

VOCAL SIGNALS OF THE VILLAGE WEAVER: A SPECTROGRAPHIC KEY AND THE COMMUNICATION CODE¹

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Abstract. Vocal signals of a species are social signals and guides to its social life. Sound spectrograms were made of 21 of the 26 vocal signals in the extensive vocal repertoire of the African Village Weaver (*Ploceus cucullatus*). A spectrographic key to vocal signals helps make these signals comparable for different investigators. Short-distance contact calls are given in favorable situations and are generally characterized by low amplitude and great brevity of notes. Alarm cries are longer, louder, and often strident calls with much energy at high frequencies, whereas threat notes, also relatively long and harsh, emphasize lower frequencies. Each male displays his newest nest in a colony with an individually distinctive call to unmated females. The most harmonic calls of the species include a loud call by a male when an unmated female first enters his nest, and also very soft, brief notes given by parent birds to attract a fledgling. Males use somewhat different songs to defend territory, for courtship, and for advertisement. Application of Darwin's (1872) principle of antithesis suggests that vocal signals are composed of basic elements that vary in duration, frequency, loudness, and tonality of notes. These variations can be arranged in pairs of opposite extremes serving to reduce ambiguity in signals, in effect a communication code. At the same time, other selection pressures can enter in according to circumstances to modify the expression of this basic code in evolution.

Key words: *code, communication, Darwin's antithesis, Ploceus cucullatus, sound spectrograms, Village Weaver, vocal signals.*

INTRODUCTION

The purpose of this report is to describe objectively the extensive repertoire of vocal signals in a highly social passerine bird (Order Passeriformes), the Village Weaver (*Ploceus cucullatus*) of sub-Saharan Africa. Other objectives are to indicate the essential stimulus situation under which these vocal signals are given, to classify the vocal signals into general categories in a spectrographic key, and then to attempt to analyze these signals into basic elements of the underlying code of communication.

The vocal signals of a bird are social signals that reflect the social life of the species, and the repertoire may often be far more extensive than is commonly realized. In very few birds has such a large vocal repertoire yet been described objectively, and this finding for one passerine species suggests how much more we have to learn about the social signals and, therefore, about the social life of many species of passerine birds. For example, in 1978, 12 vocal signals of the Black-capped Chickadee (*Parus atricapillus*) were described (Ficken et al. 1978), and with

further study the known vocal repertoire of this species has been increased to at least 17 different vocalizations (Smith 1991). In the pre-spectrograph era, Margaret Nice (1943) in her classic study of the life history and behavior of the Song Sparrow (*Melospiza melodia*) listed some 21 "chief vocalizations" for this species.

This report builds on and extends an earlier study in which 15 vocal signals were described for the Village Weaver (Collias 1963). With further observation over 20 more years of color-banded individuals in outdoor aviaries, my knowledge of this bird's vocalizations has been extended to some 26 distinct vocal signals (a three-fourths increase), as well as increasing my understanding of the various stimulus situations under which each signal is given. Sound spectrograms are depicted here for 21 of the vocal signals of this species.

This paper presents a spectrographic key to the extensive repertoire of vocal signals of the Village Weaver. This key not only shows one way to classify vocal signals, but also suggests a way of describing the vocal repertoire of birds in objective terms, comparable for different observers, by focusing on the important differences in the spectrograms of the different vocal signals.

¹ Received 16 March 1999. Accepted 20 October 1999.

In classifying the calls, I have made use of Darwin's principle of antithesis (1872, p. 50): "When a directly opposite state of mind is induced there is a strong and involuntary tendency to the performance of movements of a directly opposite nature . . ." This approach helps solve the problem of intergradation of vocal signals and minimizes ambiguity of signals.

An underlying communication code is suggested by spectrographic application of Darwin's principle to vocalizations (Collias 1963, 1987). There have been very few previous comprehensive attempts based on Darwin's (1872) principle of antithesis to analyze bird calls into their basic elements, as in my study of the vocal signals of the Red Junglefowl (*Gallus gallus*; Collias 1987). The present detailed study extends this application to a passerine bird and supports it with quantitative data. In general, attraction calls are soft (of low amplitude), brief, and repetitive, or else with definite and clear harmonics. But alarm cries and threat sounds are generally loud and harsh with a wide and diffuse spread of frequencies combined with harmonic streaks. Alarm cries have high frequencies, threat sounds emphasize low frequencies. Similar general rules of vocal communication and physical characteristics of signals may apply to both birds and mammals (Collias 1960, 1964, Morton 1977, Owings and Morton 1998). A difference between the communication code that I suggest and Morton's motivation-structural rules is that in addition to frequency and tonality I include duration and loudness of notes in the code. Morton (1977, 1982) has also emphasized the importance of intergradation between vocal signals under mixed motivations, theoretically serving to communicate subtle differences in motivation and consequent variations in behavior.

A specific and separate vocal signal can be characterized by (1) a fairly consistent spectrographic structure, (2) a typical situation or context under which this call is given, and (3) the general function or functions (message) of the call as deduced from the common element in the various situations under which the call is uttered (Smith 1969). Calls do sometimes intergrade, but in practice most calls as ordinarily given are discrete and easily recognized.

From these objective criteria of specific structure, situation (context), and function or functions, one can suggest the underlying motivation

and presumed emotional state that drives a bird or mammal in its behavior. At times, especially under intermediate stimulus situations, calls representing mixed motivations may be given.

METHODS

OBSERVATION OF BEHAVIOR

The Village Weaver nests in dense colonies in isolated trees along streams, in forest clearings, and in villages and gardens. At the start of the breeding season, the males arrive first and establish small individual territories in the colony tree, and weave the outer shell of the nests. When the females arrive, each male attempts to attract a female to his nest with special displays, and if successful he builds other nests to which he attempts to attract additional females, the species being polygynous. The female, if she accepts the male and his nest, lines the nest, incubates the eggs, and does all or most of the feeding of the young (Collias and Collias 1970, 1984). In the colony tree, whenever the male was under observation, so in general was the female because her nest was only a few centimeters to a meter or so from the male within the male's small territory in the tree. Throughout the study, particular attention was paid to the relations between the sexes.

The general method of the investigation was close observation of color-banded individuals in the field and of birds of known history in outdoor aviaries where the birds bred and largely controlled their own lives. The typical stimulus situation for the calls was determined by observing the context in which each vocal signal was given, often on hundreds of different occasions. Tape recordings and sound spectrograms were made of most of the different calls. Verbal imitations of the vocal signals are merely mnemonic aids for convenience.

Village Weavers of the West African race, *Ploceus c. cucullatus*, were observed in nature in northwest Senegal and in large outdoor aviaries at the University of California, Los Angeles (UCLA) (Collias and Collias 1970). In both field and aviary, we placed two color bands on each leg of the birds, the same color combination on each leg for more rapid identification of individuals. We watched the birds throughout one breeding season in northwest Senegal (Collias and Collias 1970), and generally throughout the breeding season over two decades in our avi-

aries (1959–1980) at UCLA. In Senegal, we especially watched one colony located in a small acacia tree just across a small irrigation canal from our observation site. The birds were accustomed to seeing people, and almost from the start paid no apparent attention to us. For two other complete breeding seasons, we also observed other races of this species in central and in southern Africa (Collias and Collias 1959, 1971). Our stock of captive weavers at UCLA originally came from Senegal, given to us in 1959 by Jean Delacour and other birds later by Gérard Morel. In California, the observer routinely hid in a blind at one end of each large aviary. The five aviaries ranged from 7.9 m long \times 6.1 wide \times 4.2 m high to 9.2 \times 5.2 \times 5.2 m, with usually 10–19 birds and similar numbers of males and females in each aviary. Details of the care and maintenance of the birds are given elsewhere (Collias and Collias 1970).

Both male and female weavers were each observed for many hundreds of hours, particularly in the outdoor aviaries where all birds were accessible to close observation, except when the female was inside her enclosed nest in the male's territory. Observation of vocal signals was opportunistic and often at irregular intervals and incidental to other projects so no precise estimate of total time observed over many years is available.

RECORDING AND MEASUREMENT OF VOCAL SIGNALS

In my initial study of vocalization in this species (Collias 1963), tape recordings of the vocal signals were made in the aviary with an Ampex Model 910 and an Electro-Voice 666 dynamic microphone. The spectrograms of the calls were made on a Kay Electric Company Sona-Graph, Model R. During subsequent years, additional calls were tape recorded in the aviaries, and sound spectrograms were made on a Kay Elemetrics Corporation Sona-Graph 6061B. Spectrograms of each call were made with the wide band (300 Hz) filter for more precise time resolution and with the narrow band (45 Hz) filter for better resolution of frequencies. In general, a note was defined as a sound that made a single continuous impression in time on the spectrogram. The harmonics of a musical note are considered part of the same note. Later, spectrograms of the calls were recorded and mechanically measured on a DSP Sona-Graph Model

TABLE 1. List of vocal signals of the Village Weaver.

