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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

VISUAL AND ACOUSTIC COMMUNICATION IN THE BLUE JAY, *Cyanocitta cristata* (Aves, Corvidae)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

SHEILA CONANT

Norman, Oklahoma

1972

VISUAL AND ACOUSTIC COMMUNICATION IN THE BLUE JAY,

Cyanocitta cristata (Aves, Corvidae)

APPROVED BY

DISSERTATION COMMITTEE

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Charles C. Carpenter for his guidance and encouragement throughout the project, and for providing space and equipment for me in his laboratory. Thanks are also due to my committee members Drs. Harley P. Brown, Gary D. Schnell and Paul G. Risser for reading and criticizing this manuscript.

My graduate work at the University of Oklahoma has been supported by a National Science Foundation Traineeship awarded to me by the Department of Zoology. Mrs. Marjorie Bradley, Assistant to the Dean of the Graduate College, has been most helpful in administering the research funds from the traineeship.

Friends too numerous to name have been helpful with many different parts of the project.

I am especially indebted to 25 patient, colorful, and endearing Blue Jays that were most cooperative research subjects.

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CHAPTER I

INTRODUCTION

The Blue Jay, one of the more familiar and widely distributed North American corvids, exhibits a wide variety of distinct acoustic and visual communication signals. Hardy (1961) made a rather thorough study of the life history of the Blue Jay, including visual and vocal communication, but he did not investigate communication in depth. Edwards (1971) investigated the ontogeny of vocalization in the Blue Jay, describing the development of various calls, ascribing functions to some.

A number of life history and behavior studies on other New World jays have been made, the most extensive of which are: Amadon (1944), Florida Scrub Jay (*Aphelocoma coerulescens coerulescens*); Brown (1963a, 1963b, 1964), Mexican (*A. ultramarina arizonae*) and Steller's jays (*Cyanocitta stelleri*); and Gross (1949) Mexican Jay. All of these studies include at least some observations and comments on communication signals of the various species.

Blue Jays lend themselves well to laboratory studies; they are easily raised, maintained and observed, and they exhibit a rich repertoire of behavior patterns. They adapt well to captivity and, apparently, show little behavioral distortion, other than a tendency to be "tame" or unafraid of humans, resulting from the necessary constraints of captive existence.

I decided to study Blue Jays because their repertoire of communication signals is large and has not been well-described. They are easily observed in the field and are excellent subjects for studies in captivity. My objectives in the study were to describe the physical characteristics of acoustic and visual displays and to determine their biological significance.

CHAPTER II

MATERIALS AND METHODS

Acquisition and Maintenance of Birds

The majority of the data presented here were gathered during observations of 25 captive, hand-raised birds. All of the birds were collected from various locations within Cleveland County, Oklahoma. They were acquired from nests at ages ranging from one to five weeks. Six birds were collected in the spring of 1969, and, in 1971, 19 more birds were taken during the spring and summer months.

From May, 1969, until December, 1970, the birds were kept at my home in an aviary with a 6 x 8 x 12 ft indoor flight and a 12 x 14 x 16 ft outdoor flight. In December, 1970, the birds were moved to the Animal Behavior Laboratory on the North Campus of the University of Oklahoma, where they were kept in an aviary with an 8 x 12 x 20 ft indoor flight and a 15 x 30 x 30 ft outdoor flight. No behavioral differences that might have been attributed to the move were apparent. Occasionally, individual birds or pairs were placed in other, smaller aviaries for special observation.

Both nestling and adult diets contained varying amounts of the following items: fresh and dried fruits and vegetables, hard-boiled eggs with shells, fresh meat, cracked corn, sunflower seeds, raw peanuts, honey, graham crackers, Purina Pigeon Checkers, Purina Dog Chow, Prunty's Mockingbird Food, Prunty's Nestling (Egg) Food, and vitamin supplements. Some live insects were available during the warmer months. Limecake, pumice blocks, and fresh water for drinking and bathing were available at all times.

All birds were banded with both U.S. Fish and Wildlife Service aluminum bands and colored plastic bands for individual recognition.

Observation--Methods and Equipment

Vocalizations were recorded with a Uher 4000 Report-L portable tape recorder (frequency response 40 to 20,000 Hz) and a Uher 514 omnidirectional microphone (frequency response 70 to 14,000 Hz). Sound analyses were made with both a Tektronix type 502A Dual Beam Oscilloscope and a Kay Sonagraph, model 1029-A. On the Sonagraph the frequency band setting used for most analyses was 80 to 8,000 Hz. The wide band pass filter, with a frequency resolution of 300 Hz was used for temporal resolution, and the narrow band pass filter, with a frequency resolution of 45 Hz was used for frequency resolution.

Motion pictures were made with a model H-16 Bolex 16 mm movie camera and a 17-85 mm Pan Cinor zoom lens.

Motion analyses of displays recorded on film were made by projecting film with a Bell and Howell Model 173 Time and Motion Study Projector.

An Esterline Angus 20-channel Event Recorder, coded in series for about 50 behavior patterns (including both visual and vocal displays), was used to record data during observation periods.

Because the birds were "unafraid" of humans, it was not necessary to use a blind for observation. Most observations were made within 10 m of the cage or even inside it. Binoculars (7 x 35) were used to facilitate identification of individual birds.

Field observations and experiments were made frequently throughout the course of the study. Data from field observations allowed me to compare the behavior of captive and wild birds, as well as to gather data under field conditions on the function of displays.

CHAPTER III

VISUAL DISPLAYS AND POSTURES

Introduction

Blue Jays exhibit at least 20 distinct visual displays or postures. The function of a given posture or display is determined by the context in which it is given, and involves fixed or moving aspects of "facial expression," head position, body position and piloerection. Movement in general, as well as movement of specific, often visually conspicuous, parts of the body or plumage, serves, at least in part, to give visual emphasis to displays. In many cases movement functions only to emphasize a visual display without changing its meaning, just as an increase in volume might emphasize an acoustic signal.

Components of Visual Signals

The components of postures and displays that function as communication signals in the Blue Jay may be grouped into three categories: 1) "facial expression" and head position, 2) body position, 3) movement and position of plumage. Each category has several variations, each of which is graded, or continuously variable.

1. "Facial expression" and head position may be modified in several ways. The position of the crest varies from erect to appressed, the position of the mandibles varies from open to closed, and the position of the head may be below, at the same level as, or above the body axis. The direction of point of the bill is important, but highly variable.

2. Body positions vary, but can be placed in several groups. The body is considered crouched when the ankle joint is bent so that an angle of less than 90° is formed by the tibiotarsus and the tarsometatarsus. When the body is in the neutral position, as during periods of mild activity or inactivity, this angle approximates 90°. In the "tiptoed" position the angle is greater than 90°.

The orientation of the body with respect to the horizontal varies among and within displays. The body is sometimes rotated from the neutral position (body at an angle of about 45° with the horizontal) so that the head and upper torso move vertically up or down. Extremes of this position occur when the body is held nearly perpendicular to the perch or when the head is lowered to a point where it is below the perch. The point of rotation of the body may be either the ankle or knee joint.

Occasionally, during a display, the feet leave the perch entirely, although the bird does not initiate flight or spread its wings, but, instead, returns to the perch. This

type of body movement is usually associated with intense excitement. Finally, the bird may be in flight at some point during a display.

3. The movement and position of plumage is an important component of visual displays. Different degrees of piloe ction are observed within and among displays and : to have communicative significance. Morris (1956) has described four degrees of piloerection, and I will adhere to his descriptions when discussing piloerection in this paper. They are as follows: 1) sleeked, the plumage is actively depressed against the body; 2) relaxed, the pluma,e is neither actively depressed nor erected; 3) fluffed, the plu..ge is partially erected and the feathers remain in contact with each other; 4) ruffled, the plumage is fully erected, and the feathers no longer remain in contact with each other.

The wings and tail are often moved during displays; they may be fluttered, flicked or held stationary. Both the wings and tail may be fanned (i.e., moved from the closed to the open position or to some point between these extremes) while they are fluttered or flicked. If the wings and tail are held stationary during a display they may be held at any point from closed to fully fanned.

The Blue Jay is a strikingly marked bird and some attributes of its coloring appear to be important in visual displays. The black facial mask and collar probably give added visual emphasis to displays, especially to those

displays involving movement of the head as well as those in which the displaying bird is within several meters of the animal to which the display is directed. Courtship and agonistic postures and displays often involve various degrees of piloerection whereby dark areas of the plumage are increased in area.

The white and black wing and tail bars are conspicuous during movement. Fluttering, flicking and fanning of the wings and tail make these bars, particularly the white ones, quite obvious.

Postures and Displays

Visual communication signals may be placed in three groups on the basis of functional and physical similarities. The first group of postures, which do not appear to function as communicative signals, includes those assumed during maintenance activities. They are characterized by relaxed or fluffed plumage, neutral body position, appressed wings and closed tail. The second group is characterized functionally as primarily agonistic and is associated with erection of body plumage and, especially, head plumage and abrupt movements, if any, of wings and tail. The last group of displays functions as submissive or solicitative signals, and is associated with sleeking of both head and body plumage and fluttering type movements of the wings and tail if these appendages are moved at all. Each of these types will be discussed below.

Maintenance Postures

Neutral posture (Fig. 1). This posture is assumed by the bird during periods of mild activity (not including long rest periods or sleeping), for example, as a bird forages on the ground or up in the vegetation.

In neutral posture, the crest and plumage are relaxed; the bill is closed and pointed forward. The body is in neutral orientation to the horizontal, and the wings and tail are fully closed. Of course, as the bird moves, aspects of the posture are necessarily modified by the nature of the activity. For example, if the bird is foraging it moves about actively looking for and picking up food items.

Sleeping (Fig. 2). While a Blue Jay is asleep, the crest is relaxed and the body plumage is usually fluffed. The body is crouched, and the bird may rest its full weight on only one foot. The head is usually turned backward with the bill nearly parallel to the body axis and tucked behind the wing. At times the head is merely lowered between the shoulders, giving the bird a hunched appearance. This hunched appearance is often seen during midafternoon rest periods. During daytime rest periods, the bill is never tucked behind the wing; whereas, during nocturnal sleeping the head is turned back and the bill tucked behind the wing more often than it is hunched with the bill pointing forward.

Thermoregulatory postures

Heat conserving posture (Fig. 3). Birds often assume

Figure 1. Neutral posture.

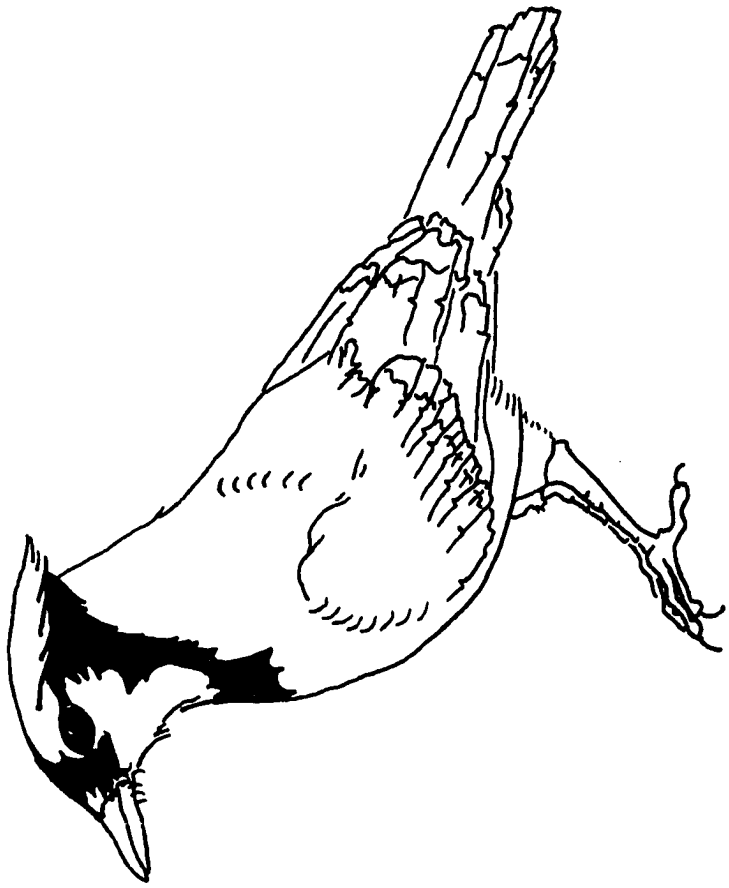


Figure 2. Sleeping.

Figure 3. Heat conserving posture.

this posture, which is characterized by fluffing of all body and head plumage, on cold days when they are inactive. According to Morris (1956) feathers in the fluffed position (feathers erect but still in contact with one another) facilitate heat conservation because the entrapped air spaces between them have reached maximum size, thus providing the greatest insulation possible.

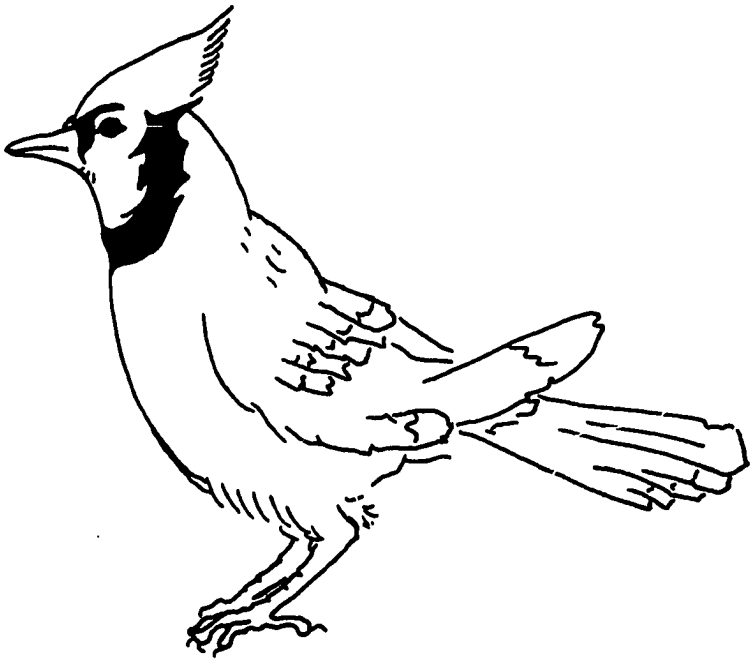
Cooling posture. On very warm days, inactive jays often perch with their feathers ruffled (fully erect and no longer in contact with one another). Morris (1956) contends that ruffling of feathers increases heat loss because entrapped air spaces and, concomitantly, insulation are lost when the feathers lose contact. A ruffled, inactive Blue Jay would look much like the one illustrated in Fig. 3, except that it would have a ragged outline.

