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Individual, brood, and sex variation in begging calls of Western Bluebirds.—Vocal differences in birds are often sufficient for recognition not only of species but of variables such as sex, age, genetic relatedness, and condition. Here we analyze begging calls of Western Bluebird (*Sialia mexicana*) nestlings and test for family, sex, and individual differences. The original impetus for this study was the finding by Gowaty and Droge (1990) that female Eastern Bluebird (*Sialia sialis*) nestlings were fed more often than were male nestlings and that female-biased broods were provisioned more frequently by the adult male attending the nest. If this result is due to an adjustment of parental behavior in response to the sex of the nestlings, then there must be a proximate mechanism by which parents can determine the sex of their offspring. Inasmuch as bluebirds are cavity nesters and nestlings are similar in size, the most likely mechanism for sex recognition is differences in nestling vocalizations or begging calls.

Subsequently, work in our study population has determined that sex-biased provisioning does not occur (Leonard et al. 1994) and, furthermore, that parents do not discriminate against unrelated offspring translocated into their nests (Leonard et al. 1995). These results prompt a somewhat different question than that originally envisioned. Given that Western Bluebird parents do not appear to discriminate among offspring, either on the basis of sex or genetic relatedness, are differences in nestling vocalizations uncorrelated with these factors? If vocalizations are not distinguishable between the sexes or between nests, then one

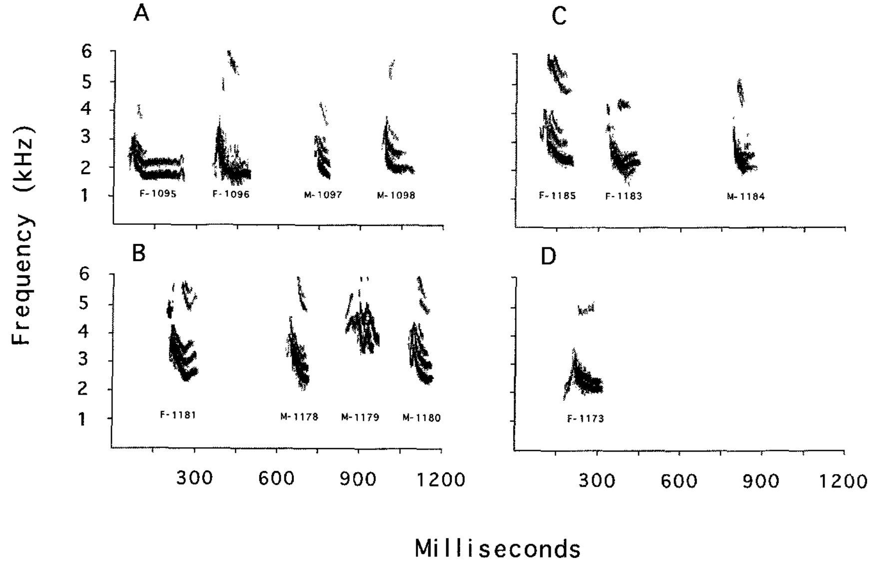

FIG. 1. Sound spectrograms of begging calls of 12 Western Bluebird nestlings from four different families (A, B, C, D). For each family, sound spectrograms on the left of the time scale represent calls of female nestlings (F-); sound spectrograms on the right of the scale represent calls of male nestlings (M-). Each sound spectrogram is a representative example for the begging calls of each nestling.

possible mechanism of discrimination would be absent in Western Bluebirds, even though such discrimination might be advantageous.

Methods.—We recorded nestling begging calls of Western Bluebirds at Hastings Natural History Reservation, Monterey Co., California, in June and July, 1989. All nestlings from three nests and one additional nestling from a fourth nest were recorded. Twelve nestlings were recorded in all, including six males and six females. Recordings were made when nestlings were between 14 and 19 days old, just after nestlings can be sexed by plumage (Pyle et al. 1987) and several days before fledging, which usually occurs when nestlings are about 21 days old.

We used an omnidirectional microphone (Sony ECM-280) mounted on the inside of the nest box and recorded several begging calls for each nestling before feeding by parents. The microphone was attached to a tape recorder operated from a blind 3–7 m behind the nest box. Nestlings were recorded individually by removing all chicks but the one that was being recorded; chicks not being recorded were held together in a bird-holding bag inside the blind. One chick after the other was placed into its nest box for recording. Chicks were kept in the nest box by themselves for no longer than 30 min., after which they were replaced with another chick from the brood. On two occasions we recorded two nestlings in the nest together to verify that chicks were giving the same calls when by themselves as when together.

Begging calls were analyzed using The Sound Analysis and Synthesis System on an AMIGA Micro-computer (Fig. 1). The calls were digitized using eight bits and a sampling frequency of 12 kHz (Richard 1991). Sound spectrograms were carried out by a fast Fourier transform using 256 points and weighted by a Hanning window (Richard 1991). Time and

TABLE 1

PROPORTION OF VARIATION AMONG INDIVIDUALS AND WITHIN INDIVIDUALS FOR PARAMETERS OF BEGGING CALLS OF WESTERN BLUEBIRD NESTLINGS

Vocalization parameter	F-ratio (df = 11,113)	P	Percent variation between	Percent variation within
DOMF	152.7	<0.0001	93.6	6.4
DF	38.5	<0.0001	78.3	21.7
DT	15.5	<0.0001	58.3	41.7
F1	765.9	<0.0001	98.7	1.3

frequency were displayed at full (1×) scale, the tape recorder was set to full speed. All settings of the amplifier were at 0 dB, except 31 Hz and 16 kHz which were both set at −12 dB, in order to reduce background noise.