	Observed in
Short-distance contact calls	
1. Soft parental notes used to lead fledgling (<i>choo choo</i>)	♂, ♀
2. Flock contact call (<i>tsuk</i>) on ground or perch	♂, ♀
3. Flight contact call (sharp <i>chick!</i>)	♂, ♀
4. Nest-material call (<i>tsuk-tsuk</i> , - etc.)	♂
5. Twitter to visiting female in nest	♂
6. Chuckling chatter greeting female's return to nest	♂
7. Rejection of male's copulation attempt	♀
8. Copulation-invitation notes by female	♀
9. Copulation call	♂, ♀
Cries of distress or alarm	
10. Hunger-distress <i>chirps</i> of nestling	♂, ♀
11. Strident squawks of hunger & location by young	♂, ♀
12. Protest squeal by incubating female when disturbed	♀
13. Low intensity alarm (<i>chirp!</i>)	♂, ♀
14. High intensity alarm (<i>kek! kek!</i>)	♂
15. Distress cry when seized	♂, ♀
Threat calls	
16. Low intensity and defensive threat (deep <i>chuck!</i>)	♂, ♀
17. High intensity threat (<i>growl</i>)	♂, ♀
18. Harsh chatter by male guarding female in nest	♂
Calls of apparently mixed motivation	
19. Initial aggressive chitter to visiting female (<i>chip chip</i> , etc.)	♂
20. Long call of male as his mate departs	♂
Courtship calls and songs	
21. Nest-invitation display to female	♂
22. Loud <i>wheep!</i> when visiting female enters male's nest	♂
23. Song to visiting female in male's nest	♂
24. Territorial song versus other male	♂
25. Perch song	♂
26. Song of juvenile male (subsong)	♂
Total	23 13

5500 (Kay Elemetrics Corporation, Pine Brook, New Jersey) and printed with a Gray Scale Printer Model 5510. This recent model Sona-Graph can display color-coded spectrograms, in which the amplitude of different frequencies are shown in different colors.

INTERPRETATION OF SPECTROGRAMS

Inspection of the spectrograms revealed a harmonic structure for several vocal signals with

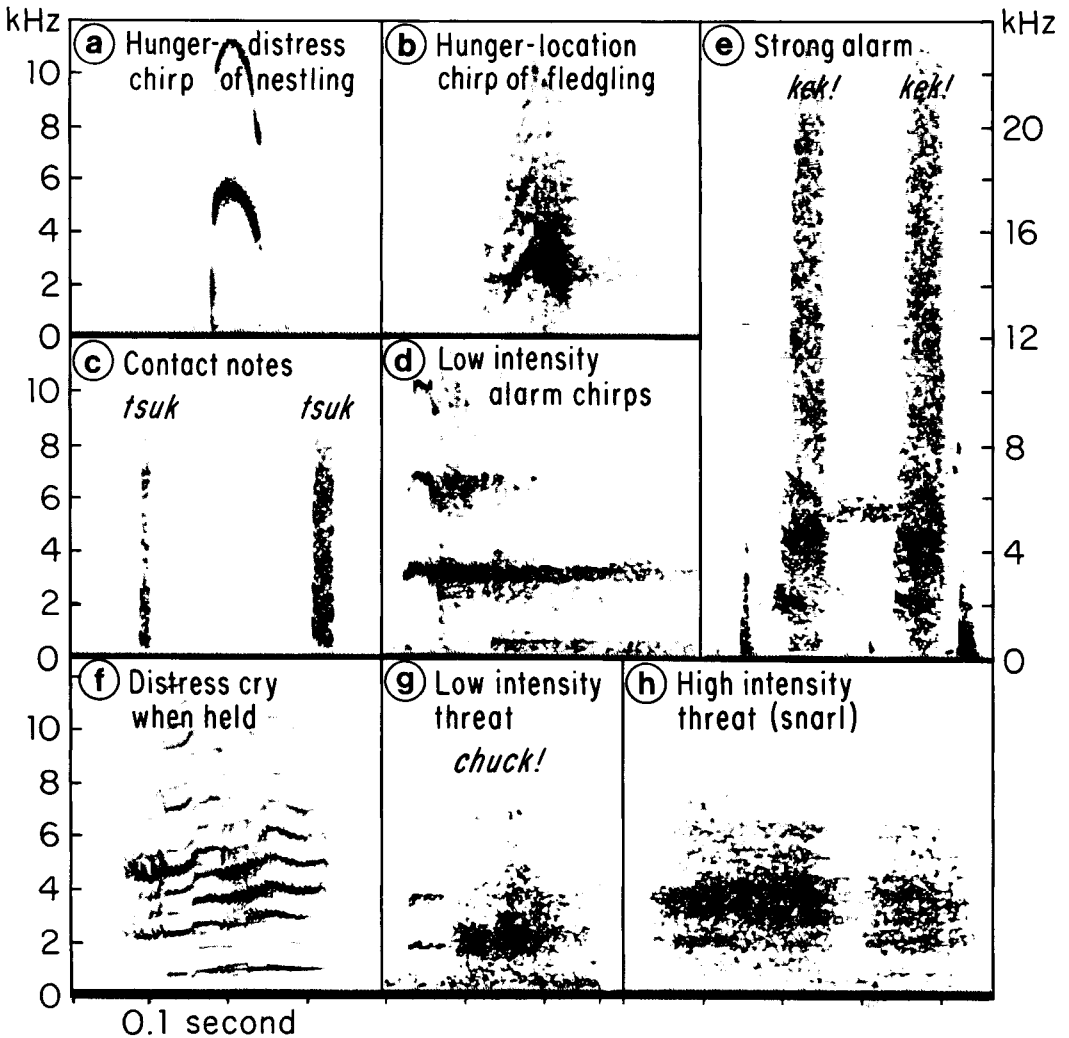


FIGURE 1. Spectrograms of some general calls of the Village Weaver. Half-normal speed with narrow filter. (after Collias 1963).

clear, distinct, and well separated frequency bands, and with overtones (harmonics) that are integral multiples of the fundamental. In contrast, many other sounds were harsh. A harsh sound may be defined spectrographically as a loud sound having a wide spread of diffuse frequencies combined with harmonic streaks (Collias and Joos 1953); the different harmonics are blurred or smudged on the spectrogram by intervening frequencies. Harsh calls are sometimes described as “noisy” (Baptista 1996).

The low amplitude of many short-distance contact calls that are brief keeps them from hav-

ing a harsh quality, and they are not necessarily tonal sounds. Hissing is a forceful, unvoiced expiration and is given by many birds (Collias 1960), but I have not detected it in Village Weavers. The spectrogram of a hiss shows a wide spread of frequencies, but, unlike harsh sounds, is not combined with harmonic streaks (Collias and Joos 1953).

Interpretation of the essential meaning or function of each call (Collias 1960) was based on the common element in the many occasions in which the call was observed.

A copy of the tape recordings of 21 vocal signals of the Village Weaver has been placed in

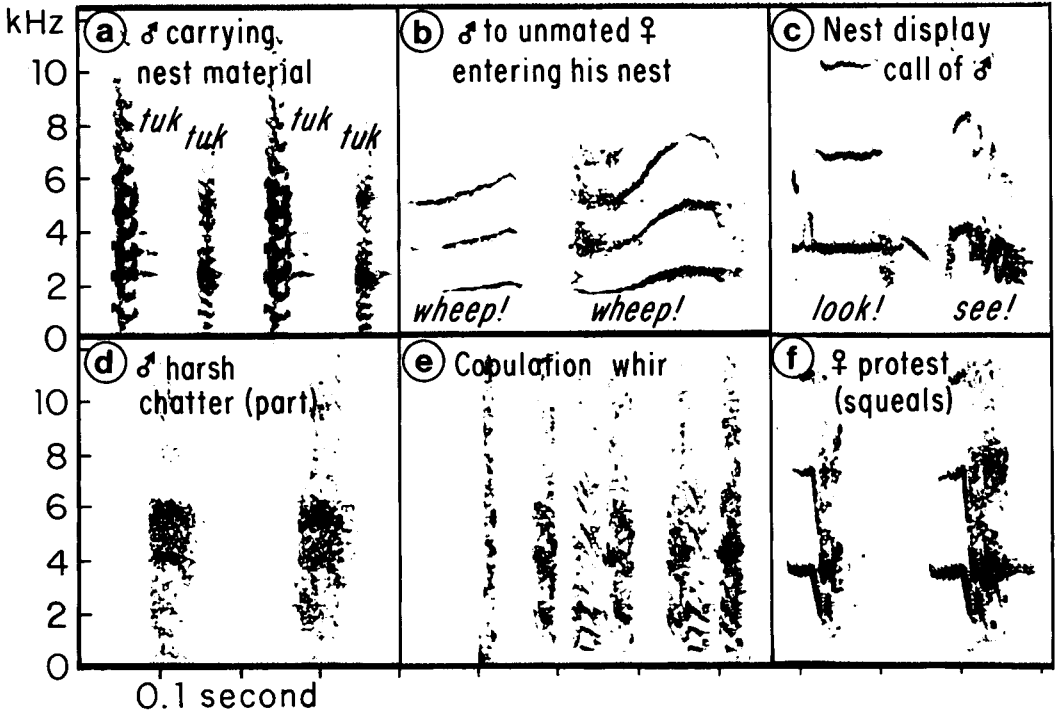


FIGURE 2. Spectrograms of some calls of the Village Weaver related to its specialized nesting behavior. (after Collias 1963). Half-normal speed with narrow filter.

the Library of Natural Sounds, Cornell Laboratory of Ornithology (Ithaca, New York).

RESULTS

The vocal signals fall into four main functional groups, except for two calls of apparently mixed motivation (Table 1).

Of the various vocalizations given by the adults, the male gives 20, the female 11. The Village Weaver is a polygynous species with intense competition between the males for mates. Most of the vocal signals that were heard only from the males reflect this competition for females. The males use different song-types, special courtship calls, and certain threat calls. In addition, the males act as sentinels to warn of approaching predators. The female spends much of her time in the colony inside her roofed nest which has a bottom entrance, where she cannot see approaching danger. On hearing the high intensity alarm call by the males, which demands instant response, the females at once dive out of their nests and move into the protection of the dense thorny branches toward the center of the

acacia tree in which the colony is located. Females were not observed to give the high intensity alarm call, and if they ever do so it must be rare.