Bathing. During both water bathing and sunbathing the feathers are ruffled and the wings and tail fully fanned. Ruffling of feathers during bathing probably facilitates wetting (by water) or warming (by the sun) of both the feathers and the skin. Preening, which always follows water bathing and occasionally follows sunbathing, is performed with the feathers ruffled. Ruffling of the feathers immediately around the cloaca occurs during defecation.

Agonistic Postures and Displays

Investigatory posture (Fig. 4). This posture, first described by Hardy (1961), is assumed by a Blue Jay

Figure 4. Investigatory posture.



investigating strange objects that may or may not pose a threat. In this posture, the bill is closed and pointed forward, the crest is fluffed, and the head is held above the tail and body axis. The body is held in neutral or slightly "tiptoed" position with body plumage fluffed. The wings are appressed and the tail is slightly fanned.

Alert posture. The alert posture is quite similar to investigatory posture except that the wings and tail are occasionally flicked. If the bird is in motion during investigatory posture or alert posture, movements are usually stiff and jerky. The bird is easily startled and appears ready for instantaneous flight.

Aggressive Postures and Displays

The characteristics of aggressive postures of Blue Jays vary with the intensity of aggression shown by the displaying bird or birds. Although this variation is continuous, it is possible to characterize the postures observed at the extremes (mild to intense) of aggression.

Mild aggression (Fig. 5). Aggressive encounters of low intensity occurred frequently among the captive jays. An example of this is the supplanting of one bird by another on a perch or at a feeding area. The posture of the aggressor in such encounters is easily recognized. The bill is closed and pointed forward and the crest is fluffed. The head is usually held above the tail and body axis while the body itself is slightly crouched. The body plumage is sleeked or

Figure 5. Mild aggression.

relaxed, the wings are appressed and the tail is slightly fanned.

Intense aggression (Fig. 6). Aggressive encounters of high intensity occurred infrequently in my captive birds except during the breeding season, when they are common. At this time the birds show an increase in the amount of defensive behavior, i.e., "claiming" or "stealing" food, nest material, mates, perching sites, etc.

A highly excited, aggressive Blue Jay assumes a characteristic posture. The bill is open and directed at the object of aggression. The crest is fully erect or ruffled, while the position of the head with respect to the body axis varies. The wings and tail are at least partially, and often fully fanned. Sometimes the wings or tail or both are flicked.

In high intensity aggression the degree of piloerection varies considerably. Infrequently, the plumage is sleeked or even relaxed. Bill snapping may accompany intense aggressive displays.

The aggressive encounter (Fig. 7). Fig. 7 is a sketch of three Blue Jays (the two shown uppermost are involved in the encounter) during an aggressive encounter. Both birds exhibit some of the characteristics of the aggressive posture. The bird on the left eventually won this encounter, which was recorded on film, by supplanting the other bird. Note the position of the winner's head with respect to its own body and the body and head of the other

Figure 6. Intense aggression.

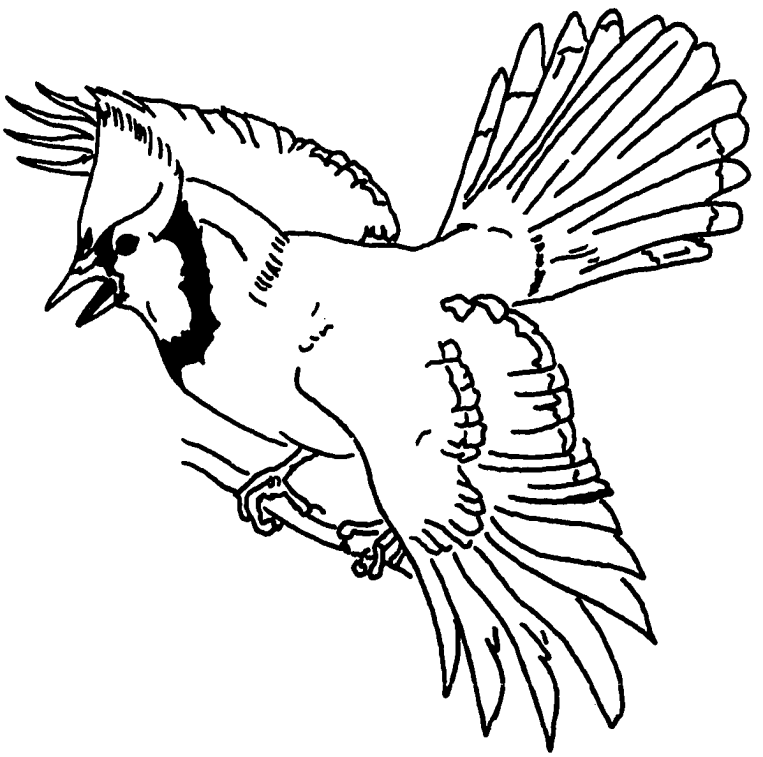


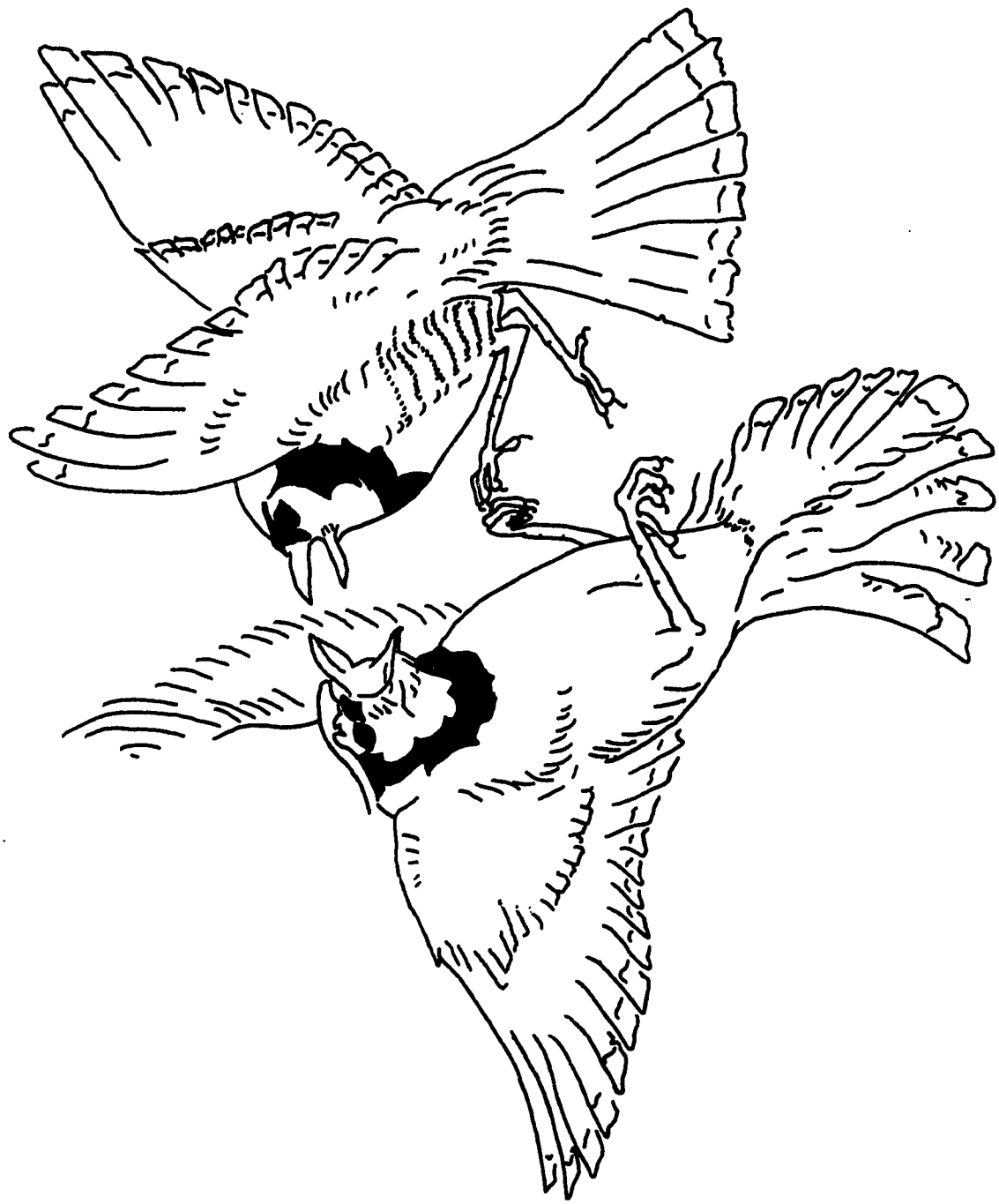
Figure 7. The aggressive encounter.

bird. Victory in an aggressive encounter can be predicted by noting the position of the winner's head with respect to the body axis and the head of the opposer. The winner's head nearly always is either horizontal to or below its own body axis and tail, and below the head of its opponent.

There are two other factors that, to some degree, predispose victory in aggressive encounters. Most important is the birds' position in the established dominance hierarchy; the subdominant in an aggressive encounter nearly always loses, presumably by choice. Frequently a bird may supplant another bird by a "surprise attack." In this case, the aggressor flies toward or approaches the attacked bird in such a way that it cannot see the approach. This serves to startle the attacked bird and, invariably, it is displaced. This kind of approach may permit a bird to win an encounter over an opponent that is higher in the dominance hierarchy.

Fighting (Fig. 8). On rare occasions, two Blue Jays will become involved in a fight. Fights usually occur when one bird refuses to be displaced from a perch or feeding station, or when there is a dispute over possession of a food item. When two birds are fighting they are in hovering flight, face to face with body plumage ruffled, clawing at each other. After a few bouts of clawing and hovering, one bird chases the other until it escapes and is a good distance from the chaser or until the chased bird is cornered and gives the appeasement posture (Fig. 14), which will be

Figure 8. Fighting.



discussed later. Body contact during fights is infrequent.

Simple bobbing (Fig. 9). This display is given in both agonistic and sexual contexts, and is the most frequent display given by Blue Jays. The simple bob, which is rarely observed unaccompanied by vocalization, functions primarily to add visual emphasis to vocal signals. Field observations reveal that when bobbing involves communication among individuals at some distance (over about 50 m) there are nearly always conspecific observers present and, in my estimation, their view of the displaying bird is good. Simple bobbing also accompanies vocalizations given among groups of birds in close proximity, but it is less consistently employed in the presence of conspecific observers at close range than those that are at a distance.

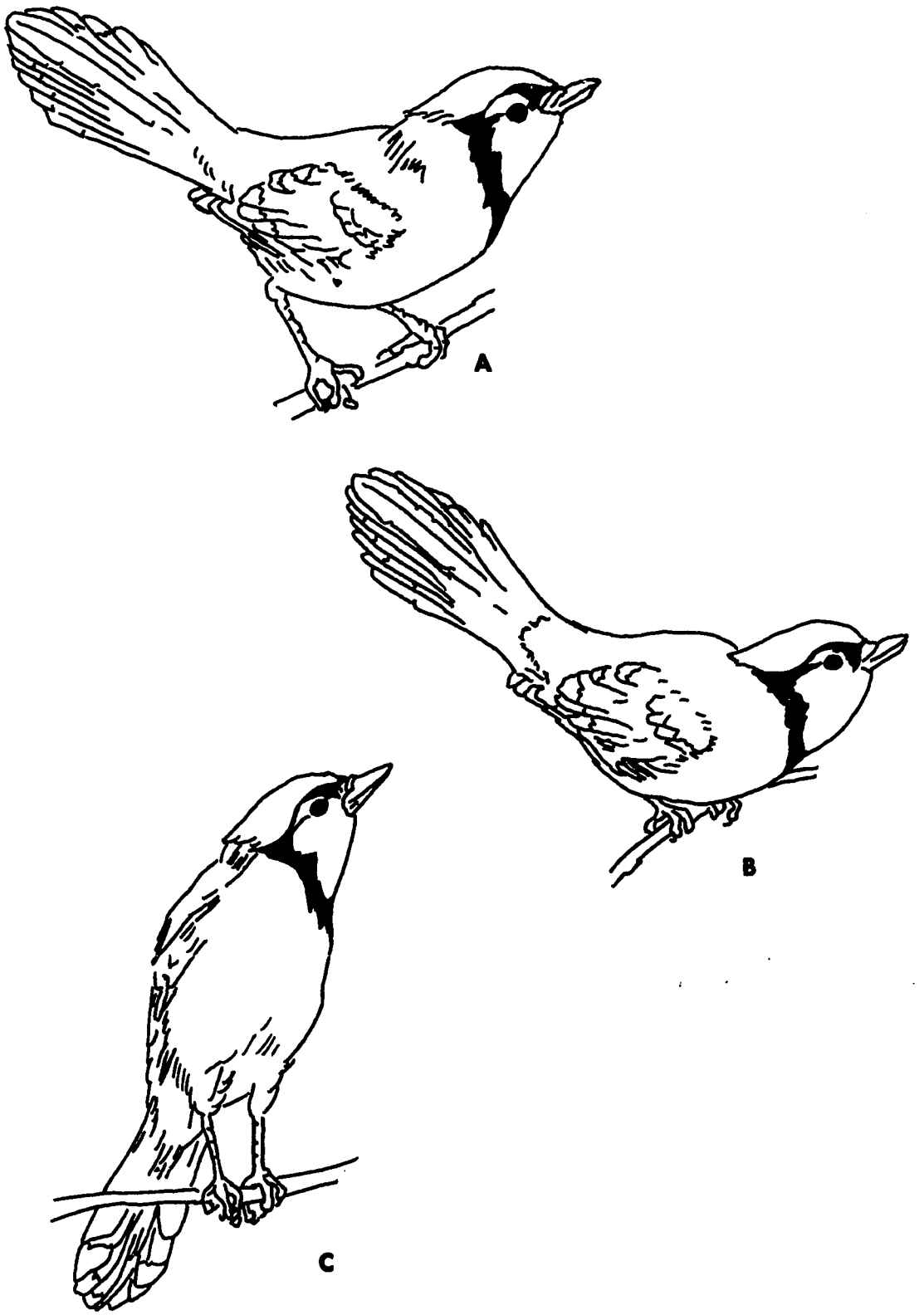
I recorded the number of vocalizations with or without bobbing displays by jays in the presence of proximate or distant conspecific observers. Of 308 vocalizations given at a distance of over 50 m from the observer, 246 (80%) were accompanied by bobbing. Only 189 of 517 vocalizations (37%) given less than 50 m from the observer were accompanied by bobbing. There is a significantly ($X^2 = 413.36$, $P < .005$) higher frequency of bobbing associated with vocalizations involving distance communication than with vocalizations involving proximate communication.

