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VOCAL DEVELOPMENT IN AMERICAN KESTREL (*FALCO SPARVERIUS*) NESTLINGS

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ABSTRACT.—We studied the acoustical characteristics of calls made by nestling American Kestrels (*Falco sparverius*). A total of 563 vocal samples was obtained from 88 chicks (49 males and 39 females) from 20 broods. Thirteen frequency, three numerical, and two temporal characteristics were measured using audio spectrography. Discriminant function analysis failed to distinguish the calls of male and female chicks, but univariate and principal component analyses suggest that vocal ontogeny proceeds more rapidly in males than in females. The acoustical characteristics of call notes changed in a consistent manner as nestlings matured, and by day 16 chicks produced calls similar to those of adults.

KEY WORDS: *American Kestrel;* Falco sparverius; *vocalization; development.*

DESARROLLO VOCAL EN POLLUELOS DEL CERNICALO (*Falco sparverius*)

RESUMEN.—Estudiamos las características acústicas de las vocalizaciones hechas por polluelos de cernícalo (*Falco sparverius*). Un total de 563 muestras de vocalizaciones fueron obtenidas de 88 pollos(49 machos y 39 hembras)de 20 nidadas. Trece características de frecuencia, tres numéricas y dos temporales fueron medidas usando audio espectrografía. El análisis de la función discriminante falló para distinguir los llamados de los pollos hembras y machos, pero el análisis univariado y de componentes principales sugiere que la ontogenia vocal procede mas rápidamente en machos que en hembras. Las características acústicas de las notas de los llamados, cambiaron de manera consistente con la madurez de los polluelos, y para el día 16 los pollos produjeron llamados similares a los de los adultos.

[Traducción de César Márquez]

Although the acquisition of species-specific song has been studied extensively in passerines (e.g., Kroodsma and Miller 1982), much less is known about the development of vocal behavior in nonpasserines. The American Kestrel (*Falco sparverius*) has a simple vocal repertoire, consisting of three main calls in adults: *klee, whine,* and *chitter,* and combinations thereof (Willoughby and Cade 1964). Vocalizations of nestlings have been described (Sherman 1913, Roest 1957, Balgooyen 1976, Smallwood and Bird 2002), but only qualitatively. Audio spectrography facilitates quantification of acoustical signals, and the variables derived from spectrographs may be analyzed with both univariate and multivariate statistical treatments. For example, discriminant function analysis was used to distinguish calls among four species of penguins (Thumser et al. 1996) and principal component analysis was used to identify individuals within a flock of Greater Flamingos (*Phoenicopterus ruber,* Mathevon 1997). Multivariate techniques also have been used to determine gender in birds whose vocalizations are not readily discernable by human observers (e.g., Whooping Cranes, *Grus americana;* Carlson and Trost 1992). No differences in vocalizations of male and female American Kestrels, either adults or young, have been reported. The objectives of this study were to analyze acoustical characteristics of calls made by nestling kestrels to (1) determine if gender can be distinguished vocally and (2) examine ontogenic changes.

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Table 1. Principal component analysis for frequency variables used to describe acoustical characteristics of nestling American Kestrel calls. See methods for descriptions of variables.

VARIABLE	EIGENVECTORS	
	PC1	PC2
Low mean frequency	0.357	−0.150
End mean frequency	0.340	−0.161
End maximum frequency	0.322	−0.194
Low maximum frequency	0.316	−0.207
Dominant harmonic	0.306	−0.115
Maximum frequency	0.300	−0.010
High mean frequency	0.283	0.335
High maximum frequency	0.270	0.347
Initial mean frequency	0.256	0.210
Low 25% frequency	0.238	−0.304
High 75% frequency	0.220	0.373
Initial maximum frequency	0.213	0.218
Frequency range	−0.044	0.549

Table 2. Age-related changes in acoustical characteristics of American Kestrel chicks (49 males and 39 females pooled) from northwestern New Jersey, 1999. For each variable, the correlation is between age category (N = 11, 0–1 d through 20–21 d) and the mean value for each age category. See methods for descriptions of variables.