PREVIOUSLY UNDESCRIBED CALLS OF THE VILLAGE WEAVER

Fifteen different vocal signals were described earlier (see Figs. 1 and 2) for the Village Weaver (Collias 1963). With more years of additional experience with the birds, I now describe 11 more calls, making a total of some 26 recognizable vocal signals for this species. Spectrograms are presented here for seven of the additional vocalizations (Figs. 3, 4, and 5) that are described below.

A basic attraction or contact call given by both parent Village Weavers to a fledgling is a very soft (low amplitude), gentle, and rather melodious *choo choo* (Fig. 3a). This call, given by a parent close to the young one, stimulates the young to follow the parent as the parent endeavors to lead the young bird from an exposed spot to a safer place.

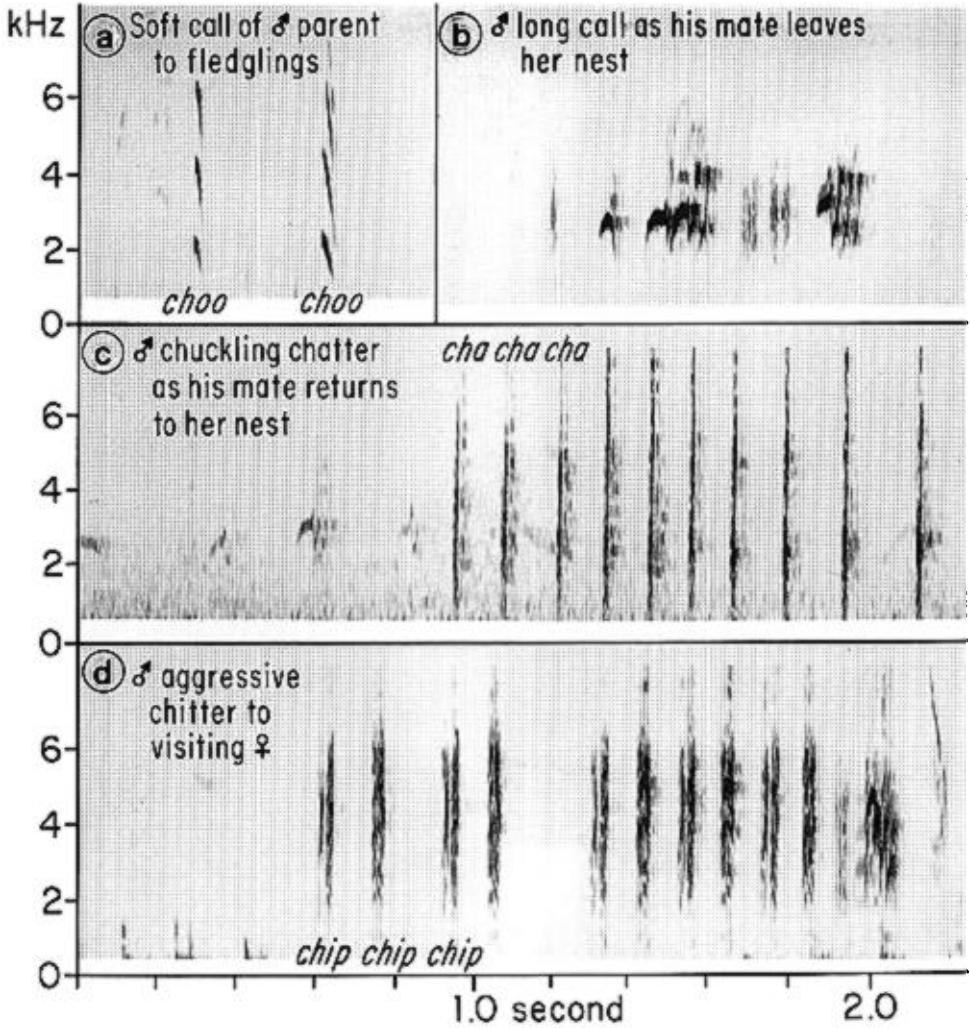


FIGURE 3. Spectrograms of some previously undescribed calls of the Village Weaver. Normal speed with wide filter.

The male gives a special *long call* (Fig. 3b) when his mate leaves her nest and flies off. This call is somewhat harsh with variable frequencies between 2 kHz and 4 kHz, and the spectrogram resembles both contact and threat sounds, but the function of this call was not determined. When his mate returns to her nest, the male utters a very different call, a *chuckling chatter* (Fig. 3c). The pulsed character and low frequencies of this call resemble the general characteristics of short distance contact calls.

When an unmated female first enters a male's small territory, instead of at once courting her, he sometimes utters an *aggressive chitter* (Fig.

3d) of sharp *chip* notes, and at the same time he chases the female out of his territory. The male normally defends his territory from intruders, and it may be that any bird other than one of his mates that enters his territory initially arouses some aggressive defense tendency in the male.

Sometimes a male songbird clearly shows mixed motivation, alternating between attack and courtship, or between aggression and sexual motivation (Hinde 1953). One male, when an unmated female entered his nest, hopped excitedly about in his territory, uttering loud single *wheep!* calls (Fig. 2b) associated with courtship.

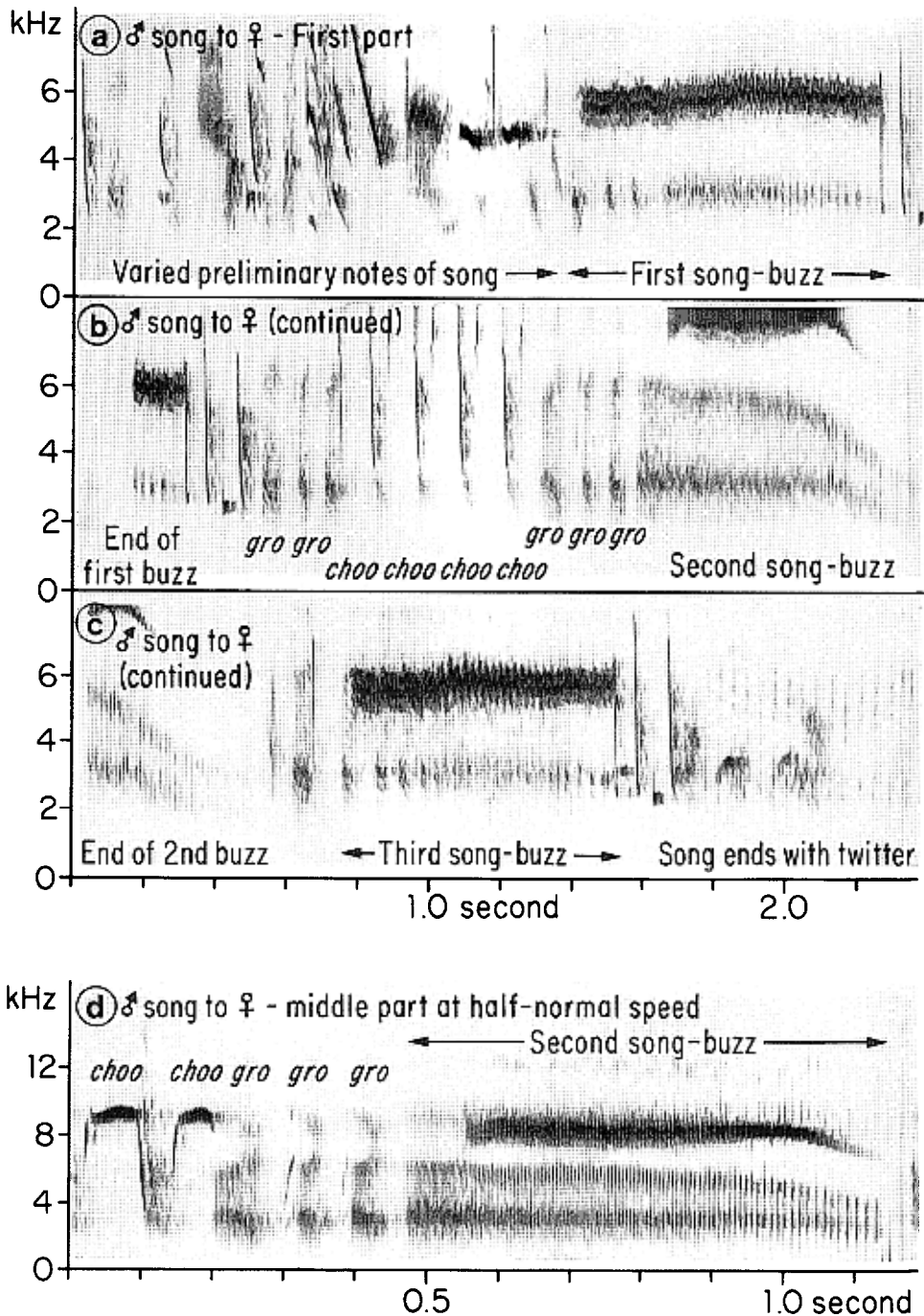


FIGURE 4. Spectrograms of song of male Village Weaver to female inside his nest. (d) shows middle part of song at half-normal speed (wide filter) to bring out higher frequencies. Normal speed with wide filter.

