*The Condor* 89:510–524


# THE VOCAL REPERTOIRE OF THE RED JUNGLEFOWL: A SPECTROGRAPHIC CLASSIFICATION AND THE CODE OF COMMUNICATION[1]

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*Abstract.* This report attempts to describe objectively the complete vocal repertoire and the vocal code of the Red Junglefowl (*Gallus gallus*), most probable wild ancestor of the domestic fowl. An unconfined color-banded flock was watched over a period of 6 years at the San Diego Zoo. The general behavior and vocalizations are essentially the same in Red Junglefowl and the domestic fowl. Different vocal signals can be recognized by their sonograms and by the common element in the various situations in which a signal is given. Twenty-four vocal signals are described but because of intergradation between some signals and between different situations no absolute size of vocal repertoire can be fixed. A spectrographic (structural) key to the vocal signals of the Red Junglefowl is given and with the sonograms should enable one to identify the typical calls.

Different elements can be combined to produce specific vocal signals, in effect a code. Brief, soft repetitive notes of low frequency are attraction calls. Loud harsh sounds with high frequencies are alarm cries. Harsh sounds emphasizing low frequencies are threat sounds. These rules hold for many other birds. Junglefowl also have special calls that appear to indicate well-being, or mild disturbance and frustration. The evolution of the vocal signals of the Red Junglefowl is discussed in relation to Darwin's (1872) three principles of communication and to modern ethology.

*Key words: Red Junglefowl;* Gallus gallus; *domestic fowl; vocal signals; vocal coding; sound spectrogram; sonogram; Darwin.*

## INTRODUCTION

This report attempts to describe objectively the vocal repertoire of the Red Junglefowl (*Gallus gallus*). A major goal is to show how the vocal signals can be analyzed into a basic code of communication. There have been preliminary attempts of this sort (Collias 1960, Morton 1977) but none have dealt with the entire vocal repertoire of a species. Some two dozen calls of the Red Junglefowl are here described and analyzed. The vocal repertoire of this species in its undomesticated form has not been described before in any comprehensive way with the aid of the sound spectrograph. I also discuss the evolution of the vocal signals.

Charles Darwin (1875) gave a great deal of evidence for his conclusion (p. 258) that all the breeds of domestic fowl of his day probably descended from the Red Junglefowl. William Beebe (1926) and Jean Delacour (1977), in their books on the pheasants of the world, agreed. The domestication of the Red Junglefowl appears to be still going on in Southeast Asia (Collias and Saichuae 1967). So far as the species-specific crowing is concerned, in the domestic breeds so far analyzed the voice resembles that of the Red Junglefowl (Miller 1978). It would be very difficult to show that no genes whatsoever have entered the gene pool of any breeds of domestic fowl from one of the other three species of junglefowl, but there seems to be no positive or conclusive evidence for the polyphyletic theory (Crawford 1984). In matings of domestic fowl with the four species of junglefowl, only those with the Red Junglefowl are fully viable and reproduce normally (Crawford 1984).

The Red Junglefowl is of special interest as the wild ancestor of most if not all breeds of the domestic fowl, which is the world's most studied bird. The vocal repertoire of the two is essentially the same as can be seen by comparing the results described here with earlier studies of the domestic fowl (Collias and Joos 1953, Baeumer 1962, Konishi 1963). Wood-Gush (1971) compared studies by several authors of the vocal signals of the domestic fowl and pointed out that it is not always clear which calls are the same as described by different authors. He emphasized

[1] Received 10 June 1986. Final acceptance 10 February 1987.

the need for more objective and detailed descriptions of the calls and of the stimulus situations.

The sound spectrograph made possible a truly objective study of animal sounds. The first announcement of the invention of this machine by the Bell Telephone Laboratories had examples of sound spectrograms (sonograms) for songs of songbirds (Potter 1945). One of the first reports by the engineers describing the sound spectrograph also showed a sonogram of crowing by a rooster (Koenig et al. 1946:45). The first spectrographic study of the vocal repertoire of a bird was of the domestic fowl (Collias 1952, Collias and Joos 1953).

Different vocal signals may often be identified by the situation in which they are given (Collias 1960, Konishi 1963), but caution is needed because the same signal may be given under a variety of specific situations. One must seek the common element in different situations or circumstances to get at the essential message and meaning of the signal (Collias 1952). Smith (1977) has made a useful distinction between the message of the sender and its meaning to the receiver. I use the term "signal" to refer to the message of the sender. Since the message is less modified by differences in ecological or behavioral context, or by learning, than is the meaning to the receiver, it is more useful for a basic classification of the vocal repertoire. Konishi (1963) found that domestic fowl deafened within 2 days of hatching still developed the normal repertoire and forms of vocalization.

One signal may grade into another, particularly under intermediate stimulus conditions. Statistical description of the variability in a number of samples of each call may help to distinguish and characterize the different calls. Using special computer techniques, Riska (1986a, 1986b) recently made one of the most precise studies of this sort on the vocal repertoire of the Brown Noddy (*Anous stolidus*) a species of tern having many graded vocalizations.

One can also attempt to analyze vocal signals, including graded signals, by simply taking any two calls with opposite structural characteristics as revealed by their sonograms and noting correlations with differences in apparent motivation of the signaler, as well as with differences in response of the receiver. This is an application of Darwin's (1872) principle of antithesis in which ambiguity is reduced between two signals of opposing motivations by evolving opposite properties of signals. Furthermore, by grouping the sound parameters in the structure of the various calls into antithetical pairs, one often finds in the Red Junglefowl apparently antithetical motivations signaled within such pairs. These different sound parameters are basic elements that can be combined in various ways to produce the different social signals, in effect a code. A preliminary report was presented at the 19th International Ornithological Congress, Ottawa, Canada (Collias 1986), and will be elaborated here.

In considering the evolution of the vocal signals of the Red Junglefowl, I have made use of Darwin's (1872) three principles of "emotional expression." Animal signals usually reflect differences in mood or motivation, and Darwin's book is still useful to ethologists. He often anticipated modern views, and his ideas helped form the original basis of modern views. Some of the many complexities in the evolution of animal communication have been summarized and related to modern ethological theory by Marler (1977).

## STUDY AREA AND METHODS

In a field study of the Red Junglefowl in its native home in India and Southeast Asia (Collias and Collias 1967, Collias and Saichuae 1967), we found the birds to be very wary and difficult to approach. They are hunted almost everywhere they occur. We found it much easier to observe details of behavior in the protected and unconfined population of Red Junglefowl which roams freely over the 49 ha of the San Diego Zoo in southwestern California. Over 2,000,000 people a year visit this zoo and the birds are so accustomed to people that some junglefowl will take food from a person's hand. For adequate study of the vocal repertoire of birds it is important to be able to observe them repeatedly at close range in all aspects of their life. While there are disadvantages in trying to record vocalizations of free-ranging birds particularly because of the prevalence of extraneous background sounds, it is important at first to let the birds control their own lives to get at all the normal vocal repertoire.