The hypothesis that bobbing is important in visual communication among birds located some distance from each

other is further strengthened by the fact that it never accompanies those vocalizations that involve communication between individuals within 10 m of each other. The food begging call of the young, the courtship feeding or copulation solicitation call of the adult female are never accompanied by bobbing. In these cases, exchange of information occurs between birds that are usually within a meter or so of each other.

Fig. 9 illustrates the movement of the bird during a simple bob. At the beginning of the display (A, Fig. 9) the bird is in neutral body position with plumage relaxed, wings appressed, tail usually closed, and head above body axis and tail tip. Bobbing is initiated as the bird begins to crouch and lower the head to a position level with the body axis and below the tail tip (B, Fig. 9). The bird next returns through the original neutral position (A, Fig. 9) and then "tiptoes," at the same time raising the head above the body axis and deflecting the tail downward (C, Fig. 9). At the height of the bobbing motion the bill may be directed vertically upward or it may remain in a horizontal position. In addition, if the bob is quite deep and/or the bird is excited, one or both feet may leave the perch at the high point of the bob. Bobbing is concluded as the bird returns again to the original neutral position. Occasionally, an additional crouch (B, Fig. 9) and return to neutral position are added. The depth of the bob varies, becoming proportionately deeper with increased excitement.

Figure 9. Simple bobbing.


A
B
C

There are several important characteristics of the simple bob: a) During the simple bob, there is no appreciable horizontal movement on perches or movement from perch to perch. b) Simple bobs are discrete single units; if several bobs are given in a short time period, there is a slight pause between bobs. c) The simple bob is a smooth, continuous movement. d) The plumage is relaxed except for an occasional tail flick. e) Simple bobbing usually involves bending of the ankle joint; it is analogous to a curtsy.

Because there was a gradation in the depth of bobs, I arbitrarily classified simple bobs into three categories:

1. Head bobbing. Some bobs involved movement only of the head and neck. During this type of bobbing there was no flexion of the ankle joint or downward deflection of the tail. This type of bob was given in situations of very low excitement. Vocalizations accompanying this display were often at a relatively low sound level as subjectively judged by the observer.

2. Body bobbing. The majority of simple bobbing falls into this category. This type of bob is one that follows the pattern illustrated in Fig. 9. The entire body is bobbed, the ankle joint is flexed both at the crouched position in the downward movement and at the horizontally elevated "tiptoed" position in the upward movement of the display. In addition, the bill is directed upward and the tail is deflected downward simultaneously at the height of the bob.

3. Exaggerated bobbing. During an exaggerated bob, the displaying bird bobs more deeply than during body bobbing, and, at the height of the bob, one or both feet leave the perch. Both feet may leave and return to the perch simultaneously or one foot may be lifted from and returned to the perch slightly out of phase with the other. Whether or not the feet move in synchrony does not seem to be communicatively significant.

Preliminary observations suggested that head bobbing, body bobbing, and exaggerated bobbing were associated with low, mild, and high levels of excitement, respectively. To test this, I chose three vocalizations that were consistently associated with bobbing and were themselves characteristic of the arbitrarily designated levels of excitement. I recorded the number of times each bob type was associated with each of the three vocalizations. Data on calls not associated with bobbing were not used in statistical tests for significant association of calls with bob types.

The alarm call is invariably associated with high levels of excitement evoked by such things as the presence of potential predators (cats, etc.). The bell song is most frequently associated with a mild level of excitement. The call is usually territorial, but occasionally functions as an alert signal that serves to call attention to an unusual object or organism in the aviary. The flock contact call is given by unexcited birds, or at least by birds that exhibit

a very low level of excitement. This call serves as an acoustic mechanism by which flock continuity is maintained.

Table 1 shows the percentage of vocalizations given with each bobbing type during observation periods.

The data in Table 1 were put in a 3 x 3 contingency table and submitted to a Chi-square test for non-random association of vocalizations with bobbing types. It was shown that the flock contact call was associated with head bobbing, the bell song was associated with body bobbing, and the alarm call was associated with exaggerated bobbing ($X^2 = 1358.20$, $P < .005$).

It seems, then, that the primary functions of simple bobbing are 1) to give visual emphasis to acoustic communication signals, and 2) to indicate the level of behavioral excitement of the bird that is bobbing.

Courtship display (Figs. 10, 11 and 12). This is the principal courtship display of the male Blue Jay, and it is always accompanied by the courtship vocalization.

Although courtship display is similar to simple bobbing with respect to the type of vertical movement during the display, it differs from simple bobbing in a number of important aspects. a) The bird changes location both vertically and horizontally as it displays. b) Courtship display consists of series of bobs with little or no pause between individual bobs. c) The bobs in courtship display are characterized by jerky rather than smooth movements.

Table 1.--Per cent of selected vocalizations given with each of the three simple bobbing types

	Flock Contact Call (n = 402)		Bell Song (n = 266)		Alarm Call (n = 324)	
	%	no.	%	no.	%	no.
Head bobbing	87.3	351	7.5	20	5.6	18
Body bobbing	5.5	23	87.2	232	12.4	14
Exaggerated bobbing	7.2	28	5.3	14	82.1	266

d) There is considerable piloerection, especially of the feathers on the head and neck, which are ruffled, and the wings and tails are frequently flicked. e) Courtship bobbing does not involve bending of the ankle joint; it is analogous to a bow rather than a curtsy.

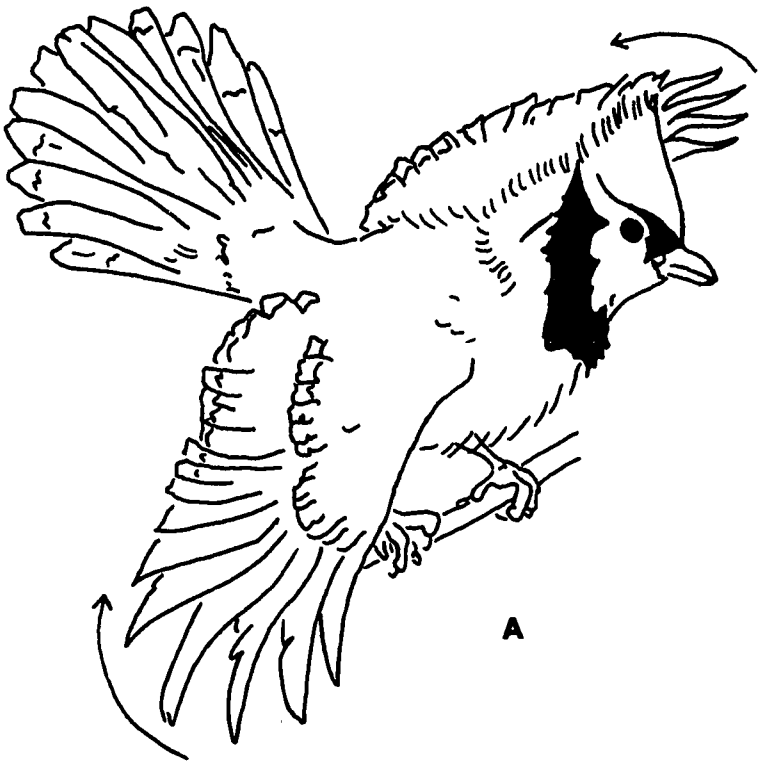
Both the degree of piloerection and abruptness of movement characteristic of courtship bobbing visually enhance this display. Head and neck feathers are ruffled, effectively increasing the apparent size of the black facial mask and collar. Flicking of the wings and tail with each separate vertical movement (Fig. 10, A, B; Fig. 11, C. D; Fig. 12, E, F) serves to flash the white markings on the feathers of these appendages. Because the bird does not bend the ankle joint to effect a crouching position, it appears to be "tall" at all times.

Courtship and agonistic displays in many animals are characterized by movements and changes of body position and shape that make the animal appear larger than it does when not displaying (Hinde, 1966). Both the aggressive postures and the courtship display of the Blue Jay exhibit this phenomenon quite well.

Submissive and Solicitative Postures and Displays

Avoidance posture (Fig. 13). When two or more birds are perched at a feeding station there is usually one individual that feeds first and then leaves. The other individual(s) present remain(s) perched at the feeder without

Figure 10. Courtship bobbing.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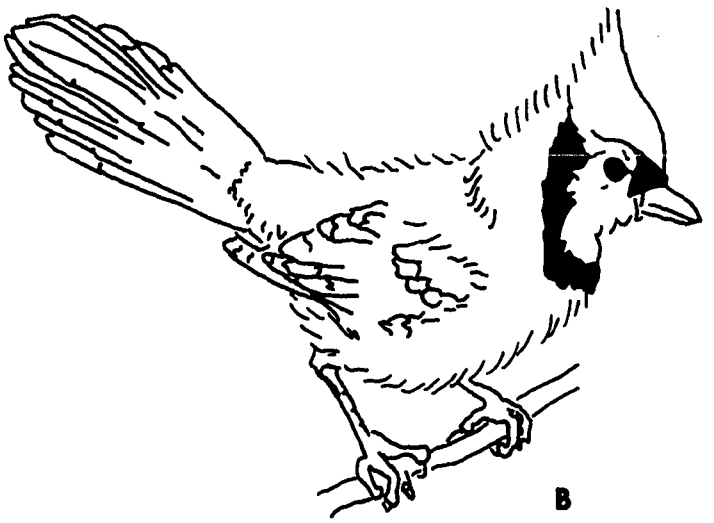
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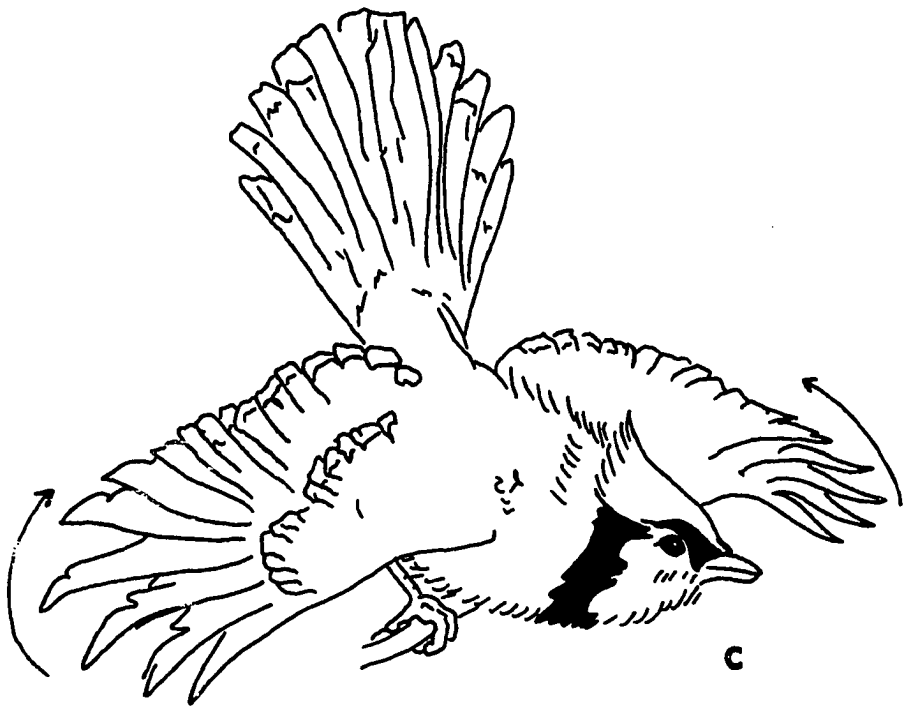
Figure 11. Courtship bobbing.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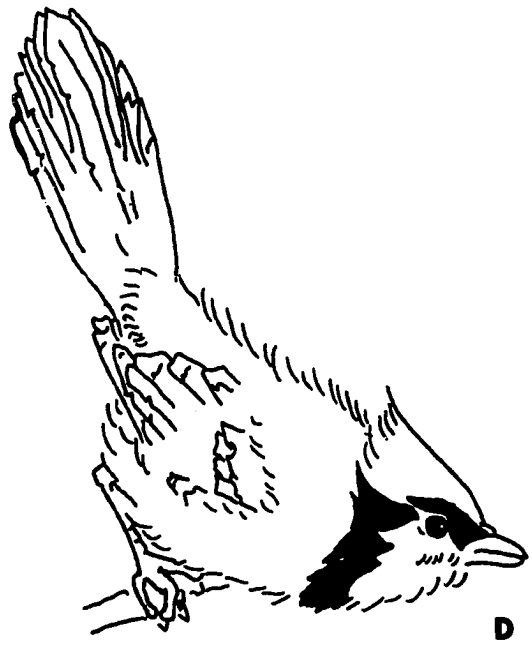
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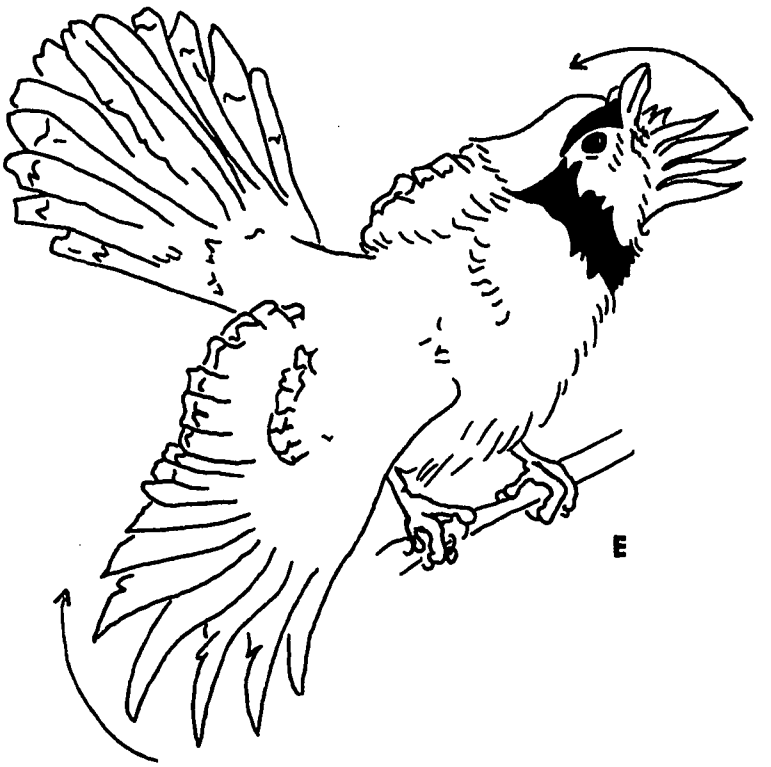
Figure 12. Courtship bobbing.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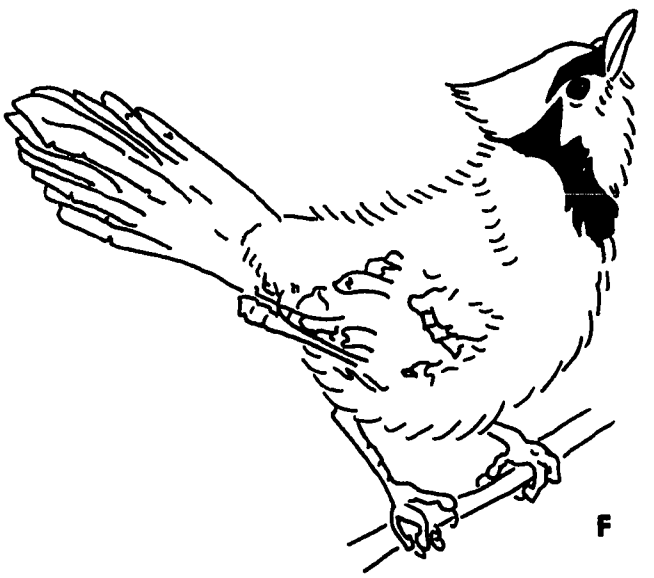
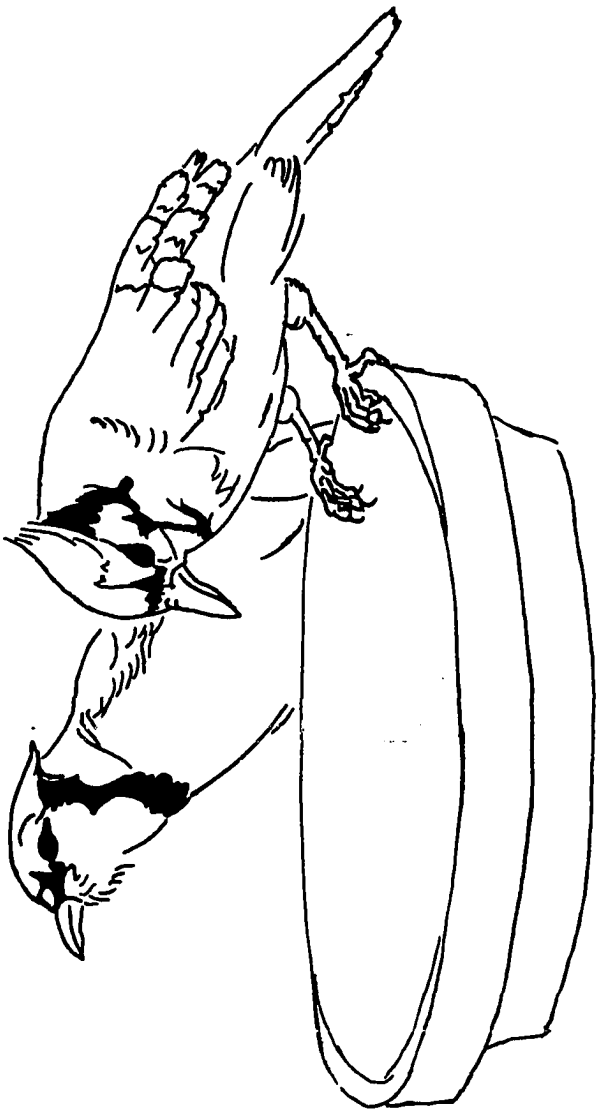