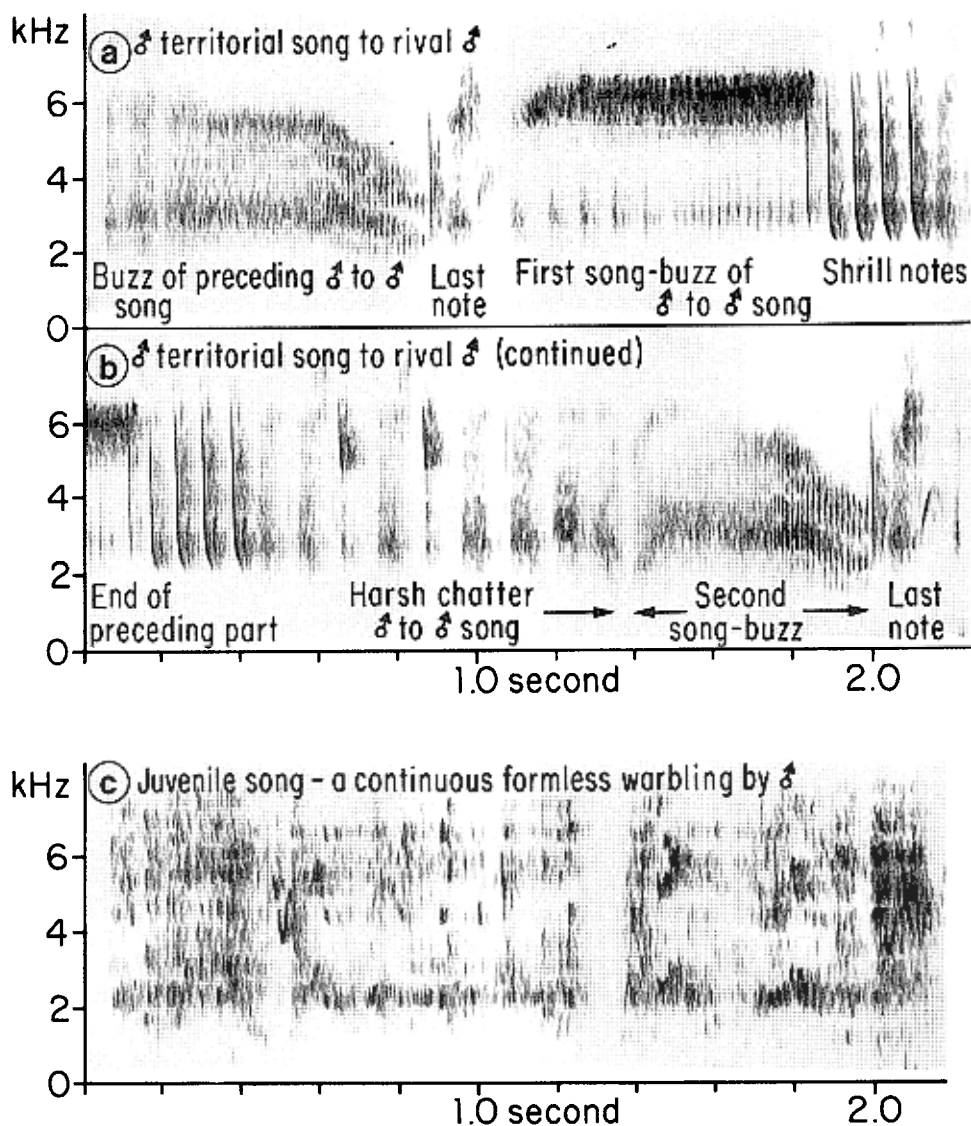


FIGURE 5. Spectrograms (a) and (b) of territorial song of male Village Weaver to a rival male. (c) song of juvenile male Village Weaver. Normal speed with wide filter.

But while perched, he also alternated these calls with sharp *chip-chip* notes (Fig. 3d) of mild aggression. Sometimes a male gives courtship calls while moving toward a visiting, unmated female, but shifts to the aggressive calls when flying away from her toward the edge of his territory.

When a visiting female, after inspecting a nest, exits and perches in the territory, the male usually flies directly to her and attempts copulation. But the female often rejects this initial

attempt at copulation by rolling under the branch and hanging upside-down by her feet. At the same time she may utter a *rejection* call (not taped), a rather high, thin and weak, double note, *see-up!*

When a female is ready to mate, normally she needs do little to encourage the male, besides perching in his territory. But one female, just outside a male's territory, was seen to invite the male to mount with definite pre-copulatory behavior. While vibrating her partly spread wings,

she pointed her beak straight up and raised her tail, at the same time uttering *copulation-involution* notes (not taped), a high piping and plaintive series of single *peeps*.

SONGS OF THE VILLAGE WEAVER

In our aviary colony, among the adult males, there was in most cases besides the species-typical form of the song, individual "signatures" in the song that were constant for each male (Jacobs 1979). When an unmated female first enters the nest woven by a male, he goes to the entrance of the nest and *sings directly to the female* with a long buzz near the end of his song. He often ends this song with a *twitter* (Fig. 4c) resembling other attraction notes in general characteristics. But when a male gives his *territorial song* to rival males, he instead often intersperses a harsh chatter (Fig. 5b) of *threat* sounds before the terminal buzz (Fig. 5b). This song type is often given at the territorial boundary where two males face and often peck at each other. Both of these song types were heard hundreds of times during each breeding season. Similarly, in the Cuban Grassquit (*Tiaris canora*) Baptista (1978) has described one pure-toned song-type signaling sexual motivation whereas a second harsh or buzzy and simpler song signals territorial aggression.

The second song buzz in the male Village Weaver's song to a female (Fig. 4d) is clearly composed of harmonics with a fundamental frequency of about 3 kHz and a harmonic at about 6 kHz. In addition, the highest frequency component at about 8 kHz is not harmonically related to the first two components of the song buzz and is likely produced by the second voice; that is, the songbird syrinx has two independent acoustical sources (internal tympaniform membranes) one in each bronchus, enabling a bird to produce two notes simultaneously (Greenwalt 1968, Suthers et al. 1999).

The adult male Village Weaver also has a *perch song of advertisement* that he gives while simply perched in one spot in or near his territory. My general impression, after hearing many of these songs, is that the perch song is even more varied than the other two types of song. For example, as I wrote one day in the large aviary: "Male RAY sings alone in the center of the south tree. He has no nest, nor even the start of one, but he sings repeatedly, giving the song-buzz, the attraction twitter (Fig. 4c), and the

scolding chatter (Fig. 5b), in most bouts of vocalization." In other words, in contrast to the two other types of song, the male may include both attraction and aggressive notes in his perch song in addition to the usual terminal long song-buzz notes. The perch song is much less common than other types of adult song, but the bird sings it for a longer period. Selection pressures for variety in the advertisement song may include different call notes of the species that could aid species recognition.

Young male Village Weavers begin to sing a *juvenile warble* (Fig. 5c) or "subsong" beginning at roughly a month of age shortly after leaving the nest (Collias and Collias, 1973). The females were never heard to sing. The song of the juvenile male is soft and sounds rather pleasant, a continuous, persistent, and formless warbling, given while perched. His singing may be spontaneous or initiated by various external sounds, for example, the sound of a vacuum sweeper or of running water from a faucet. One young male Village Weaver, hand-raised in isolation from other weavers at our home, first gave the adult male song buzz or wheeze at about five months of age. This was at first much shorter than the buzz notes in the typical adult male song. He first gave this buzz several times while pecking aggressively at my fingers when I interfered with his working at a strip of nest material.

A SPECTROGRAPHIC KEY TO VOCAL SIGNALS OF THE VILLAGE WEAVER

Specific calls are shown below in italics. See Tables 2 and 3 for measurements of call notes. Figure designations in parentheses refer to the number and letter of each call on the sound spectrograms (sonograms).

- I. *Short-distance contact calls (attraction notes)*. Not harsh; brief, generally soft (of low amplitude) notes.
 - A. Contact calls, not click-like. Very brief (<0.04 sec), soft and repetitive notes, with some lower frequencies (below 2 kHz). Given by both sexes, except as noted below.
 - (1). PARENTAL NOTES USED TO LEAD FLEDGED YOUNG (Fig. 3a). Very soft *choo choo* notes, with clear harmonic structure (distinct overtones) and sharply descending frequencies.

TABLE 2. Length and frequency of nine Village Weaver calls of a general nature. Measures are approximate because some calls start and fade out gradually. See Figure 1 for spectrograms of these calls with the same number and small letter designation for each call as in this table.

Figure (spectrogram) and stimulus situation of call [and location in spectrographic key]	n notes measured ^a	Length of note (sec)	Range of frequencies (kHz)	
			all	strongest
1a. Hunger-distress chirp (nestling) [IIA]	1	0.06	1 to >20	4.0-6.0
1b. Food-begging squawk (older nestling) ^b [IIA]	10	0.10-0.20	1.6-8.0	2.1-5.0
1b. Hunger-location squawk (fledgling) [IIA]	10	0.10-0.12	0.6-14.6	2.0-6.7
1c. Contact note (<i>tsuk</i>) when fed [IA]	7	0.01-0.02	0.04-11.3	1.3-4.3
1d. Low intensity alarm chirp [IIB]	10	0.19-0.29	2.9-7.6	3.0-3.9
1e. High intensity alarm call (<i>kek!</i>) [IIB]	6	0.06-0.08	0.2-15.1	4.0-7.0
1f. Distress cry when seized [IIB]	9	0.23-0.29	0.7-10.1	2.2-2.8
1g. Low intensity threat (<i>chuck</i>) [III]	10	0.06-0.11	1.0-5.0	1.7-3.0
1h. High intensity threat (<i>snarl</i>) [III]	6	0.06-0.15	1.0-5.6	2.0-2.9

^a Two birds were recorded for call-types 1c and 1f; one bird was recorded for each of the other call-types in this table.
^b The food-begging squawk is very similar to and develops into the hunger-location squawk.