VARIABLE	r_s	P
Notes/call	0.964	0.0001
Internote	−0.973	0.0001
Note length	0.916	0.0001
Number of harmonics	0.973	0.0001
Dominant harmonic	0.954	0.0001
Amplitude pulses	−0.706	0.0152
Maximum frequency	0.927	0.0001
Initial maximum frequency	0.891	0.0002
High maximum frequency	0.845	0.0010
Low maximum frequency	0.973	0.0001
End maximum frequency	0.936	0.0001
Initial mean frequency	0.900	0.0002
High mean frequency	0.855	0.0008
Low mean frequency	0.964	0.0001
End mean frequency	0.927	0.0001
High 75% frequency	0.827	0.0017
Low 25% frequency	0.882	0.0003
Frequency range	−0.809	0.0026

STUDY AREA

The study area was in rural northwestern New Jersey, bordered to the north and west by the Kittatinny Ridge and Delaware River, and to the east and south by residential and commercial development. This area is characterized by mixed agriculture, including corn, hay, and cattle production, and forestland in the ridge and valley physiographic region (Sauer et al. 1997). Eighty-two wooden nest boxes (internal dimensions: 20 × 23 cm floor, ca. 34 cm in height) were erected in open habitats in Sussex County (centered ca. 41°11′N, 74°38′W) between 1 April 1995 and 6 April 1999, and 103 nest boxes in Warren County (ca. 40°47′N, 75°04′W) between 5 August 1995 and 19 April 1998; 124 nest boxes were available during the 1999 breeding season.

METHODS

Data Collection. We monitored nest boxes for kestrel breeding activity at 21–28-d intervals between 30 March and 3 August 1999. Once a nest box contained at least one kestrel egg, additional visits were scheduled so that chicks would be observed within 2 d of hatching. Age was determined by body mass (Roest 1957, Balgooyen 1976, Lacombe et al. 1994, Smallwood and Bird 2002); eight chicks were still wet when first observed. To collect vocal samples, we visited nest boxes with chicks at 2–3-d intervals until the oldest chick of a brood was about 22 d old. In this study, area chicks fledge on about day 28 and are prone to premature fledging if disturbed during the preceding week (Smallwood and Natale 1998).

We made analog audio recordings with a Marantz PMD 101 portable cassette recorder. To collect vocal samples, we removed all chicks of a brood from their nest box and held each (one at a time) by hand in an upright position ca 12 cm from the recorder's built-in condenser microphone. Most chicks vocalized within a few seconds. If a chick failed to vocalize for 3 min, we ended the recording attempt and noted that the chick was silent. We identified individual chicks by coloring the down feathers of the humeral tract with permanent marking pens; gender was determined when primary feathers erupted, about day 8.

The analog recordings were digitized at a 44.1-kHz sampling rate using the sound recorder program of MicroSoft Windows 98 on a PC platform. We prepared digital spectrographs with Avisoft-SASLab Pro v. 3.4 software with an effective bandwidth of 647 Hz and a 256-point Fast Fourier Transform (FFT) size. Analytical features of this program include amplitude spectra of user-defined segments of the acoustical signals.

Acoustical Variables. All vocalizations consisted of a series of distinct notes that ranged from about 10–300 msec in duration. We defined a "call" operationally as a sequence of notes such that the interval between notes of sequential calls was at least 1.5 times greater than the interval between notes within a call; the "intercall" durations generally were at least several times greater than the "intracall" durations. We measured the following 18 acoustical variables. (1) NOTES/CALL: the mean number of notes per call. A random numbers table was then used to select one note (excluding the last note of a call; see next variable) from each vocal sample for acoustical analysis. (2) INTERNOTE: the interval (in sec) between the selected note and the following note within the same call. (3) NOTE LENGTH: the duration (in sec) of the selected note. (4) NUMBER OF HARMONICS: We examined a spectrograph of the selected note for distinct frequency bands. We then analyzed the note at the point in time when the maximum number of frequency bands