F

Figure 13. Avoidance posture (exhibited by bird at left).



feeding, apparently waiting for the dominant(s) to feed and leave. In this situation, the subdominant exhibits what I will call the avoidance posture toward the dominant bird. This is illustrated in Fig. 13, where the dominant bird is on the right. The avoiding bird perches with its bill closed, and its head and bill pointing parallel to or away from the dominant. The crest is relaxed or sleeked, and the head is above the tail and body axis. Wings are appressed, and the tail is closed and often deflected downward. At times the subdominant may lean slightly away from the dominant. Eye contact is avoided.

The avoided bird need not have assumed an aggressive posture. Assumption of an aggressive or threat posture under these circumstances would normally result in the flight of the subdominant. Avoidance behavior is strongly influenced by the position of the individuals in the dominance hierarchy. This behavior permits two or more birds to be at the feeding station simultaneously, although the dominant has first choice of food. This behavior also facilitates conservation of energy in that the dominant bird does not supplant other individuals while feeding. If the birds have been without food for several hours or if the feeder contains an especially favored food such as peanuts or graham crackers, supplanting occurs more than avoiding.

Nestling alarm freeze (Fig. 14). In response to mechanical nest disturbance or an alarm call given by an adult

Figure 14. The nestling alarm freeze.

Blue Jay, nestling jays assume what I have called the alarm freeze. In this posture the bill is closed and directed upward. The crest and body plumage are sleeked, wings closely appressed to the body, and tail closed. The head is drawn down between the shoulders and the body is fully crouched and held completely rigid. Unless the nestlings are further disturbed by handling, which may elicit a distress call, no vocalizations accompany this posture.

Appeasement posture (Fig. 15). When one bird is cornered during a fight or chasing bout by another individual that is higher in the dominance hierarchy, the cornered bird assumes a submissive stance that I have called the appeasement posture. In appeasement posture the body is held rigid, with the head and opened bill pointed upward and the tail deflected downward so that the bird's body axis, including head and tail is nearly perpendicular to the perch. The bird is fully tiptoed in this posture with body plumage sleeked and wings closely appressed to the body. While the cornered bird is in the appeasement posture, the dominant bird (on the right, Fig. 15) pecks lightly at the exposed neck and belly of its subdominant, but never enough to inflict any injury. At some point the head is slightly higher than the head of the cornered bird. At this point the dominant pecks at the subdominant's bill or even inserts its bill into the open mouth of the submissive individual.

Some elements of the appeasement posture are similar to other submissive displays of the Blue Jay. Exposure of the

Figure 15. Appeasement posture (exhibited by bird at left).

belly and neck occur during aggressive encounters because the winner of the encounter always has its head lower than the head of the loser and in a position from which it could easily peck at these vulnerable places. The open bill is characteristic of displays of adult females soliciting food or copulation (Figs. 16 and 18) and young birds soliciting food. The rigid, bill-up body position is similar to the stance of nestlings in the alarm freeze (Fig. 14). Hardy (1961) has described the postures assumed during conflicts between dominant and subdominant Mexican Jays. They are remarkably similar to the postures and movements of Blue Jays in a dominance conflict.

Courtship feeding solicitation (Fig. 16). This is characteristically a female display, although it is occasionally given by an adult male. When she is soliciting food from her mate or a courting male, the adult female crouches slightly, fluttering her partly fanned wings and tail. The crest is relaxed or sleeked and the body plumage is relaxed. The head, with slightly open bill is held nearly horizontal to the body axis and below the tail tip. An offering of food or nest material from the female may elicit a very brief courtship feeding solicitation display from the adult male. Courtship feeding solicitation display is always accompanied by the begging "keu" call.

The intensity of courtship feeding solicitation by the female varies considerably. At times she will follow her

Figure 16. Courtship feeding solicitation.

mate, giving the display with intense begging vocalizations until she is presented with a food item or a piece of nest material. At other times the male brings items unsolicited, and the female accepts them with a minimum of wing fluttering, crouching and vocalizing.

Courtship feeding (Fig. 17). Both courtship feeding and as well as courtship feeding solicitation are an integral part of pair formation, nest building, incubation, care of the young, and pair bond maintenance in Blue Jays (Hardy, 1961). Courtship feeding first appears when two birds have formed a weak pair bond during the courtship activity that precedes nesting. Before nest building begins, food items are the only type of material exchanged between members of a pair. As nest building begins, exchanges of nest material increase and, at the height of nest building, these outnumber exchanges of food. During incubation, which is entirely a female activity, the exchange of food items again increases as the male feeds his mate while she incubates. Although she continues to forage for herself during brief absences from the nest, the female receives much of her food from the male. After the young have hatched, courtship feeding continues, but at a lower rate, and the female rarely eats the food she receives from her mate, passing most of it to the young. The male also brings food directly to the young, although it may be a day or so before he gives it to them directly, rather than giving it to the female. Hardy (1961) has carefully

Figure 17. Courtship feeding.

described courtship feeding in the Blue Jay and my account does not differ from his.

Fig. 17 is a sketch of two birds about to exchange a food item in courtship feeding. At the moment of exchange, both birds give the begging "keu" call. The female may occasionally present her mate with a food item or piece of nest material. This presentation is rarely solicited by the male, although at the moment of exchange he will give a brief courtship feeding solicitation display along with the "keu" call. At times, an item may be passed back and forth several times between the pair before it is eaten or taken to the nest. During this "trading" of items there is little crouching or wing fluttering by either bird, but the begging "keu" vocalization is quite intense.

As Hardy (1961) has pointed out, the behavior patterns characteristic of courtship feeding are an integral part of the reproductive cycle from the onset of courtship through care of the young. I have noted that many of the captive jays maintained pair bonds during the entire non-breeding season after they had paired in the spring of 1971. No courtship display or copulation was observed during this period, but courtship feeding continued with high frequency and seemed to be the most important factor in maintaining pair bonds. In late winter and spring of 1972, birds that had maintained pair bonds from the spring of 1971 showed very little courtship display, if any, but continued courtship feeding, which increased as the breeding season progressed.

Nestling and fledgling food begging display. The food begging display of young Blue Jays is quite similar to the courtship feeding solicitation display of the adults. When begging for food a young Blue Jay almost always holds the bill completely open, exposing its bright pink gape, which provides an additional visual cue or "target" for the adult as it gives food to the young bird. The color of the gape in adults is black, and this color difference, in addition to obvious differences in body size and development of plumage, is a major visual characteristic that distinguishes the food begging display of the young from courtship feeding solicitation by adults.

The vocalizations accompanying food begging display in young birds are structurally quite different from the begging "keu" that accompanies courtship feeding solicitation display of adults. However, to the human observer, the two calls sound alike. Their differences will be discussed later in the chapter on acoustic signals.

Precopulatory display and copulatory position (Fig. 18). This display, given only by adult females ready for copulation, is like courtship feeding solicitation, but its features are more exaggerated. Specifically, the wings and tail are fully open and very vigorously fluttered. At the same time, the body is completely, rather than partially, crouched during the display. Precopulatory display, like courtship feeding solicitation display, is invariably

Figure 18. Precopulatory display and copulatory position.

accompanied by the begging "keu" call. Unfortunately, I have not observed copulation or recorded it on film. Its description awaits further observation.

CHAPTER IV

VOCALIZATIONS

Introduction

Many Blue Jay vocalizations have been previously described by Amadon (1944), Bent (1946), Hardy (1961, 1964, 1969), and Edwards (1971). Some of these descriptions have included sonagraphic analyses (Hardy, 1964, 1969; Edwards, 1971); however, detailed descriptions of most of the parameters of vocalizations have not been published. Similarly, although some authors have suggested functions of some of the vocalizations (Amadon, 1944; Hardy, 1961; Edwards, 1971), no study directed primarily at determining the function of Blue Jay vocalizations has been published.

Vocalization Parameters

In discussing the results of sound analyses, I will describe the following parameters of each vocalization: number of sound sources, fundamental frequency, number and frequency of harmonics, dominant frequencies (in vocalizations with harmonics or with elements produced by both sound sources), inflection, frequency modulation, and

temporal characteristics (including the number and duration of notes or clicks). Amplitude modulation is present to some degree in almost all vocalizations, and it will not be discussed.

A few terms should be defined to avoid confusion. In addition, because many terms, as well as names of vocalizations, will be used quite frequently, I will give an abbreviation or symbol for the terms the first time they are introduced, and, thereafter, use the abbreviation. The Appendix lists all the terms and their symbols in alphabetical order.

The frequency of a sound is the number of full sound waves (cycles) per second. The unit in which frequency is expressed is Hz (hertz) or KHz (kilohertz). One Hz is equal to one cycle per second, while one KHz is equal to 1,000 cycles per second. Because the narrow band pass filter of the Sonagraph has a frequency resolution of only 45 Hz, and because there are many abrupt, extensive, and irregular changes in frequency within individual calls, I have reported only ranges, rather than averages, of frequencies for the different groups of calls.

A harmonic is a sound caused by non-sinusoidal vibration of the sound source (SS), and whose frequency is some integer multiple of a fundamental frequency (F). Frequency and amplitude modulation (FM and AM, respectively) are changes, not necessarily regular, in the frequency and

amplitude of the sound. In this paper I will describe large, long, irregular changes in frequency as changes in inflection, and small, short, fairly regular changes as FM.

Birds that have a tracheo-bronchial syrinx, and this includes the Blue Jay, are capable of producing two different sounds simultaneously (Miskimen, 1951). When a vocalization is made up of two different sounds, they may be identified if they are of different F or, when they are of the same F, if each sound is amplitude and/or frequency modulated in a different manner.

Vocalizations

I have made tape recordings of all of the vocalizations given by my hand-raised Blue Jays and performed sonagraphic and oscilloscopic analyses of as many recordings as possible of each type of vocalization. In addition, I have attempted to determine the function of each vocalization by observation and, in some cases, by experimentation. The function of a particular call is influenced by 1) the physical characteristics of the call, 2) postures associated with the call, and 3) the behavioral context of the call.

Some of the vocalizations I have analyzed are similar in structure as well as function. These similarities prompted me to group the calls into four categories: 1) harmonic spectra, 2) pumphandle calls, 3) click calls, and 4) song.

The calls in the harmonic spectra group are

physically similar in that they are rich in harmonics. The physical attributes by which they differ are the number of SS, the F, inflection and the nature of modulations. Functionally these calls are indicators of alarm, frustration, and excitement associated with fear. They may also serve as contact notes within a flock, among family members, or between members of a pair.

The pumphandle calls have two SS, similar AM and FM, and a lack of pronounced inflection. They differ in F and the number of harmonics present. Functions of these calls include the indication of mild excitement and uncertainty, and they also may serve as territorial or alert calls.

The click calls are characterized by the presence of harmonics, presence of clicks, strong and regular AM and FM and terminal downward inflection. They may be distinguished from each other by their F and the number of SS present. They function to indicate excitement associated with both frustration and fear.

The physical characteristics of song are highly variable. However, it is a distinctive vocalization type in that its phrases, as well as entire singing bouts, are quite long, occasionally lasting over two minutes. Song is the sole vocalization given by the male during courtship. It is also given intermittently by birds in a calm behavioral state.