We saw no really basic or qualitative differences between the behavior of the birds in the zoo and in their native wild state. Kruijt (1964) has described the social behavior of captive Red Junglefowl with special reference to ontogeny, a topic not considered here. In appearance the zoo birds generally meet the criteria of Delacour

(1977) for wild vs. domestic Red Junglefowl, since the great majority of individuals have dark legs and the cocks moult their neck hackles in the summertime. The Red Junglefowl in the San Diego Zoo are descended from some 15 birds of the Indian race (*G. g. murghi*) purchased in 1940 from a dealer in Calcutta, and 12 birds from the Burmese race (*G. g. spadiceus*) purchased in 1941. These birds were all turned loose in the zoo in 1942, and the current population is descended from them (Lint 1971).

The different flocks in the zoo generally roost in the same trees the year round. During the day they rarely range more than 50 m from their roosts. Each flock is organized into a peck order. The dominant cock in the flock associates with one to several hens and usually keeps other adult cocks away from the hens but often tolerates the young cockerels. Details of behavior in this population are given elsewhere (Collias et al. 1966, Collias and Collias 1985). During a 6-year period (1981 to 1986) we observed one large flock (about 15 to 20 adults) and neighboring birds at 1- to 2-month intervals, visits being more frequent during the main breeding season of March to June. During each of these visits we generally watched the birds over a period of 3 days. We color-banded all the individuals in the flock selected for special study, except for a very few that were identified in other ways. The individual cocks were also recognized by their distinctive combs. To capture the birds for banding they were driven into a mist net or individually baited into a noose laid on the ground that was then drawn about their legs.

The vocalizations of the birds were recorded on a tape recorder, either a Uher 4000 Report-L, or a Sony TC 150 cassette recorder. I then analyzed the recordings on a Kay Elemetrics Corporation Sona-Graph 6061B. Sonograms were made of each call at normal speed using both wide band (300 Hz) filter for more precise time resolution and the narrow band (45 Hz) filter for better resolution of frequencies. The wide filter was especially useful for brief repetitive notes, the narrow filter more useful for the longer calls. Generally, the Sona-Graph was set to record frequencies in the 80 to 8,000 Hz range, but where calls had very high frequencies, the 160 to 16,000 Hz range was also used to detect the upper limits. The Sona-Graph shows differences in amplitude of sound somewhat crudely by different shades of gray, the louder sounds being darker. Where greater precision in measurements of intensity of sound was desired, I used the amplitude display accessory unit of the Sona-Graph, giving a curvilinear depiction of variations in intensity of sounds.

In general, a note was defined as a sound that at normal intensity makes a single continuous impression in time on the sonogram; a note is not defined here as necessarily a musical tone since many bird notes are unmusical. The harmonics of a musical note are considered part of the same note. Calls are made up of one or more notes.

## RESULTS

The calls of the Red Junglefowl will be described along with sonograms and the situations or context in which they are given. I then give a spectrographic key for the identification and structural classification of these calls.

### DESCRIPTION OF CALLS

From the common element in the different situations in which a particular vocal signal is uttered I attempted to deduce the significant aspect or general situation that stimulates that vocal signal. At the same time, from the associated behavior, one can infer or conjecture the motive or "mood" that causes the bird to give a particular signal.

1. *Chick calls expressing insecurity or security* (Fig. 1). In chicks of the domestic fowl, what we would interpret as "distress" is the only common element between the various stimulus situations that excite loud peeps or chirps with descending frequencies, for example, being lost, cold, hungry, or frightened (Collias 1952), whereas relief from these presumably distressing situations excites *pleasure notes* that tend to swing upward in pitch. The same principle holds for Red Junglefowl chicks. Here again, *distress cries* (Fig. 1a) are characterized by descending frequencies while *pleasure notes* (Fig. 1b) emphasize ascending frequencies. These two calls may grade into one another under intermediate or less extreme stimulus situations, leading toward a *chevron* type of note, for example when chicks are being brooded (Fig. 1c). In the *chevron notes,* both ascending and descending frequencies are present to varying degrees. Distress cries often have some stridency or smudging of frequencies, especially in older chicks. *Pleasure notes* are more likely to

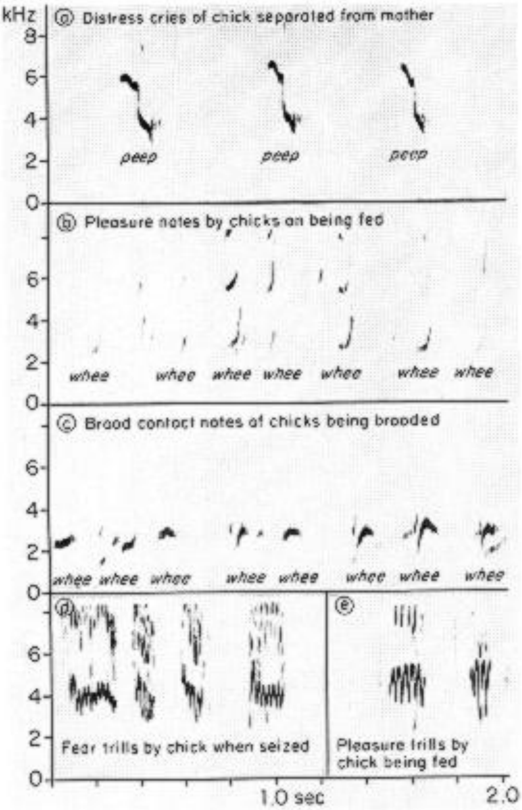


FIGURE 1. Sonograms of chick calls expressing insecurity or security. All sonograms in this figure were made at wide filter (300 kHz). Relative amplitude is indicated by darkness of marks.

show clear harmonic structure than are distress cries.

Unlike most vocalizations of adult junglefowl, the calls of chicks consist of parts of cycles or a series of complete cycles on a sonogram. In the *fear trill* (Fig. 1d) given when a chick is seized or threatened by a hand suddenly moved toward it, successive cycles mostly trend downward in average frequency. In the *pleasure trill* (Fig. 1e) by a chick being fed, the successive cycles tend to rise in average frequency. To the human ear the *fear trill* sounds startled, louder, and "worried," whereas the *pleasure trill* sounds rather pleasant and of lower intensity. *Fear trills* contain some rather irregular and some very high frequencies, going up to 16 kHz as seen in sonograms (not shown) of recordings at half normal speed when they also sound quavering to the human ear. Pleasure trills reach only about 9 kHz and also tend to have a more regular cyclic pattern.