- (2). NORMAL FLOCK CONTACT CALL (*tsuk*) (Fig. 1c). Given by young and adults when near other birds often on ground. Brief, well-separated notes, with wide spread of frequencies and no very clear harmonic structure. Given by young bird just before or after being fed, and when near parent.
- (3). FLIGHT CONTACT CALL. Sharp *chick!* (No figure). Given just before take-off and during flight. Given by young and both sexes of adults. Resembles normal brief, *tsuk* contact calls, but louder and helping to maintain contact over greater distances than do contact calls on the ground.
- (4). NEST-MATERIAL CARRYING CALL OF MALE (*tuk-tuk*, etc.) (Fig. 2a). Long series of rhythmic, humming notes with regular interval between notes. Some clear harmonics closely spaced within notes. Given by male carrying nest material back to his nest.
- (5). COPULATION CALL (Fig. 2e). Given at instant of mating. Short series of brief, soft whirring notes in irregular sequence. Notes not measured since some notes run together. Notes with a wide spread of frequencies. Also given by female with small nestlings just before she enters nest, while assuming what resembles a precopulatory posture.

TABLE 3. Length and frequency of 10 specialized calls of Village Weaver related to its complex nesting behavior. Measures are approximate because some calls start and end gradually. See Figures 2 and 3 for spectrograms of these calls with the same number and small letter designation for each call as in this table.

Figure (spectrogram) and stimulus situation of call [and location in spectrographic key]	n notes measured ^a	Length of note (sec)	Range of frequencies (kHz)	
			all	strongest
2a. Male carries nest material (<i>tuk</i>) [IA]	16	0.02-0.06	0.7-3.8	1.8-3.0
2b. Male call as unmated female enters his nest (<i>wheep!</i>) [V]	8	0.20-0.25	1.5-8.5	2.0-3.0
2c. Male nest invitation to female [V]	20	0.10-0.18	1.5-5.6	2.0-4.9
2d. Male harsh chatter [III]; female in nest	12	0.06-0.08	1.3-5.6	2.0-4.9
2f. Female protest squeal to male [IIB]	2	0.15	1-10.5	2.0-8.0
3a. Parental call to fledgling (<i>choo</i>) [IA]	9	0.02-0.04	1.1-8.2	1.7-2.4
3b. Male long call as mate leaves nest [IV]	6	0.01-0.18	2.4-4.5	2.5-4.0
3c. Male chuckling chatter as mate returns [IB]	10	0.01-0.03	0.08-7.5	3.0-4.0
3d. Male aggressive chitter to female visiting his territory [IV]	10	0.03-0.05	1.9-6.3	1.9-5.7
4c. Male twitter to unmated female entering his nest [IB]	12	0.03-0.05	0.6-10.8	1.7-5.4

^a Two birds were recorded for call-types 2b and 2c; one bird was recorded for each of the other call-types in this table.

B. Click-like notes. Extremely brief, rapidly repeated or pulsed notes.

- (1). CHUCKLING CHATTER OF MALE TO HIS MATE ON HER RETURN TO HER NEST (Fig. 3c). Some smudging immediately after each click, but the click pattern predominates.
- (2). TWITTER OF MALE, GIVEN INDEPENDENTLY OR AT END OF MALE'S SONG WHEN VISITING FEMALE ENTERS HIS UNOCCUPIED NEST (Fig. 4c). Rapid series of clear clicks with little or no smudging of each click. Twitter may overlap chuckling chatter.

II. *Cries of distress or alarm*. Generally harsh (smudged spectrogram, i.e., with wide spread of frequencies often combined with obscured harmonic streaks). Usually, loud, moderately long (0.06–0.35 sec) notes, extending into high frequencies (above 7 kHz).

A. Distress calls of very young birds.

- (1). HUNGER-DISTRESS CHIRPS OF RECENTLY HATCHED NESTLING (Fig. 1a). Spectrogram with clear loops and harmonics extending above 20 kHz. (Fig. 1a shows only fundamental and first harmonic). Call emphasizes descending frequencies. Develops into next call through begging squawk (no figure) given by young about to be fed.
- (2). STRIDENT SQUAWKS OF HUNGER AND LOCATION (Fig. 1b). Given by late nestling or fledgling. Spectrogram with wide and diffuse spread of frequencies often super-imposed on smudged loop. Given by young bird when hungry, when it fell off perch, when frustrated in attempts to obtain some object, when parent nearby moves away, and in early stages of flying when unable to find a place to land.

B. Alarm or distress cries of adults.

- (1). LOW-INTENSITY ALARM CHIRP (Fig. 1d). By male or female. Rather long (0.35 sec), sustained tone, with some blurred harmonic structure in spectrogram. Given to sudden appearance or approach of person, to hissing sound, or by captive birds when transferred to strange place often repeated.

- (2). HIGH-INTENSITY ALARM CALL (*kek! kek!*) (Fig. 1e). Observed in breeding males. Very loud, harsh, and abrupt. Rather short (0.06 sec) notes, with great range of frequencies (1–24 kHz), and with some descending frequencies in each note. Given when person climbs colony tree or moves suddenly and rapidly toward the birds, when hawk dives at colony, or to loud, abrupt and harsh sounds.

- (3). PROTEST SQUEAL OF INCUBATING FEMALE WHEN HER MATE STARTS TO ENTER HER NEST (Fig. 2f). Female pecks hard at male if he persists. Call (0.15 sec) starts with brief, constant-frequency tone followed by smudged and descending frequencies. Spectrogram with some harmonic structure.

- (4). DISTRESS CRY (MALE OR FEMALE) WHEN SEIZED (Fig. 1f). Fairly long (0.25 sec), loud, strident scream, with wide range of close-set, wavering, broken and obscure harmonic streaks on spectrogram. Given when held by person or seized by another weaver.

III. *Threat calls*. Harsh (spectrogram with wide spread of frequencies combined with harmonic streaks). Moderately long (0.06–0.4 sec) and moderately loud notes, emphasizing relatively low frequencies (below 7 kHz), with little or no energy at higher frequencies (above 7 kHz).

- (1). LOW INTENSITY AND DEFENSIVE THREAT (DEEP *chuck*) (Fig. 1g). Note (0.3 sec) with emphasis on lower (0.05–4 kHz) frequencies. Call starts and fades out gradually. Given when bird discovers some object (nest material, food item, fresh water) to be defended, or to a snake near the nests. Often *chucks* are given repeatedly, especially to predators. More often given by male than by female.
- (2). HIGH INTENSITY THREAT (Fig. 1h). A harsh growl or snarl, longer (0.4 sec) but strongest frequencies (3–5 kHz) not so low as in preceding threat call. Really two notes that sound like one to the human ear. More often heard from male than from female, while attacking con-

specific. Also given while chasing female Didric Cuckoo (*Chrysococcyx caprius*), a brood parasite, away from the colony tree.

- (3). HARSH CHATTER OF MALE (Fig. 2d). Repetitive, rather short, (0.06 sec) notes, not so low pitched (mainly 4–6 kHz) as preceding two threat calls, and each note with abrupt onset and end. Given by male in his territory while an unmated female is inspecting inside of his nest. This call often precedes his attempt to copulate after she emerges. Call possibly directed toward neighboring rival males that might interfere with copulation.

IV. *Calls of mixed motivation.* Evidently given in intermediate stimulus situations. These calls are intermediate in their structure to other major categories, and are not well understood.

- (1). LONG CALL OF MALE (Fig. 3b). Given when his incubating mate leaves her nest and flies off. Usually one series of about six notes, both short and long notes, with variable and smudged frequencies (entire call 0.4 sec, 2–4.5 kHz). The spectrogram resembles both weak contact calls and threat sounds.
- (2). AGGRESSIVE CHITTER OF MALE TO VISITING FEMALES (Fig. 3d). Brief, rather sharp *chips*. Each *chip* consists of paired notes smudged together and given at intermediate frequencies mainly 2–6 kHz. The second note tends to be the strongest in each pair of notes (unlike the chuckling chatter). Resemble short distance contact notes in brevity (0.02 sec), but a bit harsh like threat or alarm calls. Possibly reflect conflict between territorial defense and sexual interest.

V. *Courtship call and songs of male.* Complex vocalizations often of specialized different notes. Loud, long-distance calls (except for song of juvenile male). Have more distinct harmonic structure in the adult courtship notes and song than alarm or threat calls do.

- (1). NEST-INVITATION DISPLAY CALL OF MALE (Fig. 2c). Courtship call that definitely attracts female to the nest. Two-note call (*look! see!*), with long and short notes alternating. First note sustained at 3.5 kHz (fundamental), second note a brief,

descending trill. A variable and individually distinctive call (Jacobs 1979).

- (2). LOUD CALL (*wheep!*) OF COURTSHIP (Fig. 2b). Given by the males, early in season when females first arrive, and later by each male when a visiting, unmated female first enters his nest. Relatively long (0.3–0.4 sec) excited call with clear harmonic structure (distinct overtones) and predominant upswing in frequencies.
- (3). SONGS OF ADULT MALE. Much longer than other vocalizations and with wide range of frequencies. Species-specific, complex and prolonged vocalizations. Wide spread of frequencies, with various short preliminary notes, and two or three characteristic terminal buzzes. May also be individually distinctive (Jacobs 1979).
- (a). Song of adult male to unmated visiting female inside in his nest (Fig. 4a–d). Given by male at nest entrance. Terminal buzz often ends with a pleasant-sounding twitter.
- (b). Territorial song of adult male (Fig. 5a–b). This song may incorporate shrill notes and a harsh chatter, preceding terminal buzz. More emphases on lower frequencies than in song to female. Two males at their mutual territorial boundary alternate singing and pecking at one another.
- (c). Perch song of adult male (no spectrogram). Given by male perched in one spot in or near his territory. Long-continued, much varied song, often including besides the song buzz, various call notes of the species, both attraction and aggressive notes.
- (4). SONG OF JUVENILE MALE (Fig. 5c). (Sub-song of some authors). Much prolonged, continuous, formless and rather weak warbling song that lacks the typical adult song-buzz. Given by young males only, starting from about one month after hatching.