All of the illustrations of vocalizations in this paper consist of two types of sonagrams. The sonagrams on

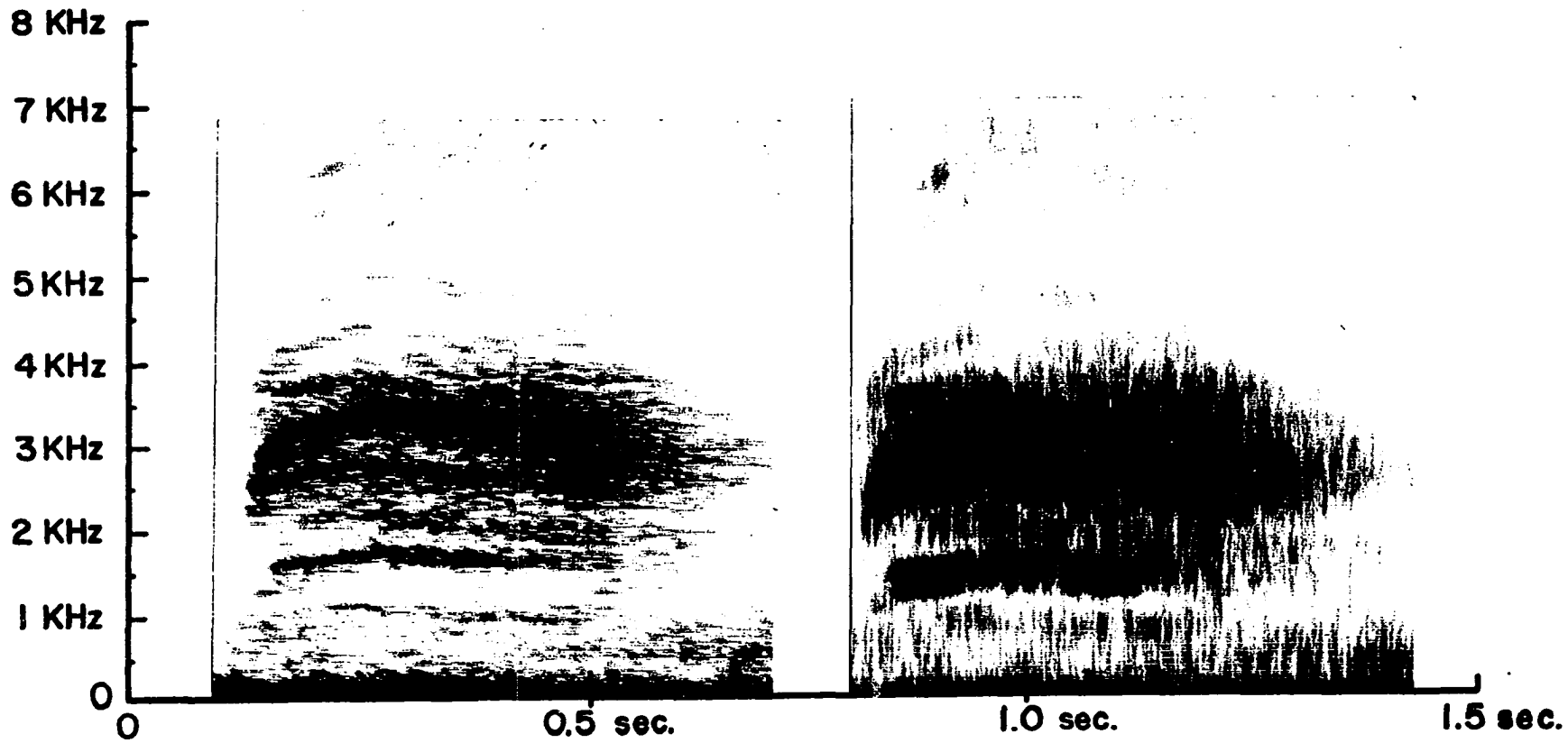
the left in each illustration were made with the narrow band pass filter, which has a frequency resolution of 45 Hz. Those on the right were made with the wide band pass filter, which has a frequency resolution of 300 Hz and a temporal resolution of 1.5 ms (milliseconds). Sonagrams made with the narrow band pass filter have poor temporal resolution. All sonagrams were made at the frequency band setting that has lower and upper effective resolutions of 80 and 8000 Hz, respectively.

Harmonic Spectra

The Distress Call (DC, Fig. 19) is given by birds that are being handled, confined (such as in a very small cage, an insect net, or a mist net), or chased. The only body posture consistently associated with this call is crouching in its most extreme form.

The DC has the form of a simple cry; that is, it has a rainbow-shaped sonagram (Davis, 1964), indicating that the frequency builds and then drops as the mandibles open and close. The call contains elements from both SS. The first and most obvious sound (S1) is responsible for the shape of the sonagram. The F of S1 starts between 0.50 and 1.60 KHz, rises a maximum of 0.30 KHz or a minimum of 0.20 KHz, and, from this point, drops 0.30 to 0.40 KHz. S1 may have from 4 to 11 harmonics, among which dominance shifts from higher harmonics at the onset of the call to lower harmonics as the frequency rises and then back to higher harmonics as

Figure 19. The Distress Call (DC).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6 KHz
5 KHz
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2 KHz
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0.5 sec.
1.0 sec.
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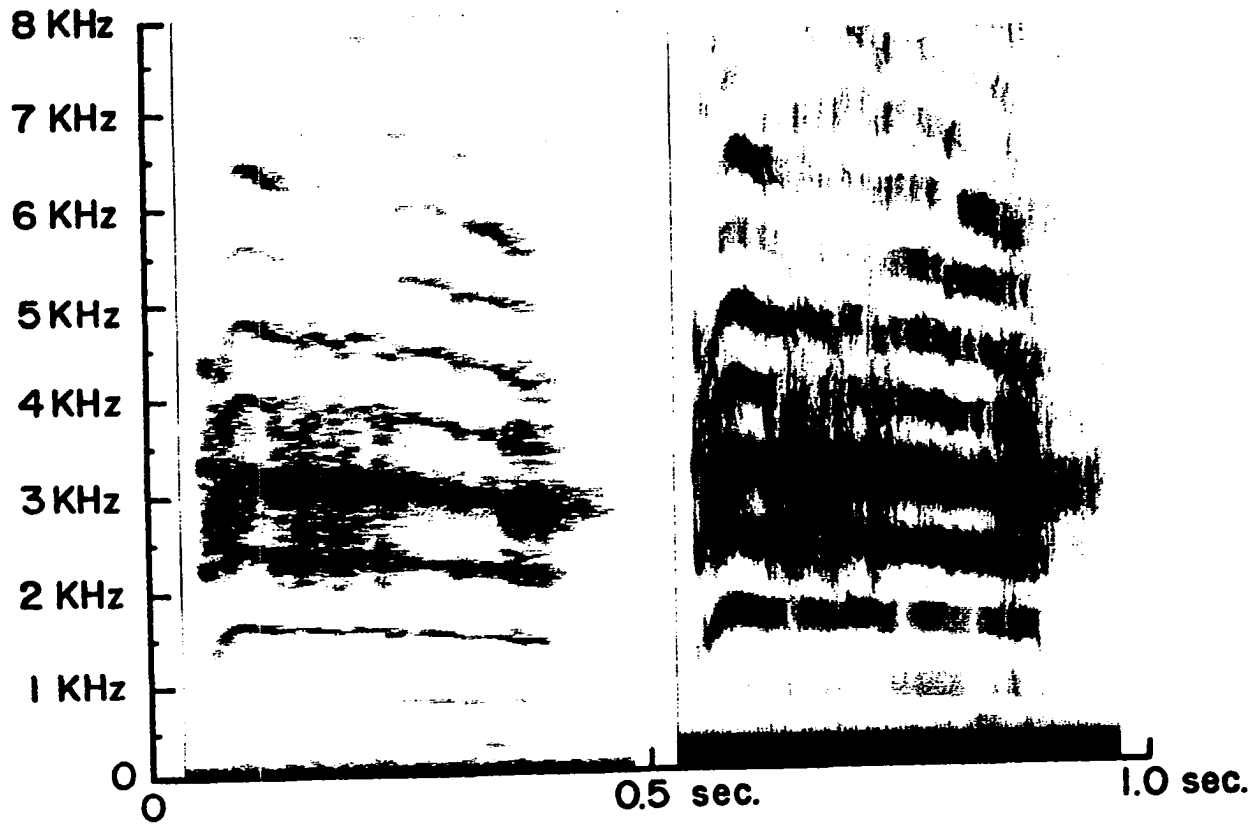
the frequency drops. The most intense harmonics are the first through the fourth (H1-H4). The duration of S1 ranges from 225 to 600 ms (avg. = 412).

The second sound (S2) begins 25 to 50 ms after the first, at a frequency between 0.70 and 1.00 KHz. It is slightly downwardly inflected (about 0.10 or 0.20 KHz) until the end of the call. This sound is usually frequency modulated during the last 100-150 ms of the call. The modulation is of about 0.50 KHz, but varies. S2 may have 6 to 11 harmonics, the most important ones being H1-H4. The duration of S2 ranges from 200 to 350 ms (avg. = 275).

The Alarm Call (AC, Fig. 20). A Blue Jay that spots a potential predator usually gives this vocalization. In 74 cases where such a potential predator was within sight of my captive birds, this call was given 63 times (85%). Calculation of the Chi-square statistic to test whether the behavior is associated with the call more than 50% of the time showed that there was an association between the two ($X^2 = 36.54$, $P < .005$). Of 213 observations when the posture associated with the call was noted, 85 calls (40%) were given with simple bobbing (usually the exaggerated type), 68 (32%) with the mild or intense aggression posture and 60 (28%) with the neutral posture.

The AC has only one SS and has from five to seven harmonics, the most intense of which are H1-H4. The F of these calls is never as intense as any of the harmonics.

Figure 20. The Alarm Call (AC).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0.5 sec.
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During the first 25 ms of the AC there is a sharp rise in frequency of 0.05 to 0.20 KHz. In the next 50 to 100 ms the frequency remains stable and then, in the next 100 to 150 ms either remains stable or drops about 0.05 KHz. The frequency continues to drop 0.05 to 0.10 KHz during the remainder (125 to 300 ms) of the call.

The call usually contains FM at two different points--from 75 to 150 ms and from 75 to 125 ms during the last half of the call. The duration of AC calls ranged from 300 to 475 ms with an avg. of 389 ms.

The Flock Contact Call (FC, Fig. 21). During the non-breeding season (August through February), Blue Jays often travel in flocks (Hardy, 1961; Sutton, 1966). When members of the flock are scattered or when they are not in sight of each other, they give the FC. By observing the context in which the FC was given, as well as by determining how often the call is given when birds were or were not in flocks, I hypothesized that the FC was used as a contact note; that is, the FC is given by birds as a means of acoustically specifying their location to other birds in the flock, who, in turn, are able to "keep track" of their flock mates acoustically.

Although the FC is heard throughout the year, it is more frequent during the non-breeding season. In 1969 and 1970, at least once a week, I recorded the number of FC given by both captive and wild birds for an hour. Observations were made between 0900 and 1100. Fig. 22 is a graph of the number of FC per hour during each month of the year.

Figure 21. The Flock Contact Call (FC).

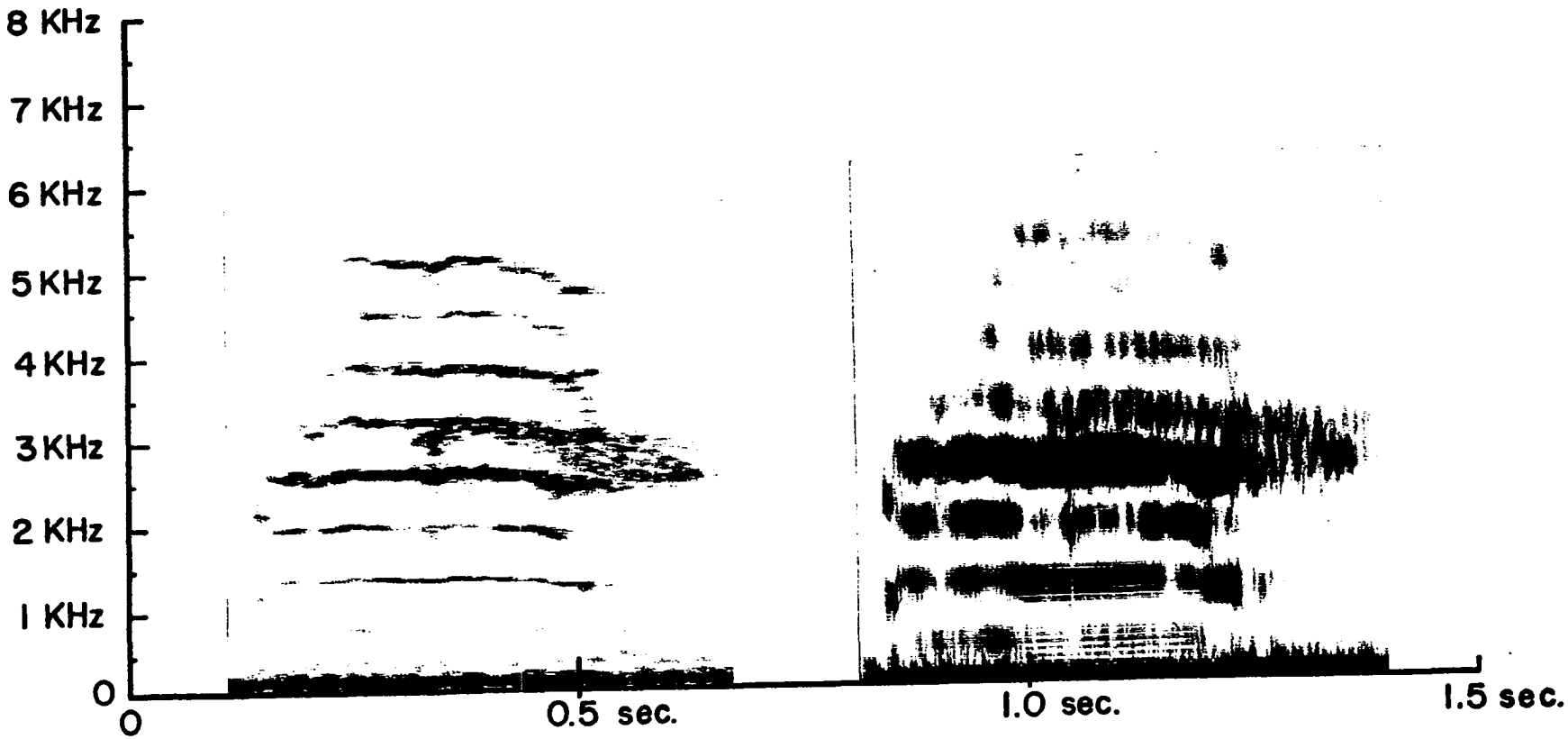
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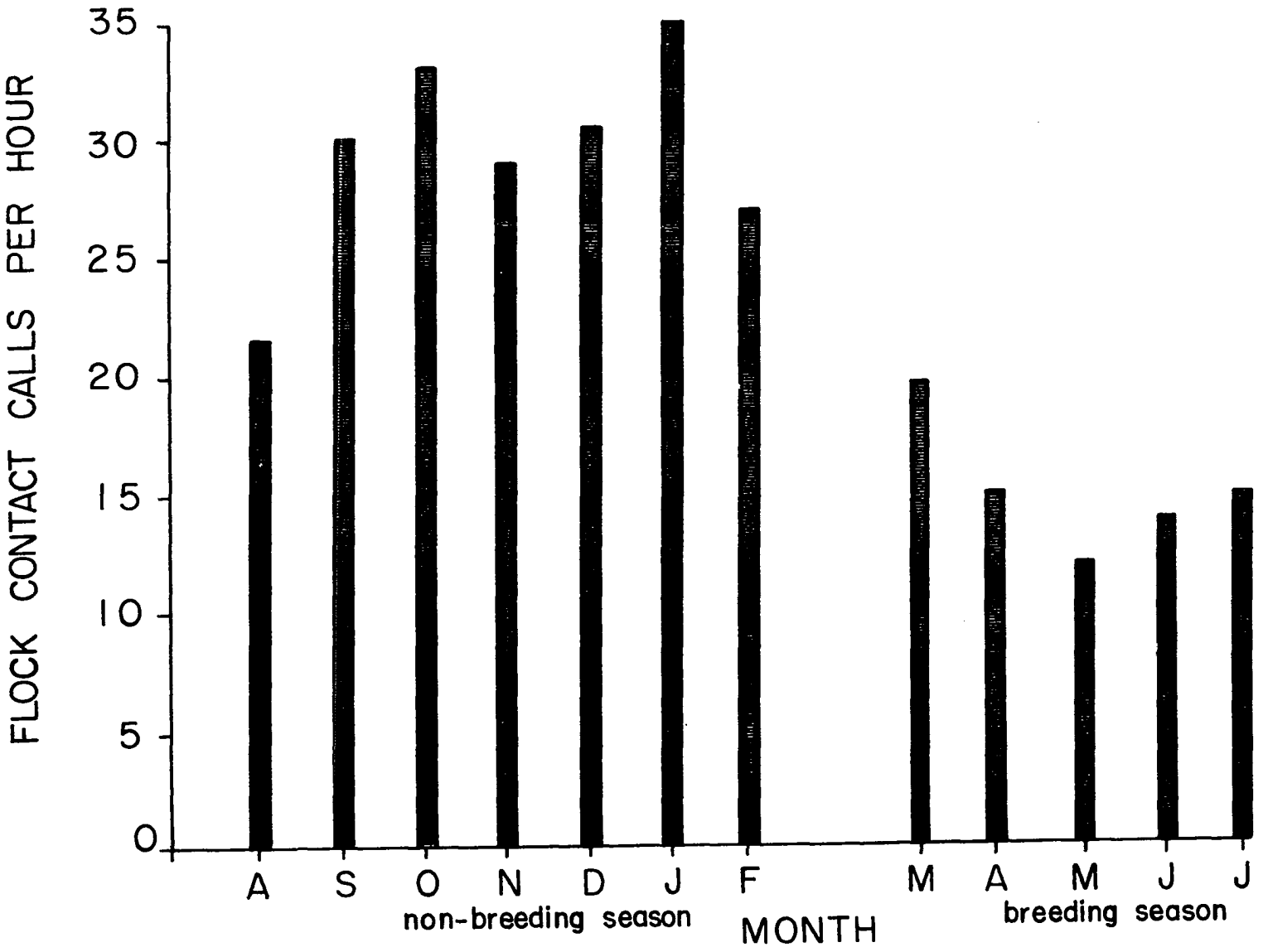
Figure 22. The number of Flock Contact Calls per hour throughout the year.