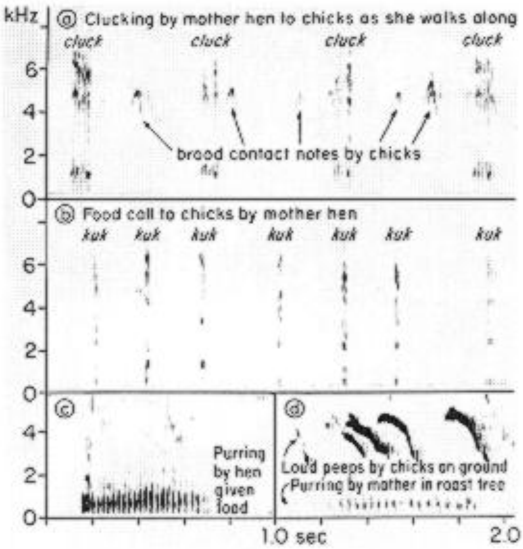


FIGURE 2. Sonograms of attraction calls of a hen to chicks (wide filter).

2. *Attraction calls of a hen to chicks* (Fig. 2). These calls consist of soft, brief, repetitive notes. Each note may have a wide spread of frequencies and includes strong low frequencies. The *clucking* by a broody hen as she walks along (Fig. 2a) with ruffled feathers stimulates her chicks to follow her. Each cluck usually consists of two paired notes differing in this respect from the single unpaired notes of the hen's *food call* (Fig. 2b) to her chicks. The notes of the *food call* are given at a more rapid and irregular rate than are *clucking notes* and attract chicks quickly to any bit of food the hen has discovered. She picks up and drops the food before the chicks and may break up large bits of food for them.

The *purring call* (Figs. 2c, d) of the hen consists of low intensity, very rapidly repeated pulses of sounds with emphasis on the lower frequencies. The hen may purr after she flies up to the roost tree at dusk. She is stimulated to purr by the *distress cries* of her chicks left abandoned on the ground. The *purring call* attracts the chicks which move toward this sound. This call probably helps train the chicks to follow their mother up into the safety of the roost tree after their wings have developed sufficiently to do so.

3. *Attraction calls of a cock to hens* (Fig. 3). The emphasis of these low amplitude, brief, repetitive notes or pulses is generally on the lower frequencies. The *food call* by a cock to a hen

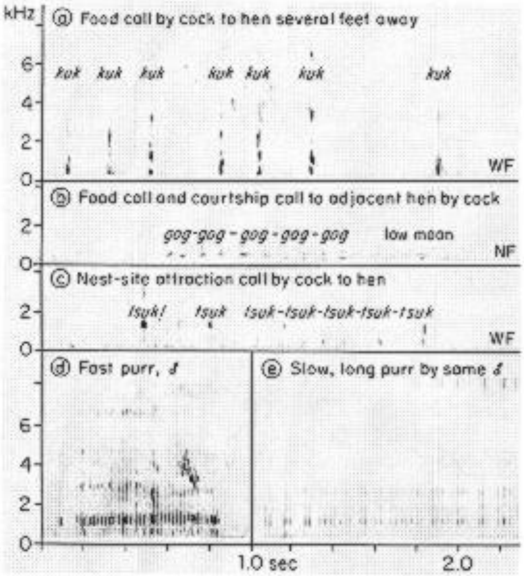


FIGURE 3. Sonograms of attraction calls of a cock to hens. All sonograms at wide filter except for Panel b (narrow filter, 45 kHz).

several feet away (Fig. 3a) has an excited quality and often draws the hen to the cock, whereupon his notes then become deeper (*gog-gog-gog* in Fig. 3b) and more rapid—almost stuttering. He may end this call with a low moan. The same call is used by the cock when courting hens by dropping and fluttering one wing as he partly circles the hen. He also courts a hen by calling her to a potential nest site with a rather similar rapid series of brief low-pitched notes (Fig. 3c), as well as by a *purring call* in which the rate of pulse delivery varies considerably (Fig. 3d, e). Stokes (1971) has made a special study of parental and courtship feeding in Red Junglefowl at the San Diego Zoo.

4. *Calls of well-being or contentment by adults* (Fig. 4). The sonograms of these calls are reproduced at narrow filter to better show their considerable harmonic structure as well as emphasis on lower frequencies. The individual notes of each call are somewhat longer than the notes of the adult attraction calls shown in Figures 2 or 3. *Contentment notes* by cocks or hens can often be induced by feeding, and particularly in the hen may develop into *singing* which consists of still longer notes uttered at a more rapid rate (Figs. 4a, b, c). *Singing* is probably the same call as the *prelaying call* of the domestic hen, described by Wood-Gush (1971:42, 44). A hen ex-

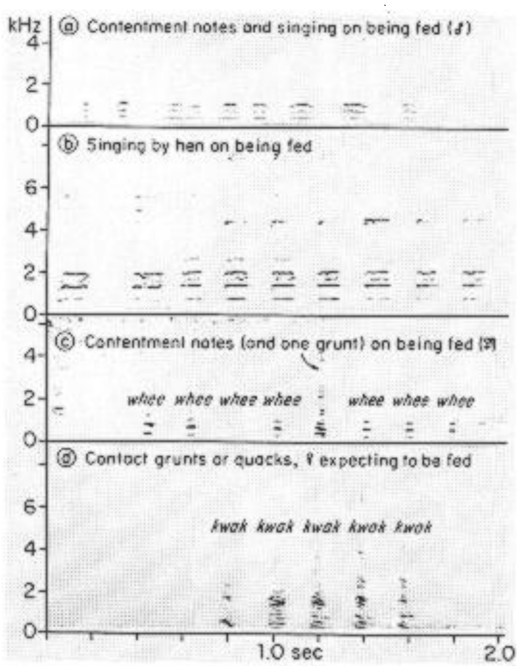


FIGURE 4. Sonograms of adult calls of well-being or contentment (narrow filter).

pecting to be fed may utter low *contact grunts* or quacking sounds (Fig. 4d) which differ from the contentment notes and singing by having less clear tones especially obscured in the higher frequencies. These notes probably function as adult social contact calls.