QUANTITATIVE ANALYSIS OF ANTITHETICAL VOCAL SIGNALS

Duration of different samples of the same call from the same bird in 15 different call-types or

TABLE 4. Different averages within five pairs of antithetical types of calls of the Village Weaver (*Ploceus cucullatus*). See Figure 6 for spectrograms of these calls.

Call-type	<i>n</i> calls ^a	Duration of notes (sec)	Dominant frequency	Loudness	Tonality
1. Young just fed (<i>tsuk</i>)	7	0.017	2.79	soft	not harsh
2. Hungry young (<i>squawk</i>)	10	0.108	3.3 ^b	loud	harsh
3. ♂ twitter to ♀ (pleasure)	12	0.040	3.07	soft	not harsh
4. High-intensity alarm (<i>kek!</i>)	6	0.066	5.69	loud	harsh
5. ♂ loud courtship call (<i>wheep!</i>)	8	0.220	2.50		not harsh
6. Distress cry (scream when seized)	9	0.249	2.78		harsh
7. Mild alarm (<i>chirp!</i>)	10	0.236	3.54		
8. Mild threat (<i>chuck!</i>)	10	0.090	2.54		
9. Parental attraction call (<i>choo</i>)	9	0.029	2.06	soft	not harsh
10. High intensity threat (<i>snarl</i>) to rival ♂	6	0.123	2.53	loud	harsh

^a Two birds recorded for call-types 1, 5, 6, and 9; one bird recorded for each of other call-types.

^b Only one sample for this dominant frequency.

vocal signals were highly correlated with each other ($r = 0.77$, $P < 0.001$), as were dominant frequencies for different samples of the same call (similarly, $r = 0.77$, $P < 0.001$). These results imply that the same call-types when sampled from the same bird are highly consistent. Different samples of the same call for loudness or tonality are subjective but similarly consistent (Table 4).

Some data supporting application of Darwin's principle of antithesis to vocal signals of the Village Weaver are presented here. Certain calls when paired as opposites in motivation and situation differ markedly in one or more of the physical components of calls: duration, frequency, loudness, and tonality (not harsh or harsh). Five pairs of clearly antithetical calls (10 calls in all) were analyzed from this point of view (Fig. 6, Table 4).

Calls 1 and 2. When a young Village Weaver has just been fed it gives a soft, pleasant *tsuk* call, but when hungry it utters a loud harsh squawk (Fig. 6). The squawk is about six times longer than the *tsuk* call, and its dominant frequency is much higher. Only one sample (3.36 kHz) of the dominant frequency of the hunger squawk is presented because of the difficulty of spectrographic measurement in this particular case, but this frequency is much greater than the mean dominant frequency (2.79 kHz) of seven samples of the *tsuk* given by a well-fed bird (Table 4). This comparison is strengthened by comparing the highest frequencies (8.7 kHz, $n = 7$ calls) in the *tsuk*'s of a well-fed bird with the highest frequencies (12.6 kHz, $n = 10$ calls) in

the squawks of a hungry bird which are again much higher.

Calls 3 and 4. A male attempts to attract a mate by displaying his most recently built nest to her and his efforts culminate successfully if the unmated female enters his nest. At that instant the male often utters a loud *wheep!* and flies about his nest and small territory. He then goes to the nest entrance and sings to the female within and frequently ends his song with a soft and pleasant twitter (Call 3, Fig. 6). This twitter is here treated as antithetical to the high intensity alarm cry (Call 4, Fig. 6). The alarm cry is harsh and longer in duration, and the dominant frequency is much higher than in the twitter (Table 4). The highest frequencies also average much higher for the high intensity alarm cry (14.0 kHz) than in the twitter (8.8 kHz).

Calls 5 and 6. The *wheep!* or loud courtship call (Call 5) given by a male when an unmated female first enters his nest is assumed to reflect "elation" and is here contrasted to the harsh scream of extreme distress (Call 6) given when a bird is seized and held (Fig. 6). In objective terms, there is not much difference in the duration or in the dominant frequencies of these two calls, but the distress cry tends to be higher and the second harmonic above the fundamental is strongest, whereas in the loud courtship call the fundamental is often the strongest as in Figure 2b. Both calls are loud and can be heard at some distance. The one strong difference between these two calls is in tonality (Fig. 6, Table 4). The loud courtship call has clear harmonic structure and sounds relatively pleasant to the human

CALLS OF VILLAGE WEAVER IN EACH PAIR OF SONOGRAMS BELOW ARE GIVEN IN OPPOSITE SITUATIONS AND DIFFER CONSIDERABLY IN THE ANTITHETICAL SOUND COMPONENTS LISTED BELOW EACH PAIR OF SONOGRAMS. Timescale 0.05 sec/unit.

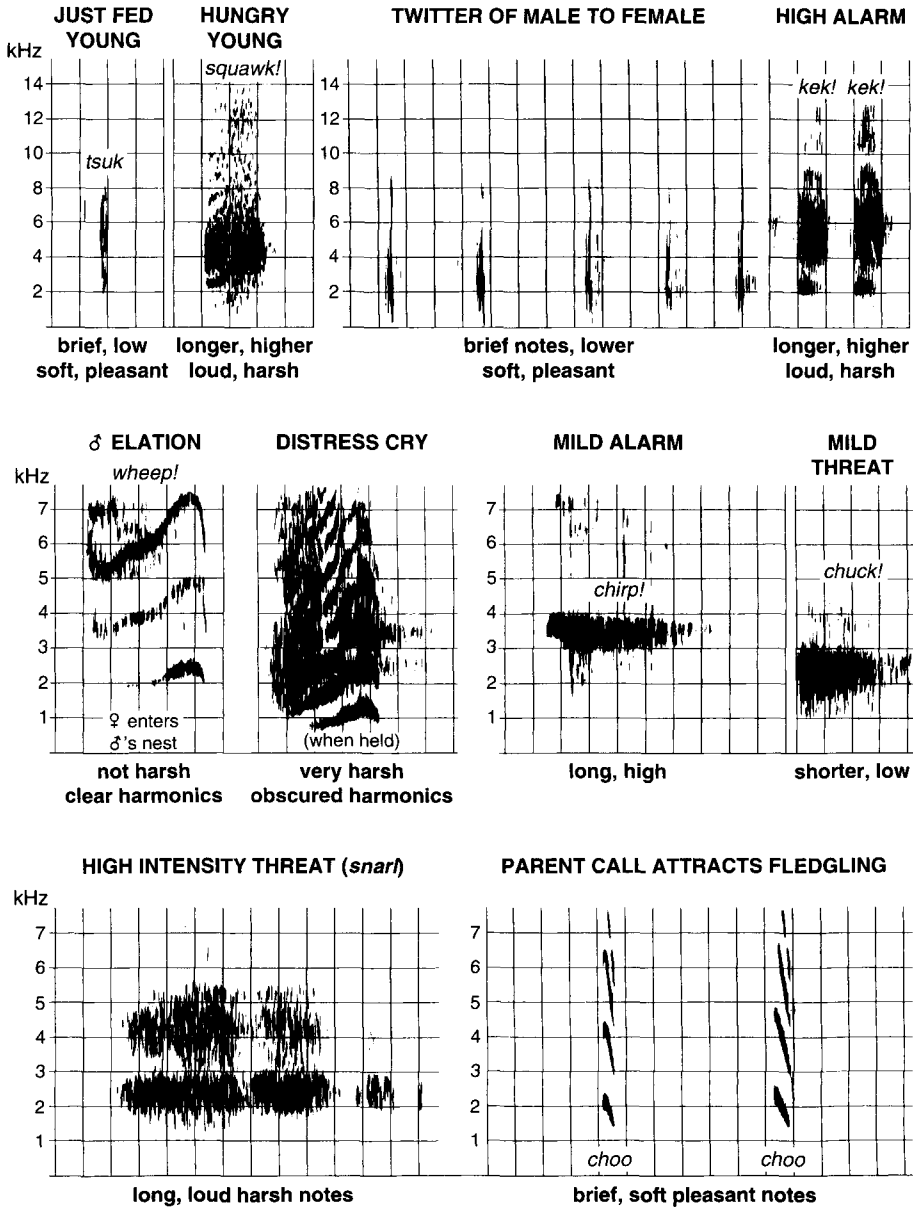


FIGURE 6. Spectrograms of five pairs of antithetical vocal signals of the Village Weaver. Wide filter.

ear, whereas the distress scream is very harsh and unpleasant.

The loud courtship call could also be considered to be antithetical in motivation to the high intensity alarm cry, but again differs primarily in that the latter call is very harsh. The high intensity alarm cry is much shorter in duration, but this may be because there is little or no time for a long drawn-out alarm cry when a hidden accipitrine hawk abruptly flies in for the kill. Natural selection may have shortened this call. Indeed, as we saw in central Africa in the race *P. c. grauri*, the weavers may sometimes instantly dive from the colony tree for cover in elephant grass without calling at all when a hawk flies in (Collias and Collias 1959).