FLOCK CONTACT CALLS PER HOUR
35
30
25
20
15
10
5
0
A
S
O
N
D
J
F
M
A
M
J
J
non-breeding season
MONTH
breeding season

The number of FC per hour during the non-breeding season is higher (avg. = 29) than that during the breeding season (avg. = 15). When the weekly means of FC per hour in the two seasons are compared, there is a significant difference ($t = 9.36$, $P < .005$) between the two groups.

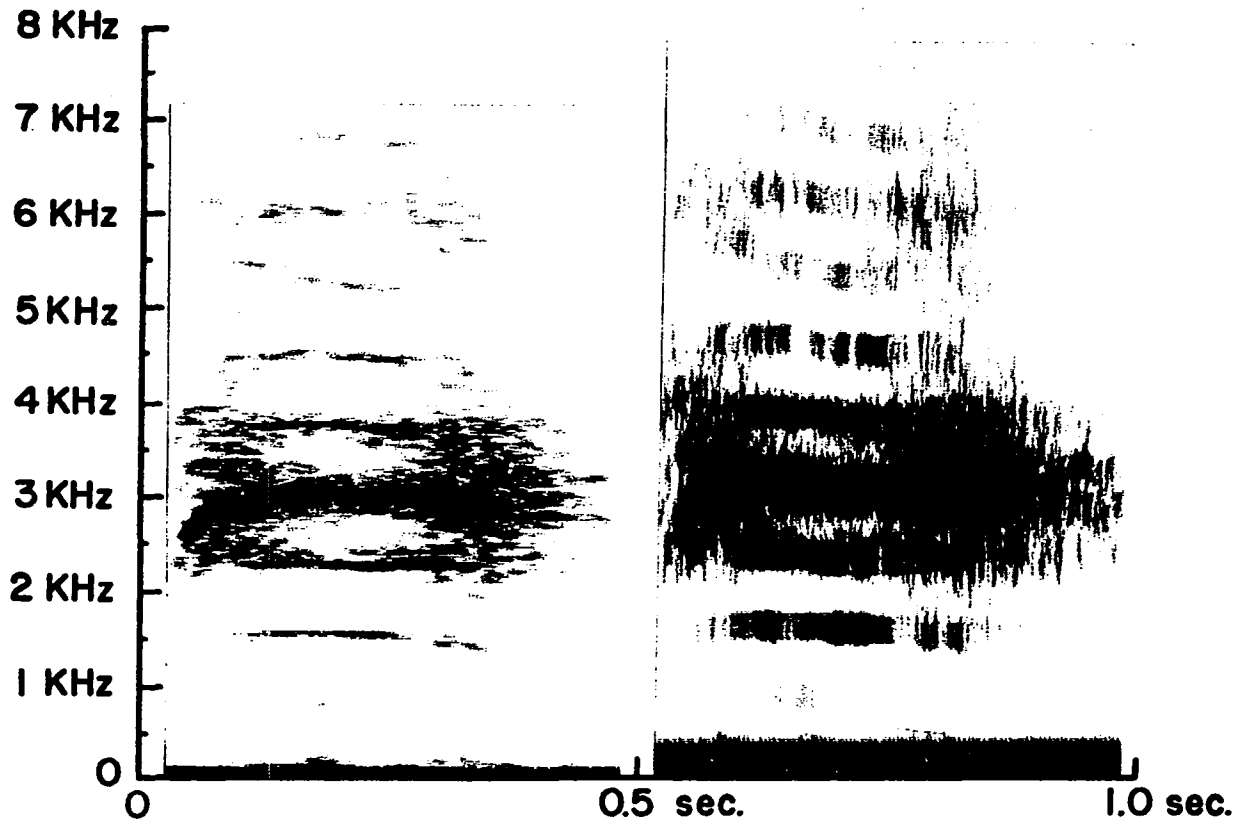
The FC is associated with simple bobbing, neutral or maintenance postures. The FC has two SS, the first being of a relatively low F (0.40 to 0.90 KHz) with five to seven harmonics. H3 is always the dominant frequency, with H1, H2, and H7 also being quite intense. The F is rarely more intense than any of the harmonics.

Regardless of the value of the F at the onset of the call, it is warbled over a range of 0.50 to 1.50 KHz above and below the initial value throughout the duration of the FC. The duration of S1 ranges from 375 to 475 ms (avg. = 432).

The value of the F of S2 in the FC ranges from 0.90 to 1.80 KHz. There are always two harmonics, either one of which may be dominant. The F is always less intense than either harmonic. S2 begins from 25 to 200 ms after S1 and is warbled throughout its duration from 0.25 to 1.20 KHz above and below the F. There is usually a terminal downward inflection. The duration of S2 is from 150 to 400 ms (avg. = 373).

The FC of young (one to three months of age) Blue Jays (YFC, Fig. 23) differs in some notable ways from that of adults. The F of S1 is generally higher in value (0.75 to

Figure 23. The Flock Contact Call of young Blue Jays (YFC).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0.5 sec.
1.0 sec.

1.65 KHz) and has fewer (none to four) harmonics. The duration of this sound has a greater range (350 to 500 ms) and it is, on the average, longer (avg. = 437).

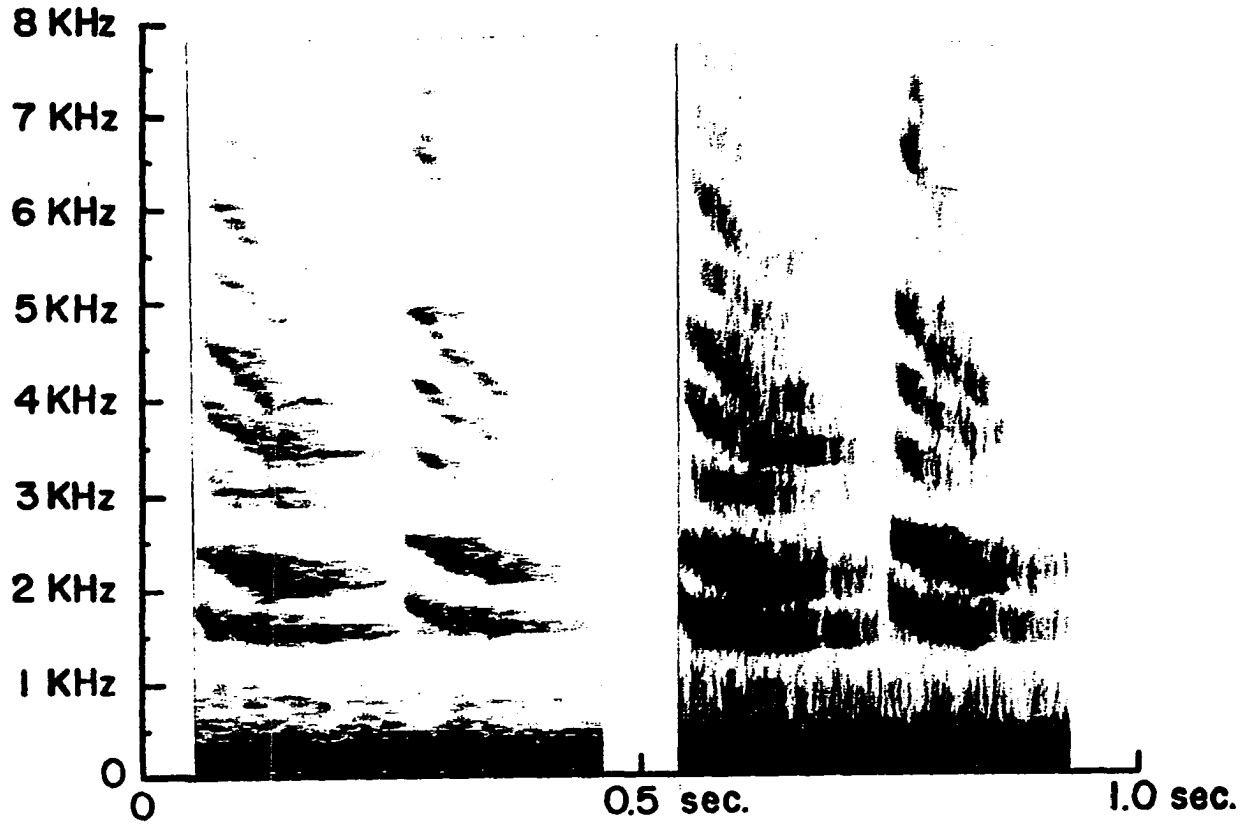
S2 in the YFC has an F higher than that of the S2 F in the adult call (1.85 to 2.40 KHz). It usually has the same number of harmonics, but the F may be more intense than either (but not both in the same call) harmonic. The duration of S2 ranges from 300 to 525 ms and it is longer (avg. = 443) than that of S2 in the adult call.

The Young Food-begging Calls (YFB, Figs. 24-27) are quite variable and I have divided them into four types: YFB1, YFB2, YFB3, and YFB4.

All YFB calls are given by nestling or fledgling birds as they beg for food. These calls are accompanied by the young food-begging posture (see Chapter III) about 50% (32 of 65 cases) of the time in two- to three-week-old nestlings and about 80% (27 of 34 cases) of the time in fledglings. YFB1 and YFB2 are given by birds that are at least about 14 days old. YFB3 calls are given by one- to three-week-old nestlings and rarely by fledglings, while YFB4 calls are given by nestlings less than about 10 days old.

YFB1 calls (Fig. 24) have only one SS, whose F ranges from 0.70 to 1.20 KHz, and they have five to nine harmonics. The order of dominance of harmonics is sequential, H1 always being the dominant, H2 second in intensity, and so on. The F is always the least intense frequency.