5. *Adult calls of mild disturbance* (Figs. 5a–e); *cry of pain when pecked* (Fig. 5f). Under various conditions with some element of disturbance Red Junglefowl utter a faint straining call or drawn out *whine* or *moan.* When a very hungry hen is shown but not given food she may utter a low *moan.* This sound consists of long, drawn out, wavering tones (a). A cock may give a *whine* of apparent frustration when offered a peanut that the observer then fails to release when the bird attempts to take it (b). A subordinate cock may *whine* as he walks away from a dominant aggressor. This *whine* may be higher-pitched in low status males (c) than when given by retreating males of high status (d). A *whine* of presumed discomfort was given by one cock when it started to rain, the *whine* soon shifting to higher frequencies apparently with increasing discomfort (e). All of these whining or moaning calls are prolonged tones of only one or a few narrow frequency bands that often waver irregularly or

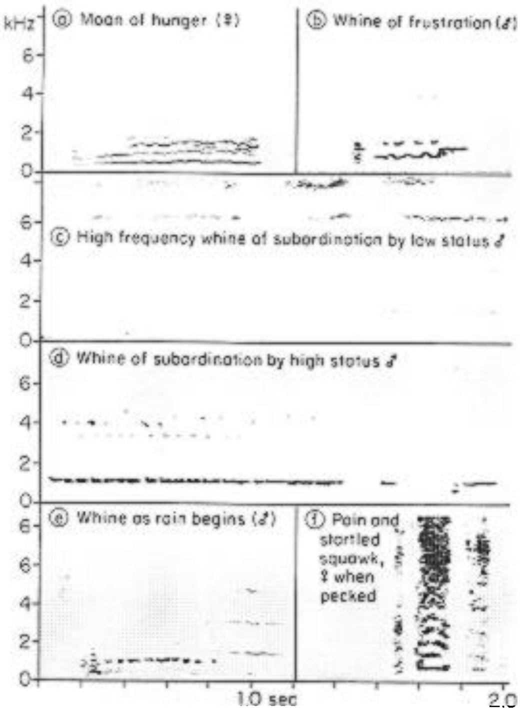


FIGURE 5. Sonograms of calls of mild disturbance by adults (a–e), and cry of pain by a bird when pecked (f) (narrow filter).

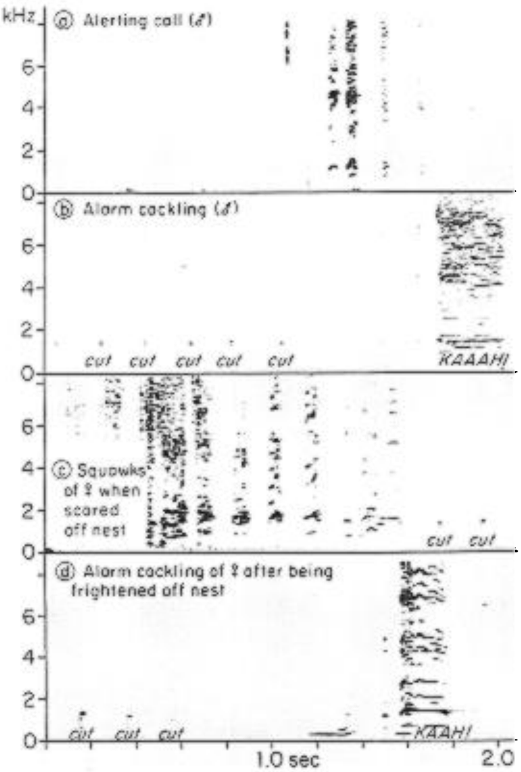


FIGURE 6. Sonograms of warning calls announcing a predator on the ground or perched (narrow filter).

are partly broken up into irregular segments on the sonogram. A cock might also *whine* and tilt his head to peer up when a relatively harmless Red-shouldered Hawk (*Buteo lineatus*) soars high overhead.

Figure 5f shows the sonogram of the startled *squawk of pain* given by a hen suddenly pecked by another. This call differs from the *whine* in that the component notes are shorter, have an abrupt onset and ending, and cover a very wide frequency range. This call is a harsh sound which stresses the higher frequencies. A harsh call is defined spectrographically as one having a wide spread of frequencies combined with harmonic streaks (Collias and Joos 1953). This call is moderately loud, not nearly so loud as the *distress* cry given by a captured bird, or *alarm* cries to predators, but spectrographically it resembles these calls rather than the *whine.*

6. *Warning calls announcing a predator on the ground or perched* (Fig. 6). These harsh *cackling* cries consist of shorter more abrupt notes than the *whine* and have a much wider range of frequencies. They may be accompanied by flying up into the safety of trees. The sudden *alerting call* (a) given on detecting a predator when the danger is not very imminent is not nearly so loud as other warning cries; the intensity of its few and brief notes quickly falls off. The typical ground predator warning (b) consists of sharp, scolding *cut-cut-cut* notes rhythmically repeated that often precede a loud, brassy, high-pitched squawk or "kaah!" Figures 6c and d show four different kinds of notes given in rapid succession by a hen frightened off her eggs: two very high explosive *hisses* succeeded by several loud *cackling* squawks as the hen abruptly left her nest half-running and half-flying, followed by a series of sharp *cut-cut* notes culminating in the very loud harsh kaah! of intense alarm while the bird holds a tense alert posture with head held high. The last note has many wavering or broken harmonic streaks.

7. *Warning announcing a flying predator* (Figs. 7a–c); *distress cries of a captured bird* (Fig. 7d). Dave Rimlinger (pers. comm.) in the course of his daily duties at the zoo has seen a Cooper's

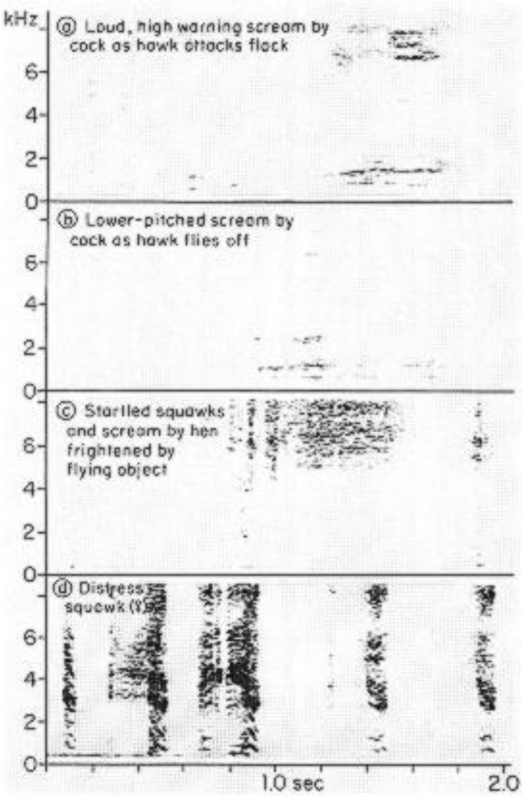


FIGURE 7. Warning announcing a flying predator (a–c), and distress cries of a captured bird (d) (narrow filter).