Calls 7 and 8. The low intensity or mild alarm call (Call 7) which is a sharp *chirp!* is treated as antithetical to the low intensity or mild threat (Call 8) which is a deep *chuck!* (Fig. 6). The mild alarm call is of longer duration, but the calls differ primarily (Table 4) in that the dominant frequency of the alarm cry (3.5 kHz) is much higher than that of the threat call (2.5 kHz). The lowest frequencies of the low intensity threat call (1.4 kHz) also average well below those of the low intensity alarm cry (2.1 kHz), as do the highest frequencies (3.3 vs. 5.3 kHz). Both calls are moderately loud and differ little in tonality or harshness to the human ear.

Calls 9 and 10. The high intensity threat (*growl* or *snarl*) uttered while attacking a rival male is one of the most repelling calls given to a conspecific, whereas the parental attraction call, a soft *choo choo*, strongly attracts recently fledged young. Therefore, these two calls are treated as antithetical to each other. Three of four basic physical components of these calls are similarly antithetical. Compared with the soft parental *choo*, the snarl of the male is much longer, much louder, and is very harsh rather than pleasant to our ears. There is not much difference in the dominant frequencies (Table 4, Fig. 6).

DISCUSSION

VOCAL COMMUNICATION CODE OF THE VILLAGE WEAVER

The spectrographic classification of the vocal signals of the Village Weaver generally includes the presumed function of these signals. Function was ascertained from the common property in the various stimulus situations under which each

vocal signal was uttered. Different elements of duration, frequency, loudness, and tonality can be combined to produce specific vocal signals, in effect a code.

The different vocal signals can be analyzed into their basic elements by pairing together elements that seem to represent opposite states of motivation (Fig. 6, Table 4). This procedure accords with Darwin's (1872) principle of antithesis as applied to animal communication and presumed emotions. The essential function of antithesis in this sense is to reduce ambiguity in signaling. This can be made clear by classifying the elements of the vocal communication code of the Village Weaver as follows: (1) brief vs. long notes, (2) low vs. high frequencies, (3) soft vs. loud notes, and (4) clear distinct harmonic tones vs. harsh sounds.

The first element in each pair is often associated with a tendency to attract conspecifics; the second element of each pair often tends to repel conspecifics. This difference in behavior probably reflects an underlying difference in motivation.

Different calls have various combinations of these elements as was exemplified in the spectrographic key to the vocal signals, and these different elements may reinforce one another's effects. For example, the normal contact notes (*tsuk!* Fig. 1c) are (1) brief, (2) low-pitched, (3) soft, and (4) not harsh; all four elements help attract conspecifics and seem to signal a positive situation. In contrast, the high intensity alarm cries (*kek! kek!* Fig. 1e) are composed of four elements that are (1) longer, (2) with strong high frequencies, (3) loud, and (4) harsh. These cries frighten the birds as is shown by their strong avoidance behavior. The intensity of a signal may be increased by being repeated at a faster rate, or given more loudly. For example, the rate at which the defensive threat or mobbing call (a deep *chuck!*) is given, increases with proximity of a predator or person.

The next step in analysis of vocal communication could be to identify the vocal elements of the code with the activities of the syrinx (Suthers et al. 1999) and of specific elements and systems in the brain and neurosensory system (Hauser 1996). In songbirds, one set of syringeal muscles controls the fundamental frequency, while another set helps control timing of sounds, each set in the two separate sound sources in each bronchus. Sound is produced during expiration

which helps govern loudness and is modified by the resonance effects of opening and closing the bill (Suthers et al. 1999).

Comparisons with some other species. The vocal repertoire of the Village Weaver has many resemblances to that of closely related species. Crook (1969) summarized the general occurrence of 10 different vocal signals of the Village Weaver that are similar to those in many other species of weaverbird, and he points out that the terminal wheeze (buzz) in the song is generally typical of the subfamily of true weavers (Ploceinae).

Speke's Weaver (*Ploceus spekei*) of East Africa has been placed by taxonomists (Hall and Moreau 1970) in the same superspecies with *P. cucullatus* and *P. nigerrimus* (Black Weaver), both of which regularly incorporate long buzz notes in the song of the males. Unlike these two species, the male Speke's Weaver has a much longer song with a great variety of notes but without a long buzz (wheeze) in it. But the song may have a brief note that spectrographically resembles a very short buzz (Fig. 7a, arrow) and possibly represents an early stage in evolution of the long song-buzz or wheeze of related weavers. The other notes in the song of Speke's Weaver vary greatly, and the great difference in song from the other species no doubt serves for species recognition. This particular song (Fig. 7) was recorded from a male Speke's Weaver persistently singing in the same tree with a nesting colony of *P. cucullatus* in Nairobi, Kenya.

The same general functional and motivational categories of vocal signals as for the Village Weaver were previously shown to apply to 24 vocal signals of the Red Junglefowl (*Gallus gallus*) with the aid of a spectrographic key, the only other species so studied. Because of the intergradation of some of the calls in intermediate situations, no absolute size of vocal repertoire was fixed (Collias 1987). But the great majority of the calls are generally discrete and characteristically given in specific situations. Furthermore, the same elements in the general communication code as for the Village Weaver were shown to apply to the vocal signals of Red Junglefowl, attesting to the generality of the code, because the Red Junglefowl is a very different kind of bird. But the rise or fall in pitch of vocal signals is more definitely a pair of antithetical elements in the communication code of

the Red Junglefowl (Collias and Joos 1953, Collias 1987) than in the Village Weaver.

A rise or fall in frequencies within a vocal signal does not seem to be a very reliable or consistent indicator in the communication code of the Village Weaver. Within some calls, presumably associated with a somewhat similar stimulus situation, the frequencies rise (male wheep! call to unmated female entering his nest), whereas in other calls (male nest-invitation display call to unmated female) the frequencies fall.

There are species of birds with much more intergradation and overlap of different calls than in the Village Weaver, for example, the Brown Noddy (*Anous stolidus*), a tern. But even here, more or less discrete vocal signals exist. The basic unit of the vocal repertoire in this species is a broad-band click, less than 4 msec long. A note here is a group of clicks that can be resolved as a group by the human ear. In one of the most precise and quantitative studies of a bird's vocal repertoire, Riska (1986) showed for this species that the nine different calls she recognized that were used in different behavior contexts by the adults could be distinguished easily and significantly from one another by a combination of factors, including note length, internote interval, number of clicks per note, and whether the call consists of a single note or a series of notes. Three types of threat calls to intruders were all much louder than three types of soft and nonaggressive close contact calls between mates, and Darwin's principle of antithesis here thus helps solve the problem of intergradation of these signals seen in other respects.

MODIFYING FACTORS IN THE EVOLUTION OF VOCAL SIGNALS

Other selection pressures besides antithesis to avoid ambiguity may enter into the evolution of vocal signals of birds. Although these selection factors help diversify vocal signals in evolution in accord with the principle of adaptive specialization, they probably still stem from the basic code of communication. These modifying factors in evolution include such things as sex differences in vocal signals, difficulty in locating a signal source, urgency of the stimulus situation, use of other signals in a new context, relation to specialized life styles, species recognition, and selection for variability to aid individual recog-