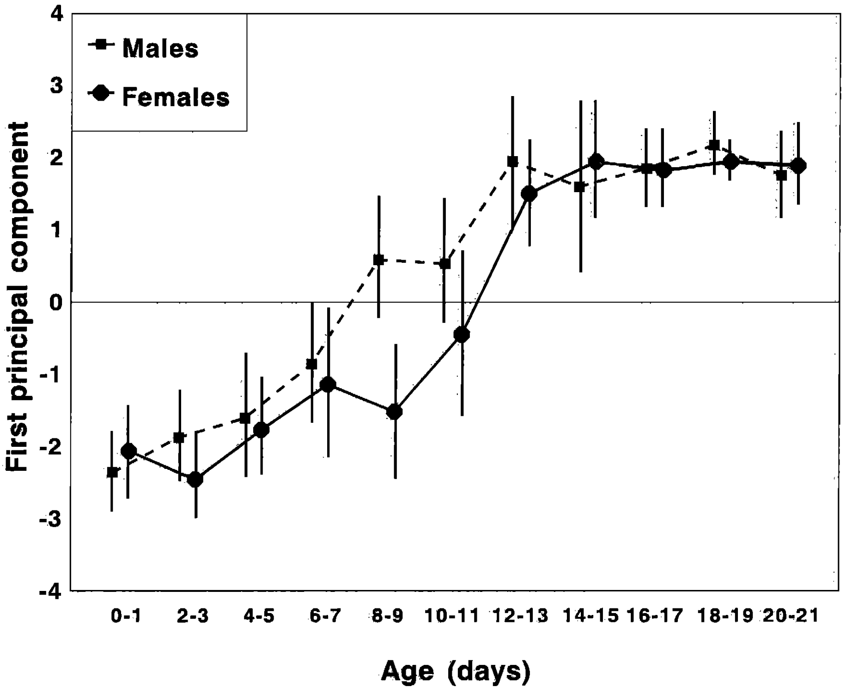

Figure 1. Vocal development of male (N = 38) and female (N = 31) American Kestrel chicks, northwestern New Jersey, 1999. Values are means (±SE) of the first principal component. Principal component analysis was performed on 13 frequency variables; PC1 eigenvectors for these variables are presented in Table 1.

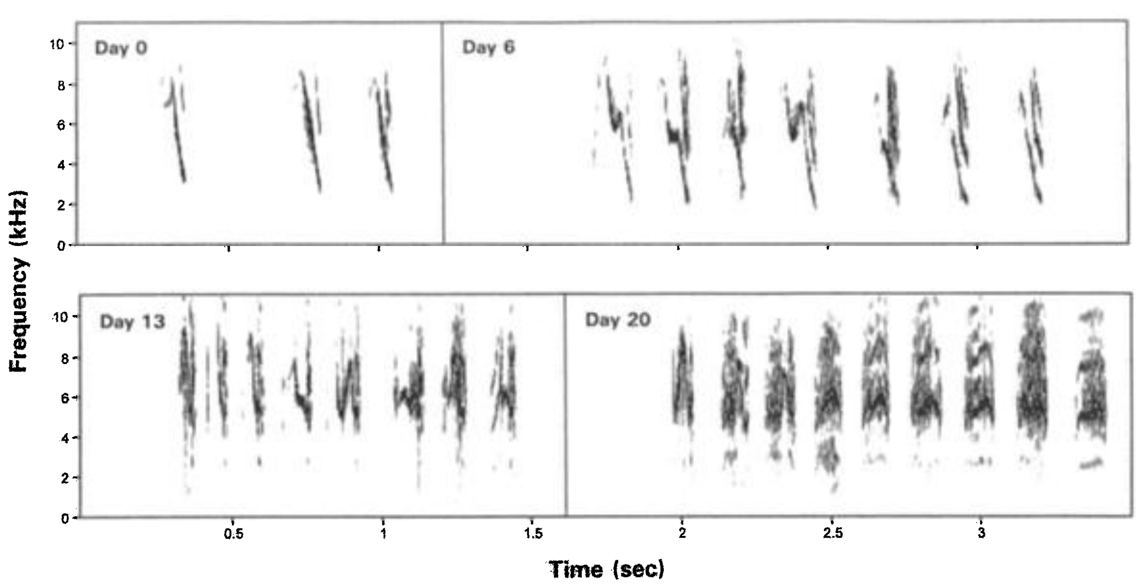

Figure 2. Age-related changes in the calls of an individual male American Kestrel chick from Sussex County, New Jersey, 1–21 June 1999. Digital spectrographs of analog recordings were prepared using 44.1-kHz sampling rate and Avisoft-SASLab Pro v. 3.4 software (with an effective bandwidth of 647 Hz and a 256-point FFT transform size). Amplitude is indicated by darkness (i.e., black indicates more energy than grey).