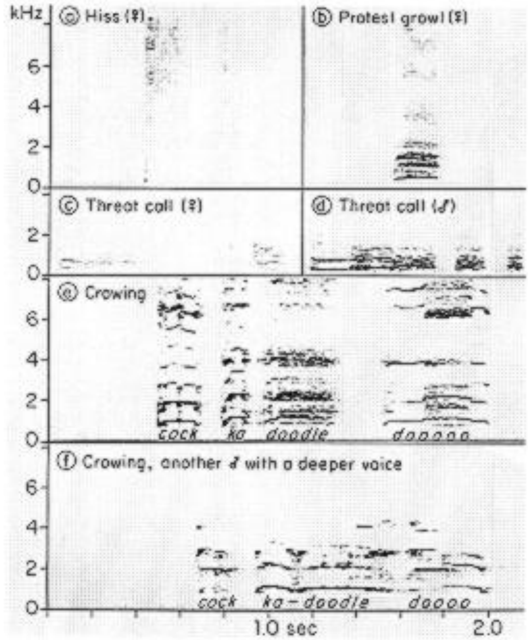


FIGURE 8. Sonograms of aggressive calls (a–d), and of crowing (e–f) by two cocks illustrating marked individual differences (narrow filter).

Hawk (*Accipiter cooperii*) capture young Red Junglefowl, and we have seen a number of unsuccessful attacks. The call warning of a flying predator has a more gradual onset than the explosive ground predator warning. A Cooper's Hawk flying in to attack demands instant response from the junglefowl. A very loud, high-pitched warning *scream* by the cock stimulates the hens and chicks to at once run to cover and hide. The cocks stand their ground in an alert, tense posture with the head high. The low- and high-frequency components of the particular call shown (a) are not harmonically related. The low-frequency component perhaps incorporates an element of defensive threat, added to the fear element in the strong high-frequency component. Since a bird's voice has two independent sound emitters (Koenig et al. 1946, Greenewalt 1968, Stein 1968), birds could readily signal aggression and fear at the same instant. When the hawk flew away in this instance after an unsuccessful attack the cock gave a *scream* or *roar* that was largely restricted to the lower frequencies (b), reminiscent of typical threat calls (Fig. 8) but much louder. To the smaller, less dangerous Sharp-shinned Hawk (*A. striatus*) flying near their roost, or in a "false alarm" to Mourning Doves (*Zenaida macroura*) suddenly flying overhead, the cocks may merely utter a rather low-pitched *roar* which is not very loud, perhaps a defensive threat. When a dangerous hawk or eagle is merely perched in a tree nearby, the junglefowl give the same cackling alarm cries they give to a ground predator. The cocks are much more likely to give the warning to aerial predators than are the hens. However, when a cloth was thrown into the air above a hen, right after a few startled squawks she uttered a loud high-pitched *scream* (c).

Very loud and harsh *distress squawks* (d) are given by a captured bird, for example by a hen held by her legs upside down by the observer. These distress cries differ from the cry of pain by a pecked hen (Fig. 5f) in that the component notes are much louder and longer, and the call is given repeatedly. Some of the notes are irregular with broken or wavering harmonic streaks (d). Both types of call have an abrupt onset and emphasize high frequencies, rising to as much as 16 kHz (as shown by recording at half-speed).

8. *Aggressive calls* (Fig. 8). The sudden *hiss* (a) by an incubating hen when disturbed is an unvoiced sound with a wide and uniform spread of frequencies lacking the harmonic or tonal streaks of harsh calls. A *hiss* is produced by strong expulsion of air from the respiratory system and is probably one of the most primitive sound signals of terrestrial vertebrates (Collias 1960). The harsh *protest growl* of a hen is also a defensive threat, and is especially given by a broody and nonreceptive hen with chicks when approached by a cock with sexual interest, or when disturbed by a person. Like the harsh threat sounds it is a fairly long note with low frequencies predominating and is not nearly so loud as are most alarm cries. The sonogram (b) made with narrow filter appears mostly as a system of vague horizontal bands. In a sonogram made with the wideband filter (not illustrated) the same sound appears as a series of pulses which being combined with noise, gives a rough, growling impression to our ears. The *low threat* uttered by a dominating hen (c) to a subordinate competing for food, closely resembles the threat sound of a cock (d) but usually is less intense and less prolonged. Neither of these threat sounds is at all loud; both are harsh sounds of relatively low frequencies. The head is often held rather low and the beak tends to be directed toward the opponent while a bird is uttering a threat. The threat may be followed by a peck. Occasionally, as before mentioned, cocks give what seems to be a much louder threat, when apparently threatening a hawk that is flying away (Fig. 7b).

9. *Crowing. Crowing* (Figs. 8e, f) of the Red Junglefowl is a loud, complex vocalization, usually with three or four notes or four energy peaks, that advertizes the presence of a cock on his territory. A cock decisively beaten in a fight ceases to crow near the dominant cock. Two cocks may engage in *crowing* duels at territorial boundaries, or when competing for a hen. The voices of different cocks may vary greatly in pitch, in number and length of notes, and in clarity of tones (e, f; Miller 1978), and it seems probable that crowing serves for the recognition of different individuals. A dominant cock will respond to *crowing* by his chief rivals even when they are out of sight on the periphery of his territory, but he will generally ignore *crowing* by the young subordinate cockerels that he tolerates in his flock. While *crowing* has been interpreted as an aggressive call, its sonogram indicates considerable complexity and it may have other functions as well. Possibly, like the song of song birds, *crowing* attracts females as well as advertising ownership of a territory to other males. *Crowing* has considerable harmonic structure.

*Crowing* is closely correlated with a stereotyped sequence of head movements. While holding the head horizontal the cock stretches his neck up and forward and utters the first note, then he sways his head and neck backward while giving the second and third notes, the latter being the loudest of the notes; finally, he swings his head and neck forward again while giving the fourth and final note. Notes 2 and 3 may be discrete in one cock (e), united into one note in another cock (f). It has been shown in the domestic cock that the trachea as a unit is strongly retracted downward by tracheal muscles during *crowing* (Brackenbury 1982). The significance of the correlations of tracheal and syringeal movements and changes in air sac pressure with the externally visible movements of the head and neck does not seem to have been studied.

Figure 9 illustrates the species-specific characteristics of *crowing* by the four species of junglefowl, the Red Junglefowl in the Siwalik foothills of the Himalayas in northcentral India, the Gray Junglefowl (*G. sonnerati*) at the Mt. Abu Game Sanctuary in western India, and the Ceylon Junglefowl (*G. lafayettei*) in Wilpattu National Park, Sri Lanka (Collias and Collias 1967). The *crowing* of the Green Junglefowl (*G. varius*) of Java was kindly recorded for me in his aviaries in southern California by Mr. Paul Schneider. The sonograms show how *crowing* of the four species characteristically differs in number of notes, length of *crowing,* accent on different notes, structure and pitch of notes, and interval between notes.