Figure 24. The Food-begging Call of young Blue Jays, Type 1 (YFB1).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7 KHz
6 KHz
5 KHz
4 KHz
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1 KHz
0
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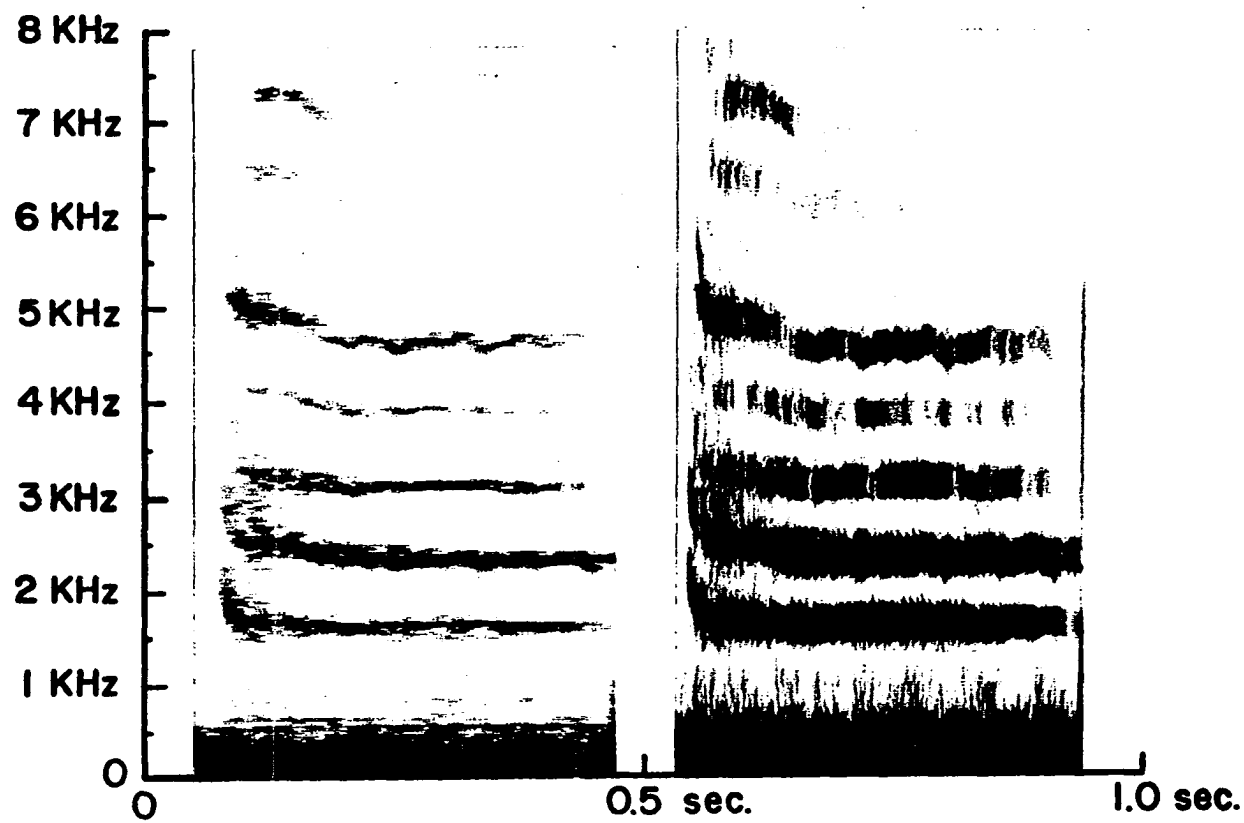
0.5 sec.
1.0 sec.

Figure 25. The Food-begging Call of young Blue Jays, Type 2 (YFB2).


8 KHz
7 KHz
6 KHz
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4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.

There is a decrease in frequency throughout most calls that is abrupt during the first 0 to 50 ms and then slower for the rest of the call. Total decrease in frequency ranges from 0.05 to 0.50 KHz, but is usually less than 0.10 KHz.

YFB1 calls are relatively short in duration, lasting from 100 to 300 ms (avg. = 209).

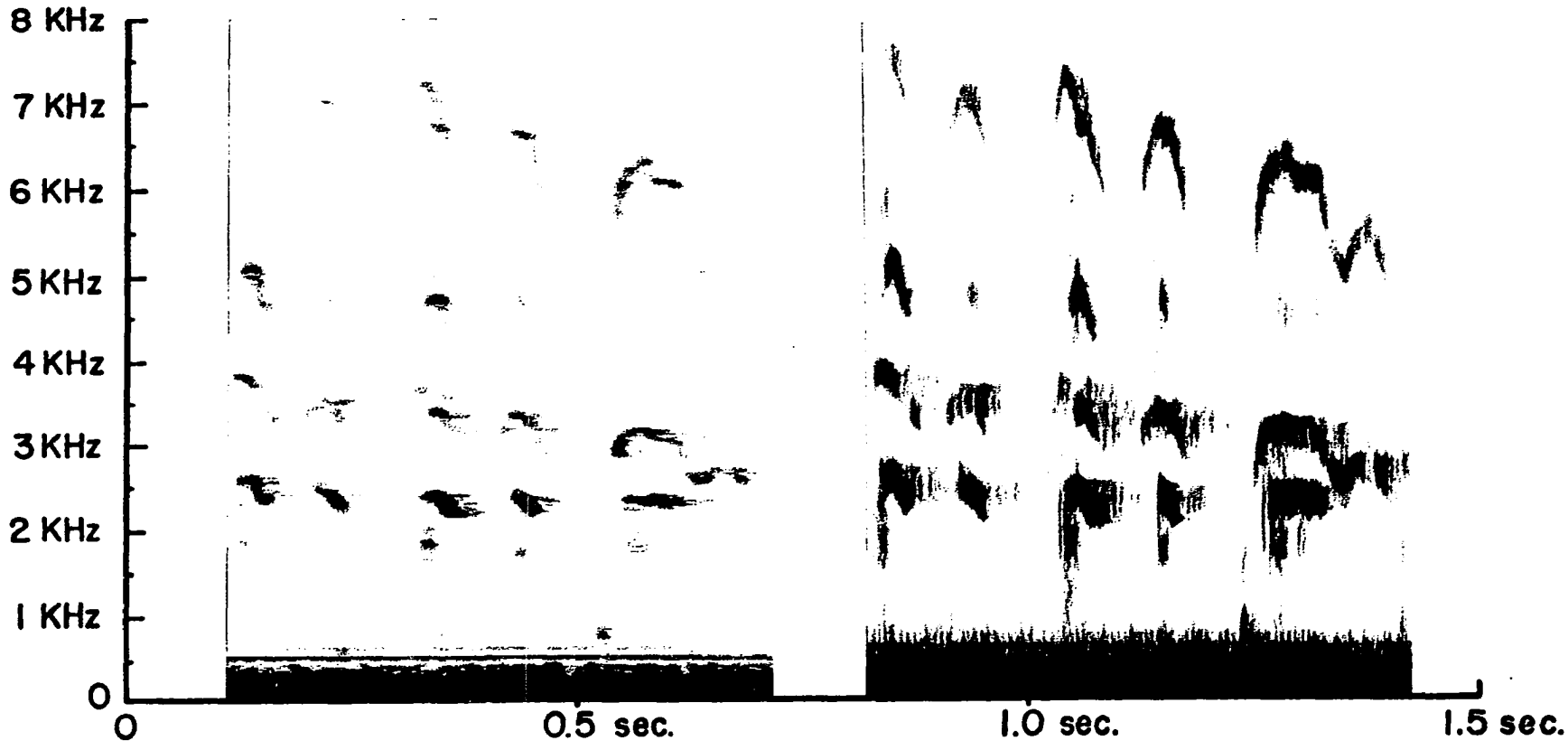
YFB2 calls (Fig. 25) may have one or two SS, the first of which has an F of from 0.30 to 2.00 KHz, but usually between 0.60 and 0.90 KHz. The sound is often warbled from 0.50 to 1.50 KHz above and below the F, but the F may be constant throughout the call. There are from one to ten harmonics (usually five to eight), and H1 is dominant, H2-H4 also being quite intense. The F is never more intense than any of the harmonics.

The duration of the first sound is from 75 to 1000 ms (avg. = 395).

S2, which appears in 5 out of 16 calls, begins 100 to 450 ms after S1. It has an F of 0.50 to 3.30 KHz, and remains constant in three out of five cases. When it does not remain constant, it is warbled from 0.25 to 0.30 KHz above and below the F. There are no harmonics. S2 has a duration of 100 to 350 ms (avg. = 225).

YFB3 calls (Fig. 26) are short notes given in series. Of 21 YFB3 analyzed 14 had two SS. S1 has a F of 0.90 to 2.80 KHz. During the first 25 ms of most calls the frequency

Figure 26. The Food-begging Call of young Blue Jays, Type 3 (YFB3).


8 KHz
7 KHz
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3 KHz
2 KHz
1 KHz
0
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0.5 sec.
1.0 sec.
1.5 sec.

is inflected upward 0.10 to 0.80 KHz and then drops back down 0.20 to 0.40 KHz. Occasionally, the F may simply drop 0.10 to 0.40 KHz. The F may simply drop 0.10 to 0.40 KHz in the first 25 ms. For the next 50 ms the F remains the same or is inflected downward 0.10 to 0.30 KHz. If the note is longer than 50 ms there may be another warble of the F through about 0.10 or 0.20 KHz or it may remain the same. S1 of YFB3 calls is quite short in duration, ranging from 25 to 150 ms (avg. = 69).

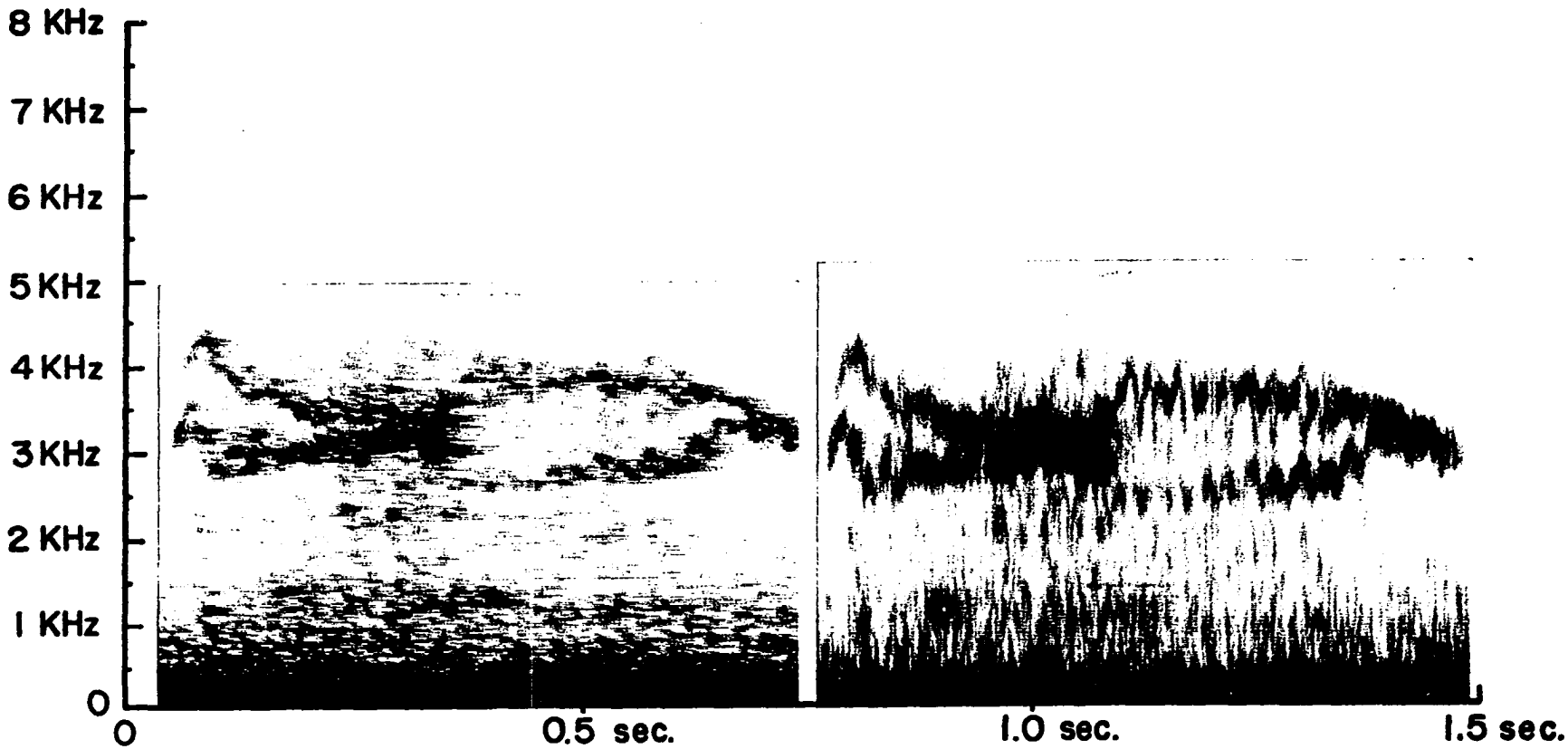
S2 of YFB3 calls have a F of from 2.70 to 3.90 KHz. In the first 25 ms the F drops 0.10 to 0.20 KHz or is sharply inflected upward 0.10 to 0.70 KHz and then drops 0.10 to 0.20 KHz. In the next 25 ms the frequency continues to drop another 0.10 to 0.20 KHz, and, thereafter, remains the same if the call is longer than 50 ms. S2 is short, except in a few cases, lasting from 50 to 150 ms (avg. = 77).

Both S1 and S2 characteristically have one harmonic, although in 6 of 38 cases there are no harmonics and in 3 of 38 calls S1 had five harmonics. The F is the dominant frequency except in the three calls which had five harmonics. In those cases the order of dominance of harmonics is sequential, H1 being the most intense and the F least intense.

YFB4 (Fig. 27) vocalizations have two SS, neither of which has harmonics, and both of which have strong FM.

S1 in the two calls examined started at 3.40 and 4.00 KHz and was warbled throughout the call over a range of 0.30

Figure 27. The Food-begging Call of young Blue Jays, Type 4 (YFB^4).


8 KHz
7 KHz
6 KHz
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3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.
1.5 sec.

to 0.50 KHz. The duration of S1 in one call was 100 ms, in the other, 700 ms.

S2 in the first call started at 3.10 KHz, in the second at 2.70. Both sounds were warbled continuously from 0.20 to 0.40 KHz. The duration of S2 in one case was 600 ms and in the other 700 ms.

The Begging Keu Call (BK, Fig. 28) is the vocalization that characteristically accompanies courtship feeding and probably copulation. Although I have not observed copulation, in 209 of the 256 cases (82%) when I recorded the vocalization accompanying courtship feeding, it was BK. The remaining cases were either unaccompanied by vocalization or were accompanied by the SK. Calculation of Chi-square shows BK to be associated with courtship feeding more than 50% of the time ($X^2 = 105.08$, $P < .005$).

Three BK were analyzed, and their F values were 1.70, 1.70 and 1.80 KHz. In the first 100 ms each call was inflected downward 0.10 KHz and then remained at that frequency for the rest of the call. All of the F were warbled or frequency modulated about 0.60 KHz above and below the F throughout their duration. There were two harmonics in each call; H1 was the dominant frequency and H2 the least intense frequency. The three calls lasted 125, 150 and 200 ms (avg. = 158).

The Soft Keu Call (SK, Fig. 29) functions as a contact note between members of a pair or among members of a

Figure 28. The Begging Keu Call (BK).