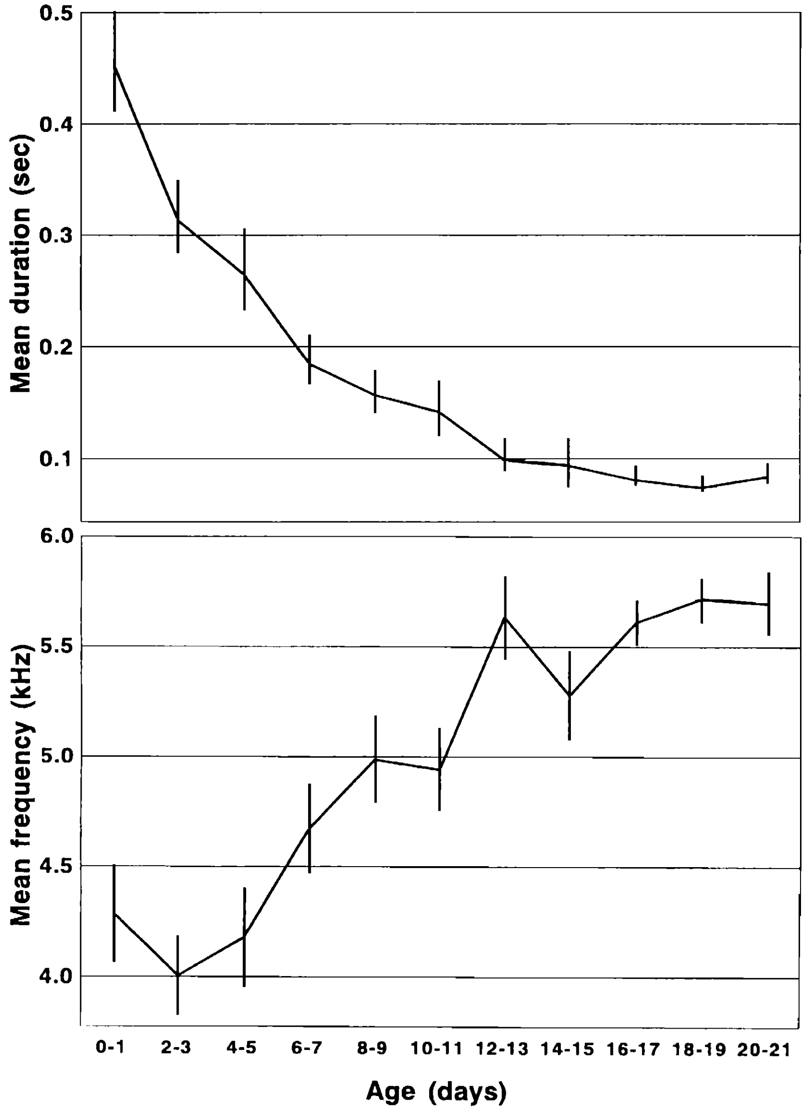

Figure 3. Call notes of American Kestrel chicks ($N = 69$), northwestern New Jersey, 1999. (Top) Call notes are given with increasing rapidity during the nestling stage. Values are means (±SE) of internote durations. (Bottom) The frequency (pitch) of call notes increases during the nestling stage. Values are the frequencies (mean ±SE) that have the highest amplitude within a call note.

were separated by the greatest differences in amplitude. (5) DOMINANT HARMONIC: the frequency (in kHz) of the harmonic with the greatest amplitude. (6) AMPLITUDE PULSES: the number of distinct amplitude pulses within the selected note. (7) MAXIMUM FREQUENCY: the frequency with the highest amplitude, measured from the cumulative amplitude spectrum generated from the entire selected note. We measured the remaining variables from the spectrograph, in which curves were generated denoting specific properties of the signal for each point in time within the selected note. (8) INITIAL MAXIMUM FREQUENCY: the frequency that had the maximum amplitude at the start of the note. (9) HIGH MAXIMUM FREQUENCY: the highest frequency on the maximum amplitude curve within the selected note. (10) LOW MAXIMUM FREQUENCY: the lowest frequency on the maximum amplitude curve within the selected note. (11) END MAXIMUM FREQUENCY: the frequency that had the maximum amplitude at the end of the note. (12) INITIAL MEAN FREQUENCY: the