The crows of Red and Gray junglefowl shown here (Fig. 9) each has four notes, but there is most energy in the third note of the Red, in the second note of the Gray. The Ceylon Junglefowl has a three-note crow which also differs from the other species in having a long interval between the first and second notes. The Green Junglefowl has a two-note crow, higher pitched than the *crowing* of the other species.

The verbal description of the *crowing* given on the sonograms are from different authorities: Gray and Ceylon by Baker (1928), and Green by Beebe

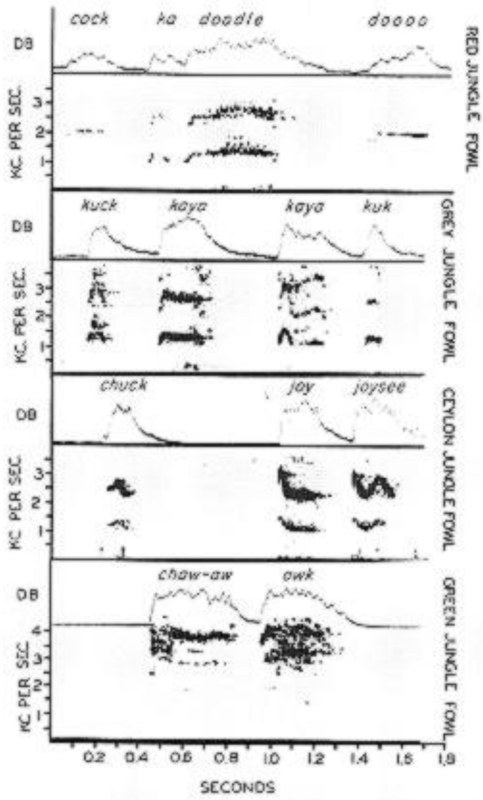


FIGURE 9. Sonograms of the species-specific crowing by the four species of junglefowl, the Red (*Gallus gallus*), Gray (*G. sonnerati*), Ceylon (*G. lafayettei*), and Green junglefowl (*G. varius*). Sonograms made at narrow filter. Amplitude display in decibels.

(1926), and are merely mnemonic aids. The traditional English rendition, *cock-ka-doodle-dooo* of the Red Junglefowl is transliterated as *Er-er-erk—er!* by Beebe (1926), who, in agreement with our sonogram (Fig. 9) states "the accent was all on the third note."

## A SPECTROGRAPHIC KEY TO RED JUNGLEFOWL CALLS

This artificial key, combined with the preceding detailed descriptions and the labelled sonograms for comparison, should enable one to identify the typical calls. It is an attempt to make the calls comparable for different observers since the key relies entirely on the sonograms of the vocal signals. Since the key is purely structural, the description of each call is essentially independent of the stimulus situation. One can then compare the common elements in the different situations under which each call is given in seeking the essential message encoded in each call.

I. (Fig. 1) *Chick calls.* Consist of successive cycles or parts of cycles on sonogram.
  A. Mainly descending frequencies, partial (*distress cries*) or complete (*fear trills*) cycles.
  B. Mainly ascending frequencies, partial (*pleasure notes*) or complete (*pleasure trills*) cycles.
  C. *Chevron notes* with ascending and descending frequencies both strongly marked (*brood contact notes*).

II. (Figs. 2–4). *Adult attraction calls.* Soft, brief (<0.2 sec) repetitive notes generally with wide frequency range; often emphasize low frequencies (below 2 kHz). Given by both sexes, except as noted.
  A. Notes with definite clear harmonic structure.
    1. Clear, fairly steady harmonics at all frequencies of call; many notes in call (*contentment notes*; *singing*).
    2. Clear tones only in lower frequencies; fewer notes in call (*contact grunts* or quacks by hen).
  B. Very brief notes without very clear harmonic structure.
    1. Notes usually paired or nearly so; about 1 to 2 pairs/sec (*clucks* by broody hen).
    2. Notes single, about 4 to 10/sec (*food call, nest-site call*).
    3. Pulsed calls, 30 to 60 pulses/sec (*purring call* by cock or hen).

III. (Fig. 5). *Adult mild disturbance calls.* Prolonged notes (often 0.5 to over 1 sec long), neither harsh nor loud; distinct and narrow frequency bands, frequently wavering irregularly or broken (*whine* or *moan*). Given by both sexes.

IV. (Figs. 6–8). *Adult repulsion calls. Hiss* or harsh calls. Wide range of frequencies smudged together. Either with long notes (>0.2 sec) in call, or if notes brief, with emphasis on relatively high frequencies (above 2 kHz). Variable calls, not consistently of three or four notes. Given by both sexes, except as noted.
  A. White noise; wide, largely uniform spread of frequencies (*hiss* by hen on nest).

B. Harsh; wide frequency bands with harmonic streaks.
   1. Low intensity calls; with some long (0.2 sec or more) notes; largely restricted to low frequencies (mostly below 2 kHz) (*threat calls*; *protest growl* of female).
   2. Moderately loud, short notes only (<0.2 sec); with some strong high frequencies (*alerting call*; *startled squawk*).
   3. Loud calls; with some long notes (0.2 sec or more); wide frequency range, with strong high frequencies (>2 kHz) in individual notes (high intensity alarm cries).
      a. Abrupt onset of individual notes (*distress cries*; *cackling alarm*). Longest note less than 0.4 sec long.
      b. Gradual onset and increase in intensity of long (>0.4 sec) note; (*flying predator alarm scream*).
   4. Loud call (male *roar* or loud threat), similar to above (3b); like a *scream* but with emphasis on lower frequencies.

V. (Figs. 8–9). *Species and sex-specific call of cock.* A loud, stereotyped call, generally with three or four notes or energy peaks; accent on third note or on third energy peak; with both clear harmonics and some harshness. (*Crowing*: advertises species, sex, location, territorial ownership and dominance.)

## CONCLUSIONS AND DISCUSSION

### VOCAL COMMUNICATION CODE OF THE RED JUNGLEFOWL

There appear to be certain basic sound parameters or elements in the calls that can be combined in various ways to produce the different vocal signals in the repertoire of the Red Junglefowl. We can attempt to get at these elements and their function in communication by pairing these elements in accord with Darwin's principle of antithesis in communication (1872, reprinted 1955:50): "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." I take the term "state of mind" here to refer to motivation or "mood" in the sense of an increased tendency of the signaler to react in a certain way under a given type of stimulus. Twenty different elements in the basic vocal communication code of the Red Junglefowl are listed below in 10 pairs, each pair composed of opposing elements with their probable functions indicated.

