDDÉ. 1979. Song differences and map distances in a population of Acadian Flycatchers. *Wilson Bull.* 91:29-41.
- SLATER, P. J. B. 1983. Bird song learning: theme and variation. Pp. 475-499 in *Perspectives in ornithology* (A. H. Brush and G. A. Clark, Jr., eds.). Cambridge Univ. Press, Cambridge, England.
- SMITH, W. J. 1969. Displays of *Sayornis phoebe* (Aves, Tyrannidae). *Behaviour* 33:283-322.
- . 1977. *The behavior of communicating*. Harvard Univ. Press, Cambridge, Massachusetts.
- STEIN, R. C. 1963. Isolating mechanisms between populations of Traill's Flycatchers. *Proc. Amer. Phil. Soc.* 107:21-50.

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