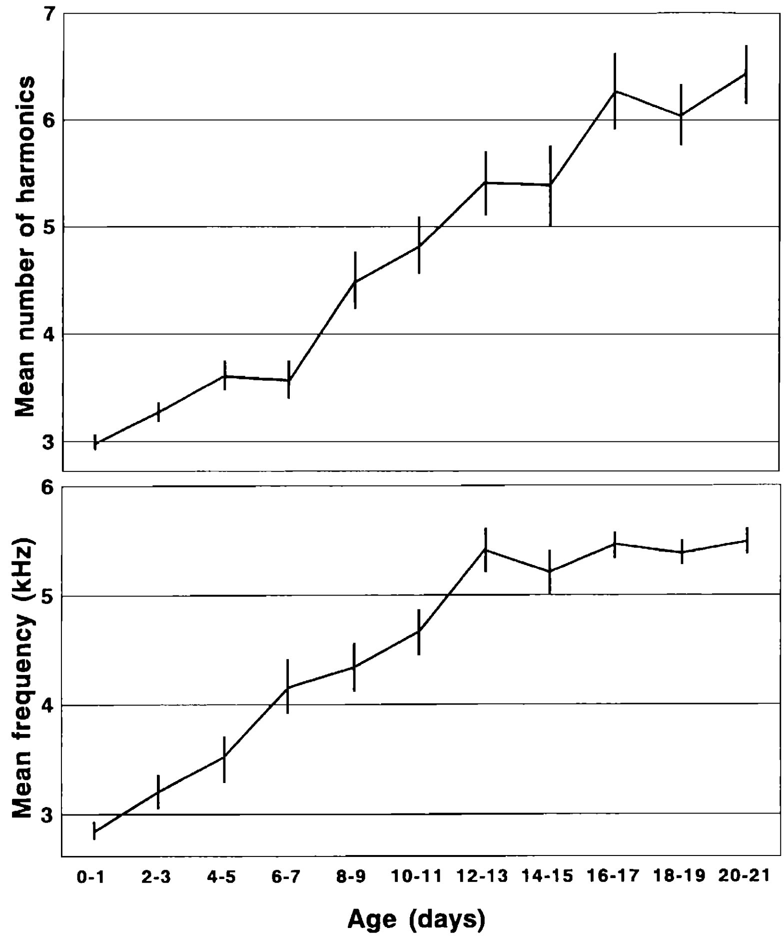

Figure 4. Call notes of American Kestrel chicks ($N = 69$) from northwestern New Jersey, 1999. (Top) The number of distinct harmonic frequencies increases during the nestling stage. Values are means ±SE. (Bottom) The frequency (pitch) of the dominant harmonic increases during the nestling stage. Values are the frequencies (mean ±SE) of the harmonic that has the highest amplitude within a call note.

mean frequency at the start of the note. (13) HIGH MEAN FREQUENCY: the highest frequency on the mean frequency curve within the selected note. (14) LOW MEAN FREQUENCY: the lowest frequency on the mean frequency curve within the selected note. (15) END MEAN FREQUENCY: the mean frequency at the end of the note. (16) HIGH 75% FREQUENCY: the highest frequency on the 75th percentile curve within the selected note. The 75th percentile curve denotes, for each point in time, the frequency below which 75% of the acoustical energy is present. This variable, and the next two variables, provide measures of frequency ranges that are not dependent upon recording level. (17) LOW 25% FREQUENCY: the lowest frequency on the 25th percentile curve within the selected note. (18) FREQUENCY RANGE: an index of frequency range, 75% HIGH FREQUENCY minus 25% LOW FREQUENCY.

Statistical Analyses. We divided the data set into 11 2-d age categories, allowing each age category to be examined separately and ensuring that no individual kestrel was represented by more than one vocal sample per age category. The data were tested for normality. Because we detected significant deviations, we used nonparametric statistical treatments for all univariate comparisons between males and females. The results of comparisons of gender within one age category were not independent of the comparisons within another age category because the same individual birds were represented in each, therefore, we adjusted the P-values using Bonferroni's probabilities (Snedecor and Cochran 1980). We performed a discriminant function analysis, with gender as the single classification variable, separately for each age category. The 13 acoustical variables denoting frequency (measurements in kHz) were subjected to a principal component analysis, and we employed univariate treatments to compare males and females with respect to the first two principal components separately for each of the 11 age categories; again, we adjusted the *P*-values due to the nonindependence of these tests. Finally, we tested age-related changes in the acoustical properties of vocalizations with nonparametric correlation analyses; age category ($N = 11$) was correlated with the mean values (of each age category) for each variable.

RESULTS

Gender Comparisons. A total of 563 vocal samples was obtained from 88 chicks (49 males and 39 females) from 20 broods. We sampled individual chicks from 1–9 times ($\bar{x} = 6.4$, mode = 8). The tendency to vocalize was similar for males and females; mean response rates were 89.8% ± 2.17 (SE) and 90.2% ± 2.46, respectively ($Z = 0.374$, $P = 0.71$, Wilcoxon rank sums test).