For all but two nestlings, we measured 11 different sonograms using calls that were maximally separated in time during the recording. In the remaining two cases we were able to obtain 10 and five calls, respectively.

We measured four parameters from each sonogram (comparable to Medvin et al. 1992, 1993): (1) the frequency at which the begging call is loudest (the dominant frequency, DOMF), (2) the duration of the begging call (DT), (3) the frequency range of the strongest band on the sonogram (DF), and (4) the lowest frequency of the strongest band on the sonogram (F1).

For each of the four vocalization parameters, we partitioned the variance within and among individuals with a one-way ANOVA in which "individual" was used as the main factor. Coefficients of intraclass correlations were calculated following Sokal and Rohlf (1981).

To test for a sex effect, we used a one-way ANOVA with "sex" as the main factor; means for each of the 12 nestlings were used rather than individual calls. The results of this analysis indicated no significant sex differences ($0.18 < P < 0.68$) (Table 2), and therefore we pooled across sex to the test for a nest effect. We tested for a nest effect using a one-way ANOVA with "nest" as the main factor.

Results.—Vocalization parameters were highly consistent within individuals, and most of the variation was found among individuals. For each of the four variables, a large (between 58.3 and 98.7%) and highly significant proportion of variance was attributable to individual differences (Table 1). Thus, nestlings had highly distinctive begging chirps.

Vocalization parameters exhibited no differences between the sexes (Tables 2, 3). In contrast, DOMF, the frequency at which begging was loudest, differed significantly among nests (Table 2). Variation among nests for F1, the lowest frequency of the strongest band, also approached significance.

Discussion.—These analyses indicate that begging calls of nestling Western Bluebirds differ significantly among individuals and among nests but not between male and female nestlings. Our failure to detect differences in the vocalizations of nestlings between the sexes is concordant with the results of Leonard et al. (1994), who found no evidence for biased provisioning with respect to sex of nestlings in the Hastings population.

Because we did not record begging calls of cross-fostered nestlings, we do not know the degree to which within-nest similarities in begging calls are determined by genetic similarity or by the common nest environment. If begging calls are primarily genetically determined, then parents could gain fitness advantages if they were able to recognize reliably and subsequently avoid wasting parental effort on unrelated nestlings (Owens 1993). Such unrelated

TABLE 2

RESULTS OF ANOVA TESTING FOR SEX AND NEST DIFFERENCES IN VOCALIZATIONS OF WESTERN BLUEBIRD NESTLINGS

Vocalization parameter	Sex effect		Nest effect	
	F-ratio (df = 1,10)	*P*	*F*-ratio (df = 3,8)	*P*
DOMF	0.403	0.54	5.545	0.024
DF	0.187	0.675	0.546	0.665
DT	2.076	0.18	0.496	0.695
FI	0.823	0.386	3.241	0.082

nestlings do not arise via brood mixing in this cavity-nesting species, but rather from extra-pair fertilizations, which are relatively common in this population (J. L. Dickinson, unpubl. data). However, discrimination by bluebird parents between nestlings from their own nests versus nestlings translocated from other nests does not occur (Leonard et al. 1995). Thus, it is unlikely that adult bluebirds use brood-specific begging calls or individual differences in begging calls during the nestling stage to distinguish between related and unrelated young.

In contrast, mixing of family groups can occur following fledging while offspring are still dependent on their parents (D. Monk, unpubl. data). Thus, it is possible that parents use brood-specific and individual-specific begging calls at that stage to identify and discriminate against fledglings from other families mixed in with their own brood (Beecher 1990, Barg and Mumme 1994). Alternatively, brood-specific and individual-specific calls may confer no selective advantage when birds are young but may be used later in life for social interactions between mates and neighbors. Additional studies will be necessary to test possible fitness functions of brood-specific and individual-specific nestling calls as well as to understand the intriguing differences in parental behavior that have been reported for Western and Eastern bluebirds.

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TABLE 3

MEANS AND 95% CONFIDENCE INTERVALS (USING STUDENT'S *T*-TEST FOR SMALL SAMPLE SIZES) FOR VOCALIZATION PARAMETERS OF BEGGING CALLS OF FEMALE AND MALE WESTERN BLUEBIRD NESTLINGS

Vocalization parameter	Female nestings			Male nestlings		
	N	Mean	95% Confidence intervals	N	Mean	95% Confidence intervals
DOMF	6	2722	570	6	2994	873
DF	6	1802	336	6	1729	273
DT	6	137	27	6	120	18
FI	6	2155	378	6	2493	839

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Communal roosting behavior of the Cave Swallow in El Salvador.—In autumn 1994, I located more than 5000 Cave Swallows (*Hirundo fulva*) at each of two nocturnal roost sites in El Salvador. Here I provide information on the communal roosting behavior of the species and roost-site characteristics on previously unknown wintering grounds in Central America. Roosting of many species of New World swallows has not been described. The winter roosting habits of migratory North American swallows likewise are sparsely known. This study provides the first description of the winter roosting habits of the Cave Swallow.

Study area and methods.—I conducted the study in a 2500 km^2 region of the coastal plain of El Salvador below 100 m elevation, from Río Paz, Ahuachapán, in the west (13°45′N, 90°08′W), to Estero El Espino, Usulután, in the east (13°10′N, 88°15′W). This area is mostly agricultural flatlands with little natural habitat, except for 38,000 ha of man-