1. Rising vs. falling pitch (chicks) — Pleasure vs. distress
2. Clear tones vs. white noise (hiss) — Attract vs. repel
3. Low vs. high pitched notes — Attract vs. repel
4. Brief vs. long notes — Attract vs. repel
5. Soft vs. loud notes — Attract vs. repel
6. Slow to fast repetition rate of notes — Increased stimulus intensity
7. Regular to irregular repetition of notes — Increased stimulus intensity
8. Gradual or abrupt onset of call — Set to respond vs. startle
9. Steady vs. wavering tones — Secure vs. disturbed
10. Consistent vs. inconsistent number of notes — Stereotyped vs. flexibility

The essential function of antithesis in Darwin's sense is to reduce ambiguity in signalling. This is especially clear for the first five pairs, in which the first member of each pair reflects what could be considered a positive or "pleasure" state in the signaler, the second member a negative or "unpleasant" state. Thus, rising vs. falling pitch in a chick call is associated with either a state of well-being ("pleasure") or conversely with some objectively specified stressful condition ("distress"). Some objective, experimental evidence for the antithetical effects of Pairs 2 to 5 has been given for the responses of domestic chicks to systematic variations in stimuli (Collias and Joos 1953). These pairs are antithetical in that the first member of each pair tends to induce approach, while the second is more likely to stimulate avoidance by a chick.

Integradation between opposing elements under intermediate stimulus situations induces ambiguous or ambivalent responses. At the same time the delicate balance between opposing motives permits a quick, adaptive response as the situation swings one way or the other. The *chevron*, or *brood contact* calls, of chicks consist of both rising and descending frequencies and seem to be given usually under conditions that are rather favorable or only mildly disturbing. Combinations of harmonic tones and white noise (*hiss*) perhaps induce some internal conflict and, to our ears at least, sound harsh. Harsh sounds are associated with alarm cries or threat notes.

Combinations of elements that induce approach would be expected to reinforce each other. Notes that are low-pitched, brief, soft, and repetitive strongly attract chicks, whereas high-pitched, long, and loud notes frighten them. Greatly increasing the loudness (Pair 5) of a sound may reverse the effect on the receiver; playing the normally attractive clucking sounds to chicks at a very high intensity will frighten away instead of attracting the chicks. Red Junglefowl commonly have two main classes of calls: soft or light calls for close-up comunication, and loud alarm or advertisement calls, effective at a distance.

A moderate increase in loudness, or an increase in the rate of repetition (Pair 6) of notes increases the likelihood of a response. Increase in the length of alarm notes (Pair 4) may also give graded stimulus intensity as Konishi (1963) suggested, and probably a graded response as well. An irregular rather than a regular rate of repetition of notes (Pair 7) probably reduces sensory refractoriness, and reminds us of Hartshorne's (1973) anti-monotony principle for the attractiveness of bird song.

Gradual vs. abrupt onset of a call (Pair 8) can be related to Darwin's (1872, reprinted 1955:p. 66) second principle of "emotional expression" (or communication) for the origin of social signals in evolution: "the principle of direct action of the excited nervous sytem on the body, independently of the will and in part of habit." The *distress cries* of a captured Red Junglefowl (Fig. 7d), the startled cry of a hen suddenly pecked (Fig. 5e), and the *alerting call* (Fig. 7a) of a cock suddenly aware of possible danger are all examples of calls with an abrupt onset and with minimal dependence on habit. They form a continuum of decreasing intensity and length of notes. The *alerting call* serves as a routine signal of potential danger. In contrast, the *brood contact* or *chevron notes* of a chick (Fig. 1c) often have a gradual onset, and the chick is set for rapid changes in response.

In contrast to steady tones, long wavering tones (Pair 9) which have a whining or moaning quality (Figs. 5a–e) are given in disturbing or conflict situations, as when a subordinate retreats from a dominant bird, or when a bird is frustrated in its attempts to get food.

The greatest consistency in number of component notes (Pair 10) in any of the calls of the Red Junglefowl is in the cock's crow. The stereotyped number of three or four notes or energy peaks is an example of the principle of ritualization, the increase in evolutionary adaptation of a signal to its function (Tinbergen 1952). One explanation for the evolution of stereotyped species-specific behavior patterns in communication was suggested in 1872 by Darwin (1872, reprinted 1955:p. 27) as one of his three principles of emotional expression "Serviceable actions become habitual in association with certain states of mind, and are performed whether or not of service in each particular case." And again: "Actions, which were at first voluntary soon become habitual, and at last hereditary" (p. 356).

Modern genetics, which of course post-dates Darwin's time, suggests a mechanism for Darwin's principle in terms of population genetics, the genetic assimilation theory of Waddington (1961). The heritability of an acquired trait, whether based on learning or not, can be increased in a population by the action of natural selection. There is evidence for both learned and genetic differences in song dialects among passerine birds (Baker and Cunningham 1985), but this promising research area has not been investigated in the Red Junglefowl. A high degree of heritability for duration of *crowing* calls has been demonstrated among certain breeds of domestic fowl (Siegel et al. 1965). There are significant geographic differences for the *assembly* call (frequency and internote interval) of the Northern Bobwhite (Goldstein 1978), but their heritability is unknown. Significant differences in duration of this call in different covies of bobwhite may develop, and these differences are probably learned (Bailey and Baker 1982). We need to investigate whether or not the heritability of a given type of call has actually been increased by natural selection in a specific population of birds in nature.

## NEED FOR EXPERIMENTAL VERIFICATION

There is need for experimental verification and further analysis of the communication code of the Red Junglefowl and the signals described here. We can vary the stimulus situation systematically to uncover the optimal stimulus situation for each call. Some experiments of this type in relation to the *pleasure notes* and *distress cries* of recently hatched chicks of the domestic fowl were reported earlier (Collias and Joos 1953). In experiments with Red Junglefowl, Sherry (1977) found that a broody hen which can see her chicks, whether she can hear them or not, *food-calls* for a significantly longer time before eating the mealworm presented to her, than does a hen prevented by a partition from seeing her chicks. Playbacks of chick sounds given when the chicks were feeding, being brooded, or at rest, had no effect on the hen's food-calling. Under a different state of motivation, a broody domestic hen will respond with defense reactions to the *distress cries* of a chick that she cannot see, but ignores an isolated chick plainly visible under a bell jar but inaudible (Brückner 1933).

In experiments with domestic fowl cocks exposed to a hen who could not see the food automatically presented to the cock, the rate and number of *food calls* given by the cock increased with the preference ranking (palatability) of the food. A hen was more likely to approach the male when he was calling than when he was silent after food was presented to him (Marler et al. 1986a). A cock would *food-call* significantly less with no audience than in presence of a hen; he would even *food-call* to a hen over non-food items especially in the presence of a strange hen (Marler et al. 1986b). Since a cock often refrains from ingesting a food item after calling a hen to it, just as a hen does after calling her chicks to food, a possible inference is that the behavior is intentional and implies that the caller plans ahead of time to share the food with the receiver (Marler et al. 1986b).