Univariate analysis of the 18 acoustical variables (for 11 age categories; 198 comparisons in all) revealed three significant differences between males and females, all for age 8–9 d: INITIAL MEAN FREQUENCY ($\bar{x} = 5.26$ kHz ± 0.20 and 4.35 kHz ± 0.24, respectively, $Z = 2.865$, $P = 0.046$, Wilcoxon rank sums test), LOW 25% FREQUENCY ($\bar{x} = 3.69$ kHz ± 0.34 and 2.78 kHz ± 0.24, respectively, $Z = 2.896$, $P = 0.042$), and DOMINANT HARMONIC ($\bar{x} = 5.08$ kHz ± 0.28 and 3.59 kHz ± 0.30, respectively, $Z = 3.330$, $P = 0.010$).

The discriminant function analyses for each age category had error rates that ranged from 7.9% (age 14–15 d, 1 of 11 females classified as a male and 1 of 15 males classified as a female) to 37.4% (age 20–21 d, 10 of 25 females classified as males and 8 of 15 males classified females). The error rate was not correlated with age category ($r_S = -0.109$, $P = 0.75$). Pooled results of the 11 age-specific analyses had an error rate of 26.0% (63 of 249 samples from females classified as males and 79 of 297 samples from males classified as females).

A principal component analysis of the 13 acoustical variables denoting frequency generated a first principal component (PC1) that accounted for 50.03% of the sample variability (eigenvalue = 6 504) and a second principal component (PC2) that accounted for an additional 17.92% of the sample variability (eigenvalue = 2.329); thus, over two-thirds of the sample variability was explained by the first two principal components (Table 1). Univariate analysis of PC1 and PC2 for 11 age categories (22 comparisons in all) revealed only one significant difference between males and females: for age 8–9 d, mean PC1 values were 0.58 ± 0.42 and −1.52 ± 0.48, respectively ($Z = 3.083$, $P = 0.022$, Wilcoxon rank sums test; Fig. 1).

Age Comparisons. Figure 2 is a composite spectrograph of the vocalizations of an individual male kestrel chick at ages 0, 6, 13, and 20 d. The day 0 call notes were "thin" (harmonically simple, with a narrow frequency range at any point in time), clear tones that dropped in pitch, sounding like *peep* or *cheep*. The day 6 call notes were given more rapidly and had more energy in the upper frequencies. The pitch was slurred downward and the notes were more *cheep*-like. The day 13 call notes were delivered faster still and had more energy concentrated into distinct harmonic frequencies. The pitch, no longer slurred downward, instead was either steady or tremulous, sounding like *chee* or *kee*. The day 20 call was similar to that of an adult *klee*. Distinct harmonic frequencies were well developed and the frequency modulation, although distinct in the spectrograph, was rapid and slight, such that the notes did not sound particularly tremulous.

Each acoustical variable was significantly correlated with age category (Table 2). All correlations were positive, except for INTERNOTE, AMPLITUDE PULSES, and FREQUENCY RANGE. The relationship between age category and INTERNOTE, MAXIMUM FREQUENCY, NUMBER OF HARMONICS, and a DOMINANT HARMONIC are given in Figs. 3 and 4.

DISCUSSION

Acoustical characteristics of call notes changed in a consistent manner as chicks matured. Notes became longer and increasingly complex with respect to harmonic structure, and both the number of notes per call and the rate at which they were delivered increased. In general, vocal characteristics changed most rapidly during the first two weeks (Figs. 1, 3, and 4). By about day 16 chicks were able to produce calls that sounded similar to the *klee* calls of adults. Roest (1957) noted that chicks of this age were able to utter the adult-like "*killy-killy*" cry, although some chicks were silent when handled.

The discriminant function analyses did not perform well in distinguishing gender. The pooled error rate of 26.0% was slightly closer to that of random classification (50% error) than to perfect discrimination. Vocalizations of males and females were essentially indistinguishable from each other with respect to the acoustical characteristics we measured, except that males appeared to progress toward adult-like vocalizations more rapidly than females, especially during the second week (Fig. 1). The first principal component (derived from frequency variables and most strongly influenced by LOW MEAN FREQUENCY, END MEAN FREQUENCY, and END MAXIMUM FREQUENCY; Table 1) differed significantly between 8–9-d-old males and females. Three other frequency variables (INITIAL MEAN FREQUENCY, LOW 25% FREQUENCY, and DOMINANT HARMONIC) also differed significantly at this age. These results suggest that males may develop adult-like frequencies (higher pitch; Table 2) sooner than females.

Although possible, it is unclear if individual variability in vocalization patterns is sufficient for individual recognition by kestrels. Such vocal recognition is widespread in both passerines and nonpasserines (e.g., Falls 1982, Stoddard 1996, and citations therein). Additional research is required to document if this behavior occurs in American Kestrels.

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