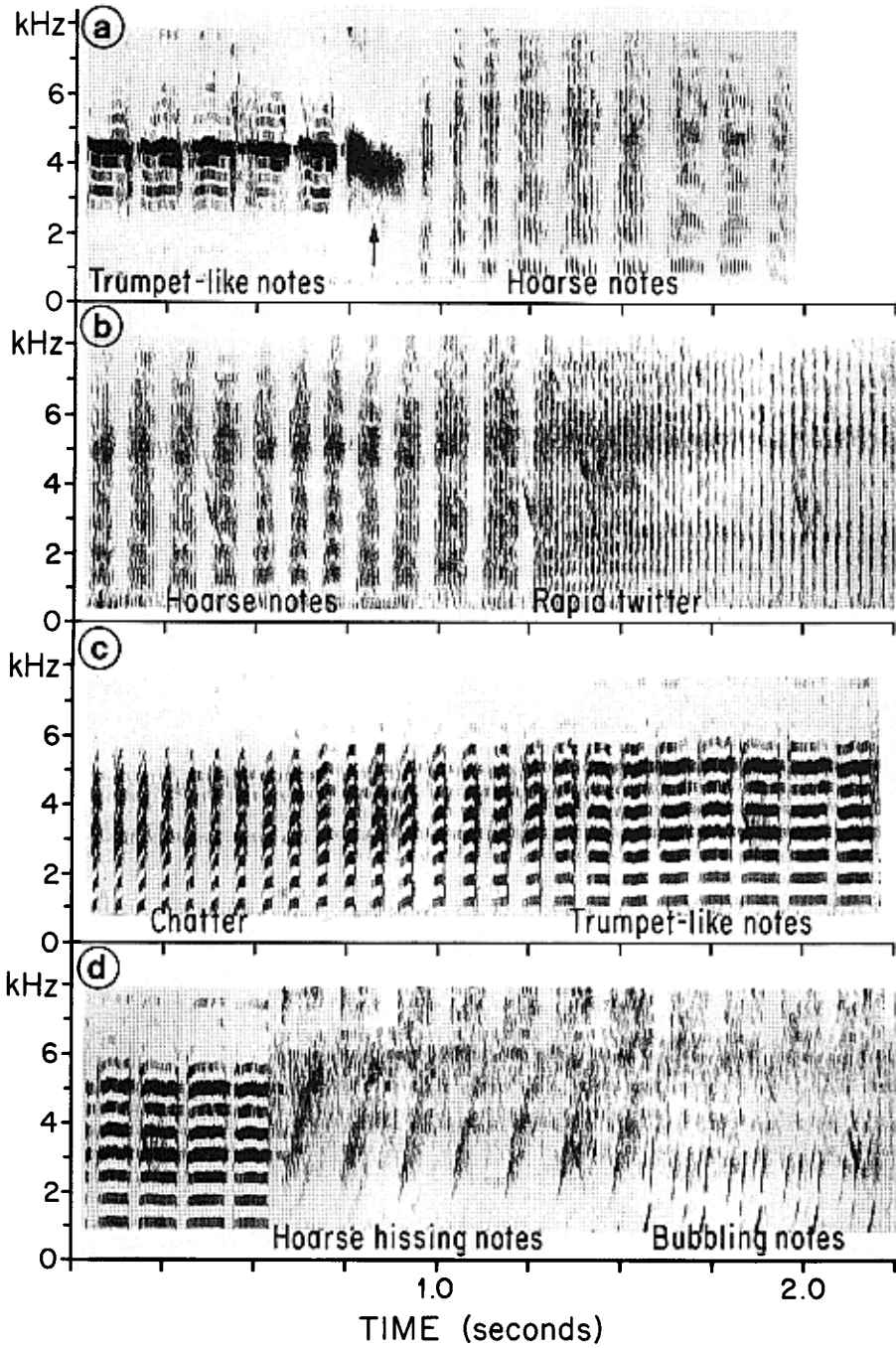


FIGURE 7. Spectrograms of prolonged song of a male Speke's Weaver (*Ploceus spekei*). Arrow points to a very brief buzz-like note. Note great variation in length and harmonic structure of component notes of song.

nitition. These modifying factors will be exemplified below.

Out of 26 vocal signals, the adult male Village Weaver gives a total of 20 calls, whereas 11 are given by the adult female. Vocalizations apparently given by only one sex include 12 by the adult male, 3 by the adult female. These sex differences are associated particularly with intense competition for mates by the male in this polygynous species. Vocalizations apparently restricted to the male include three different song types, four special courtship calls or a greeting to the female, two of the threat calls, one special call indicating nest material, and finally, the high intensity alarm call. The three special calls of the female include rejection or solicitation of copulation and a protest call when the male disturbs an incubating female.

In the Black-capped Chickadee, of 11 calls by adults as described by Ficken et al. (1978) and summarized by Smith (1991), 6 are given by both sexes, but in over 90% of instances, only the male sings and gives 2 specific threat calls, as well as the high intensity alarm call. Like the Village Weaver, only the female incubates in an enclosed nest from which she cannot see the approach of a predator and she relies on the male to act as sentinel. Skutch (1954) has described similar sentinel behavior by male Montezuma Oropendolas (*Gymnostinops montezuma*) of Central America in the nesting colonies in which the female alone incubates in a deep bag-like nest.

Discrepancy in number of calls by the two sexes is especially associated with competition for mates by the male. In the Prairie Warbler (*Dendroica discolor*) (Nolan 1978), 13 vocal signals are given by the adult male, 9 by the adult female. Only the male as a rule sings the two basic song types and gives two specific threat calls. Sex discrepancy in sound signals is even greater than in the Village Weaver in the Wire-tailed Manakin (*Pipra filicauda*) (Schwartz and Snow 1979), a lek species where the male in addition to several courtship and territorial vocalizations produces various mechanical sounds, so that eight sound signals are given by the male and only four by the female.

The hawk warning or high-intensity alarm cry in some species of small passerine birds is a very high-pitched and long continued tone that is very difficult to locate (Marler 1956, 1957, Brown 1982). In contrast, the high-intensity

warning call of the Song Sparrow is a high-pitched *tik-tik-tik*, i.e., a segmented or repetitive call that is easier to locate (Nice 1943). The common element in these two different types of alarm call is the high frequency of the calls.

High frequencies in alarm cries are often reinforced by harshness of the cries, as has been described here for the Village Weaver. Alarm cries also are often relatively long, but sometimes there may not be enough time for long alarm cries, as when a hidden accipitrine hawk abruptly flies in to attack. The notes of the Village Weaver's high intensity alarm cries (*kek!*) are relatively short (Fig. 1e), compared with the low-intensity alarm chirp (Fig. 1d).

Utilization of calls usually used in other contexts may be another factor influencing evolution of vocal signals (Tinbergen 1952). Female passerines of many species when soliciting copulation may imitate the begging notes of a baby bird. The loud "cheep" of a male House Sparrow (*Passer domesticus*) courting a female or advertising a nest site (Summers-Smith 1963) resembles the food begging note of a fledgling or nestling, as does the second note in the *look-see* courtship call of the male Village Weaver (compare Fig. 1b and 2c). The snake-like hiss given by the Black-capped Chickadee and other parids when surprised at the nest hole, usually by a predator, is a deceptive signal that probably helps deter predators and may be an adaptation for hole nesting (Ficken et al. 1978, Smith 1991).

Highly specialized calls related to a special life style have evolved in some species of birds. An example in the Village Weaver is the pleasant, humming series of brief notes (Fig. 2a) given by the male as he flies back to his nest while carrying a long strip of nest material before weaving it into his nest. It is a reasonable assumption that this call alerts and orients other males of the breeding colony to a good source of nest material. Another example of a specialized call from a bird with a totally different life-style is the *huddling* call of the Goldcrest (*Regulus regulus*), given as the birds come together to roost in warm physical contact at onset of the cold night (E. Thaler, in Cramp 1992). This species, the tiniest bird of Europe, may winter as far north as northern Scandinavia. The Village Weaver is ordinarily a resident species, unlike many other birds which undertake long migrations. According to Berthold (1993), a whole

range of migratory species possess special contact calls uttered only during migration.

Another selective factor in evolution is for difference in vocalization including call notes to facilitate identification or recognition of the species when in proximity to other similar species. Coutlee (1971), in one of the first such studies, made a comparative and spectrographic study of the entire repertoire of vocal signals of the Lawrence's Goldfinch (*Carduelis lawrencei*) and the Lesser Goldfinch (*C. psaltria*) in southern California. She found that threat, alarm, and distress cries are similar in the two species, but that the flock contact calls and courtship calls are the most distinctive for each species. The flock call notes of Lawrence's Goldfinch are much higher pitched and with a more narrow frequency range than the flock contact notes of the Lesser Goldfinch. These two species often flock together during winter months. Although the Village Weaver often nests in the same tree with other species of weaver, species differences in call notes have not been investigated in much detail.

The highly variable nest-invitational display calls (Fig. 2c) of male Village Weavers are, with few exceptions, individually very distinctive, both to the human ear and to spectrographic analysis. The young males develop this call from a variable chatter, and once developed the individual differences in the call remain constant from year to year (Jacobs 1979). Jacobs found that learning does not appear to play a role in the development of nest-invitation calls, unlike the case in the male's song. Four males taken from the nest at 10 days and reared together for their first year, each developed different and distinctive nest-invitational display calls, but their songs were very similar.

SONG DEVELOPMENT IN YOUNG WEAVERS

Much work has been done on the development of song in young songbirds (Baptista and Gaunt 1994, 1997, Catchpole and Slater 1995), which cannot be reviewed here. As in the Village Weaver, many songbirds have a juvenile song (subsong) that begins as a soft continuous warbling about the time the young bird leaves the nest or shortly after (Nice 1943). As normal development proceeds in the Song Sparrow (Nice 1943), or in the Village Weaver (Jacobs 1979), the juvenile warble becomes segmented into discrete notes with periods of silence between them. Some adult-type call notes may be incor-

porated into the juvenile song of the Village Weaver, as is known to be the case in some estrildid finches in a related family (Baptista 1996).

Young songbirds after dispersal to a potential breeding site may copy songs of their territorial neighbors (Baptista and Gaunt 1997). Indigo-birds (*Vidua chalybeata*), viduine finches related to weavers, often copy the songs of older (adult) males having the greatest mating success (Payne 1985).

In the only experiments on song development in the Village Weaver, Jacobs (1979) showed for young males taken from the nest at 5–10 days of age and hand-reared that the most characteristic feature of the song, the length of the song-buzz is learned, and learning the details of the complex pattern of introductory notes to the song from other birds reveals a remarkable ability for time resolution of vocal signals (less than 0.01 sec), far exceeding human capacity. At the age of 11 months, the young males in two groups of five were placed in separate outdoor aviaries and allowed to breed. Interestingly, within each group, all the young males copied precisely the song of the most dominant male (cf. also Baptista and Gaunt 1997). In contrast, Zebra Finch (*Taeniopygia guttata*) males learn their songs from the male parent (Zann 1990). The difference in the species may relate to the fact that on fledging, young weavers leave with the mother while the father remains in the colony tree.

ACKNOWLEDGMENTS

For help in care and observation of our weaverbird colony at UCLA and for stimulating discussion, I thank many research assistants and colleagues, including especially during the later years of the study: Catherine H. Jacobs, Cathleen Cox, and Florence McAlary McFarland. My wife, Elsie C. Collias, helped in every aspect of the study, particularly in raising many young Village Weavers, and also in valuable comments on the manuscript. Greg Budney and Robert Grotke of the Cornell Library of Natural Sounds, and W. E. Lanyon, helped greatly with advice on sound recording equipment. Peter Narins helped with the interpretation of spectrograms. I thank him for use of his DSP Sona-Graph Model 5500 and Huong Nguyen for operating it. Narins also made helpful comments on the manuscript, as did Luis Baptista. Mike Eng and Diane Riska helped maintain our earlier model of Sona-Graph. I thank Jeffrey Gornbein for help with the quantitative analysis, Margaret Kowalczyk for artwork, and Bonnie

Phan for typing. The research was supported over the years by grants from the National Science Foundation and from the Research Committee of the UCLA Senate.

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