Further experimental analysis of the communication code could be in terms of physiology. Animal vocalizations reflect the motivational state of animals or "emotion" as Darwin (1872) termed it and may often arouse emotional responses in people. The objective correlates of emotional experience in humans probably often correspond to rather similar patterns of observable behavior in the higher animals. This observation and the fact of a common vertebrate phylogeny suggest a basic similarity in communication, if not a common language of emotional expression of humans with the higher animals. What emotions animals actually experience makes little difference for scientific analysis. We can proceed to analyze the physiological basis of the general principles of communication as established by objective evidence and by homologies of brain structure. The present report by attempting to bring out some of the basic elements of the code of communication should help bridge the gap between behavior and the underlying basis of communication in the brain and sense organs.

## COMPARISON WITH OTHER SPECIES

The same basic principles that relate different motives to the structure of different calls appear to apply to many species. Among Red Junglefowl, attraction calls are generally soft, brief, low-pitched and repetitive notes. Alarm cries and threat calls are often harsh; alarm cries being usually louder and tend to include more high frequencies than do threat calls which instead often emphasize relatively low frequencies. The vocal behavior of the other three species of junglefowl is as yet poorly known (Johnsgard 1986), but these same rules hold for other species of the same family (Phasianidae) whose vocalizations have been best studied with the aid of sonograms, the Ring-necked Pheasant, *Phasianus colchicus* (Heinz and Gysel 1970), Northern Bobwhite, *Colinus virginianus* (Stokes 1967), and the California Quail, *Callipepla californica* (Williams 1969), as can readily be seen by perusing these reports. Greater generality of the rules is indicated by corresponding similarities between the vocal repertoire of the Red Junglefowl and so different a bird as a passerine species, the African Village Weaver, *Ploceus cucullatus* (Collias 1963), and even more generality is shown by the frequent parallels of the same sort between the vocal signals of birds and mammals (Collias 1960). In conclusion, there seems to be a common substrate in the principles of communication from which the various diverse repertoires of different species have evolved.

The quail mentioned above are good examples of how differences in social organization have led to new functional specializations in vocal signals. In contrast to the polygynous Red Junglefowl and Ring-necked Pheasant, the monogamous and highly social quail have a special *assembly call* that brings mates and other members of a covey together again after being scattered by a predator. This *assembly call* has apparently developed out of the call given by a chick when lost or cold (Stokes 1967).

Important similarities and differences between responses to the same calls in different species can be investigated with playback tests. Williams (1969:653) found that chicks of the California Quail readily came to food calls of a bantam domestic hen. However, incubator-hatched and maternally naive bobwhite chicks simultaneously exposed to maternal leadership calls of their own species and of domestic hens (clucking) preferred their own species (Heaton et al. 1978).

## SIZE OF VOCAL REPERTOIRE OF THE RED JUNGLEFOWL

Calls can be identified to a considerable extent by the general situation in which they are given and by their sonograms. Because of the existence of graded signals and of intermediate stimulus situations it is not possible to specify any absolute limit to the size of the vocal repertoire. However, in practice, specific calls recur frequently and characteristically in certain situations, enabling one to give a rough but fairly accurate estimate of the size of the vocal repertoire.

Based on the above criteria, I feel that I can recognize about 24 different calls given by the Red Junglefowl. Calls of chicks include: (1) *distress cries,* (2) *pleasure notes,* (3) *fear trill,* (4) *pleasure trill,* and (5) a *fear note,* which is a sharp cry given by a chick when it is abruptly seized. Guyomarc'h (1962, 1966) who has described variations in the calls of small chicks in some detail gives a sonogram of this last call (1962: 294). Additional calls, given by adult Red Junglefowl, include: (6) *clucking* by hens, (7 and 8) *food calls* of two types, (9) *purring,* (10) *courtship call* (two parts) of cock given while wing-fluttering to hen, (11) *contentment calls,* (12) *contact grunts,* (13) *singing,* (14) *whine* or *moan* of disturbance or frustration, (15) *alerting call,* (16) *startled squawk* when pecked, (17) *distress squawks* when captured and held, (18) *alarm cackling* (two parts) to ground predator, (19) *alarm scream* to flying predator, (20) *loud defensive threat* to flying predator, (21) *hiss* by hen on nest, (22) *protest growl* by broody hen when disturbed, (23) *threat calls* of low intensity by cock or hen, and (24) *crowing* by the cock.

In the domestic fowl, which has essentially the same vocal repertoire as the Red Junglefowl, Baeumer (1962) who has given the most comprehensive verbal account of the calls described 30 different calls, based on close observation over many years. Konishi (1963) who had access to Baeumer's tape-recordings, made sonograms of many of these calls. In general, the calls recognized by Baeumer and by myself appear to be about the same. The probable reasons for the difference between his count of 30 and mine of 24 can often be specified: (a) he classifies as two signals (his 6 and 7) what I have called two parts of a compound call in the case of alarm cackling to a ground predator, the preliminary cut-cut notes and the loud kaah!; (b) what I have at times labeled the same call in different situations he apparently labels as different calls in the different situations: the distress cries of a hen when seized (Baeumer's 10, B10) and or when held (B11); or the *protest growl* of a broody hen to avoid copulation (B13), to defend her nest (B14), and to defend her chicks (B16); or *clucking* by a hen when leading chicks (B18) and when brooding chicks (B19), admittedly variants of the same call; and (c) labeling different intensities of one call as different calls, such as short (B25) or long (B26) *threat notes* of a hen. Baeumer recognizes different categories (B20, B21) of the *alarm cry* to a flying object, which Konishi (1963) has identified as different intensities of the same call especially as indicated by length of the call. I also suggest an additional category (no. 20 on my list), the loud, relatively low-pitched *defensive threat* ("*roar*") to a flying predator that is departing or is relatively nonthreatening. In general, as with "lumpers" and "splitters" in taxonomy, the decision whether to distinguish one or two similar calls that sometimes intergrade, can be rather arbitrary. The important thing is not the absolute size of the vocal repertoire that is estimated, but rather that the physical characteristics of each call and the situations under which it is given be accurately and adequately described so that the same call when described by different observers can be recognized as such.

## ACKNOWLEDGMENTS

I thank the Zoological Society of San Diego for permission to do the research at the San Diego Zoo, and the zoo personnel for their help especially A. C. Risser, L. Ordonez, and D. Rimlinger. We are grateful to E. N. Flint, Mr. and Mrs. K. Morgan, Mr. and Mrs. E. Taylor, and K. Collias for helping net some of the birds for banding. My wife, Elsie, helped in many ways, and with our daughter, Karen, helped make some of the tape recordings. Paul Schneider kindly recorded the crowing of the Green Junglefowl in his aviaries for me. The research was funded by University of California Los Angeles Grant 1623.

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