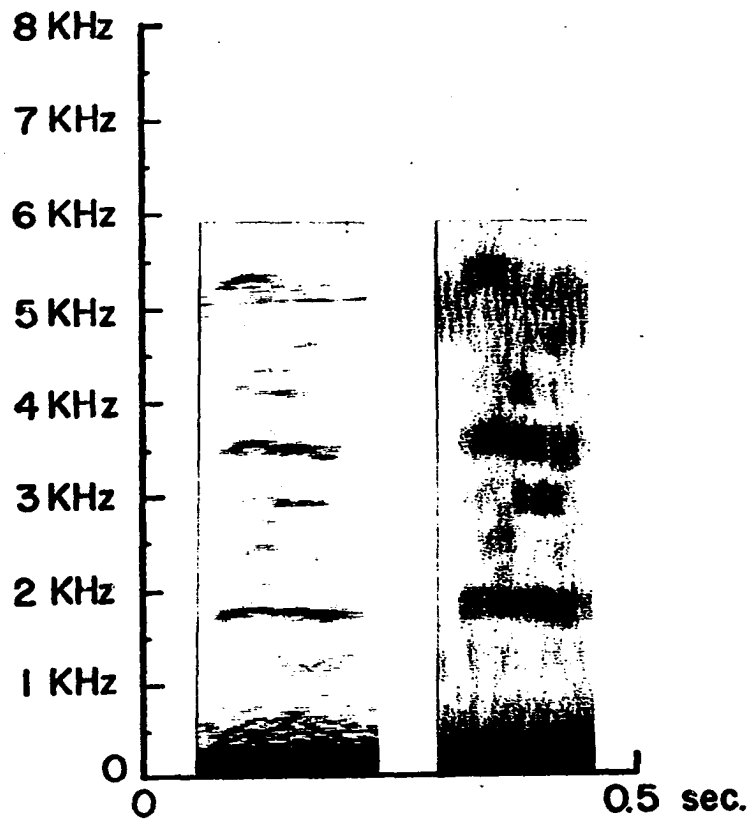
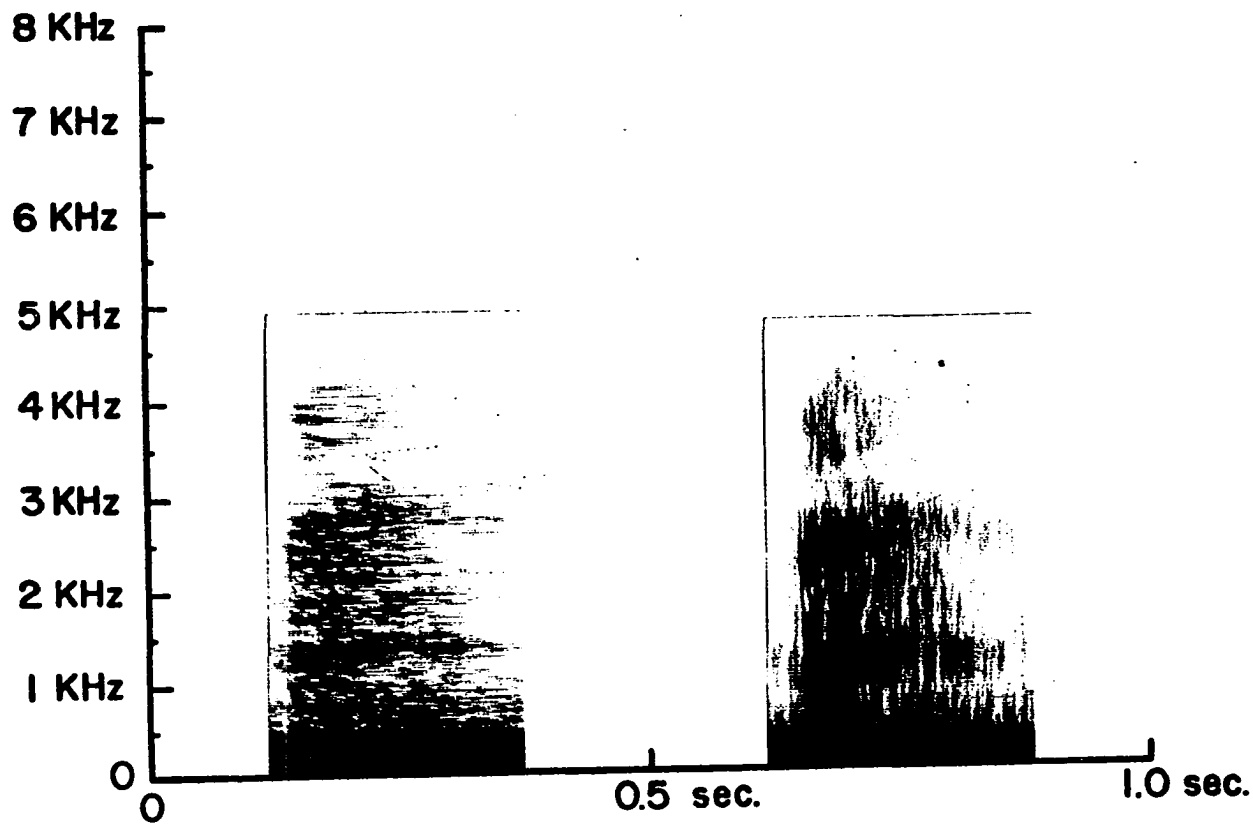

8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.

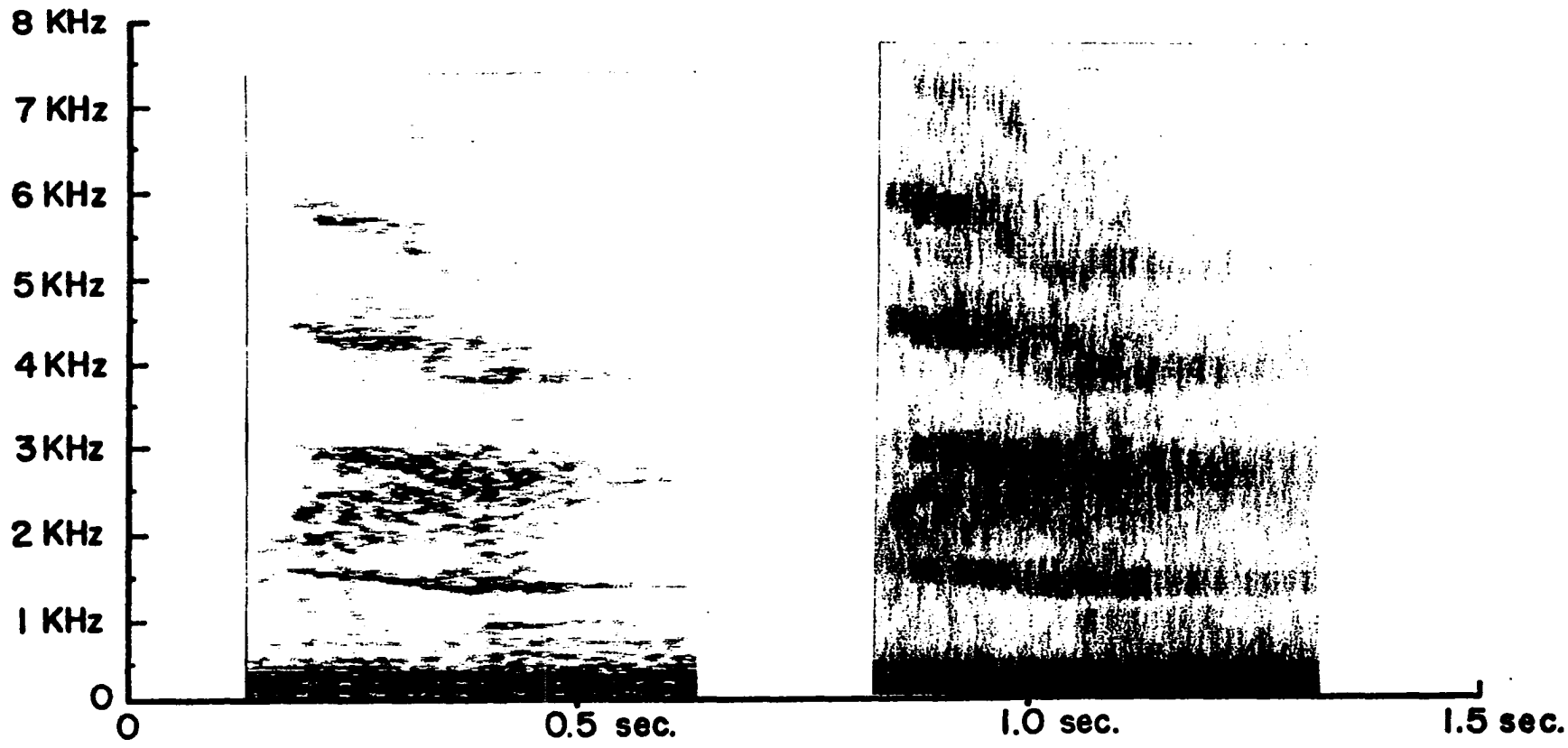
Figure 29. The Soft Keu Call (SK).


8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.

family group when birds are relatively close to each other. I tested the hypothesis that the SK functioned in this manner by recording the number of times the SK was given by members of a pair or family of captive or wild birds when they were less than 10 m apart and when they were more than 10 m apart. Of a total of 731 SK recorded, 627 (85%) were given by birds less than 10 m apart. This is significantly more (X^2 = 374.18, $P < .005$) than the number of SK (104 or 14%) given by birds more than 10 m apart. Birds giving the SK are usually in neutral or maintenance posture. Occasionally, they are involved in courtship feeding. The SK is a very simple call with no inflection of the F, constant FM, a rich harmonic spectrum and a short duration. F ranges from 0.60 to 2.00 KHz and is modulated 0.10 to 0.30 KHz throughout its duration. There are from two to five harmonics with the dominant frequencies being H1 or F. Other harmonics of high intensity are H2 and H3. The SK varies in length from 25 to 300 ms (avg. = 193).

The Loud Keu Call (LK, Fig. 30) may connote frustration (as when a bird can see, but cannot get to a food dish or its mate) or hunger (in adult birds). In these cases, especially the latter, the call is occasionally accompanied by fluttering of slightly fanned wings. Simple bobbing was recorded in 17 of 113 cases (15%) when the posture associated with the LK was noted. The LK serves most often as a contact note between members of a pair that are more than about 10 m apart.

Figure 30. The Loud Keu Call (LK).


8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.
1.5 sec.

Of 324 LK, 267 (73%) were given by birds more than 10 m away from their mates. The Chi-square test shows this to be significantly ($X^2 = 136.11$, $P < .005$) higher than the number of LK given by birds less than 10 m from their mates.

The F of LK varies from 1.20 to 1.50 KHz. During the first 100 ms the call is inflected either up or down 0.10 KHz or remains at the same value. Regardless of whether the call is inflected up or down at its onset, after the first 100 ms the frequency drops continuously 0.10 to 0.40 KHz for the rest of the call.

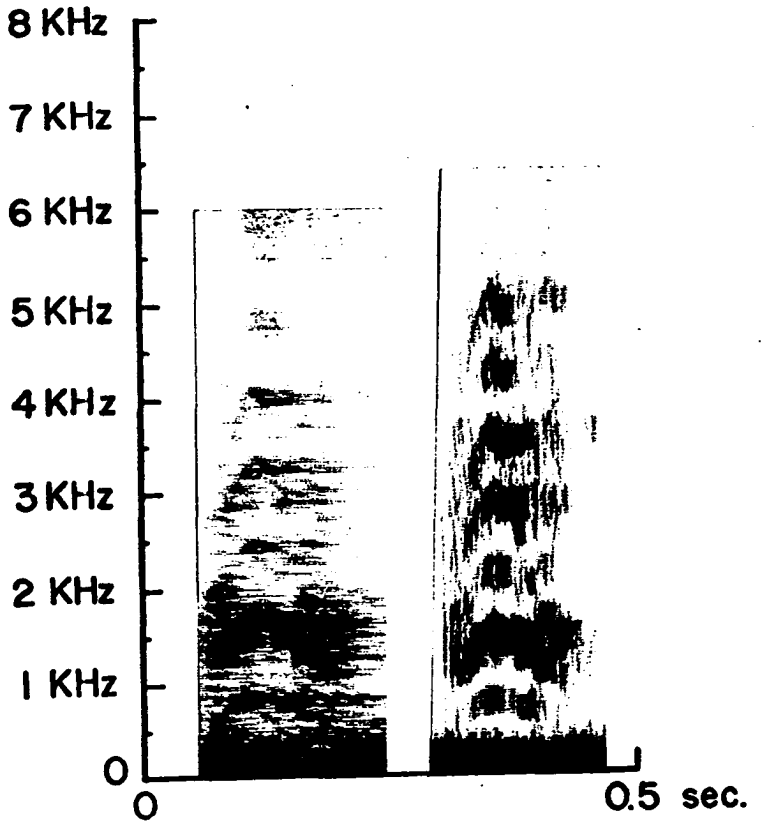
There are from two to five harmonics in LK. The order of dominance of harmonics is usually sequential except that F is usually between H1 and H2 in intensity.

The duration of LK ranges from 400 to 650 ms (avg. = 486).

The Crow Call (CC, Fig. 31) is one of many examples of mimicry in the vocal repertoire of my captive Blue Jays. The jays learned this call from Common Crows (Corvus brachyrhyncos) which fed near their outdoor flight. The call is given intermittently and I have not been able to determine its function, if, indeed, one exists.

The CC has the form of a simple cry and the F ranges from 0.50 to 0.70 KHz. During the first 50 ms the F increases by 0.10 KHz, and, in the second 50 ms it drops back to the original value. Thereafter, the F either remains constant or is deflected downward another 0.10 KHz.

Figure 31. The Crow Call (CC).


8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.

The CC is rich in harmonics, each call having from 6 to 11. Dominant frequencies are H1 and F. Other frequencies of high intensity are H2-H5.

The duration of all the CC analyzed is 150 ms. The mimicked calls compare quite well with published sonagrams (Chamberlain and Cornwell, 1971), with respect to physical characteristics.

The Meow Call (MC, Fig. 32) is another example of vocal mimicry that has no apparent function. During the time I kept them at my home, the captive jays learned to imitate the meow of a pet Siamese cat (sonagram, Fig. 33).

The cat's MC has an F of 0.40 KHz that remains constant throughout the 1200 ms call. There are five harmonics, H3, F, and H1 being most intense in that order.

The Blue Jay MC calls have F of from 0.40 to 0.70 KHz and take the form of a simple cry. During the first 300 to 400 ms, the F is inflected upward 0.10 KHz and then drops back to the original value during the rest of the call. There are from three to seven harmonics and the dominant frequencies are the same as for the cat's MC.

The duration of Blue Jay MC calls ranges from 700 to 1100 ms (avg. = 871).

With the exception of changes in inflection, the Blue Jay MC calls are very similar to the cat MC calls in structure.

Table 2 is a summary of the physical characteristics of the calls in the harmonic spectra group, and Table 3 lists the functions and postures associated with these vocalizations.

Figure 32. The Meow Call (MC).

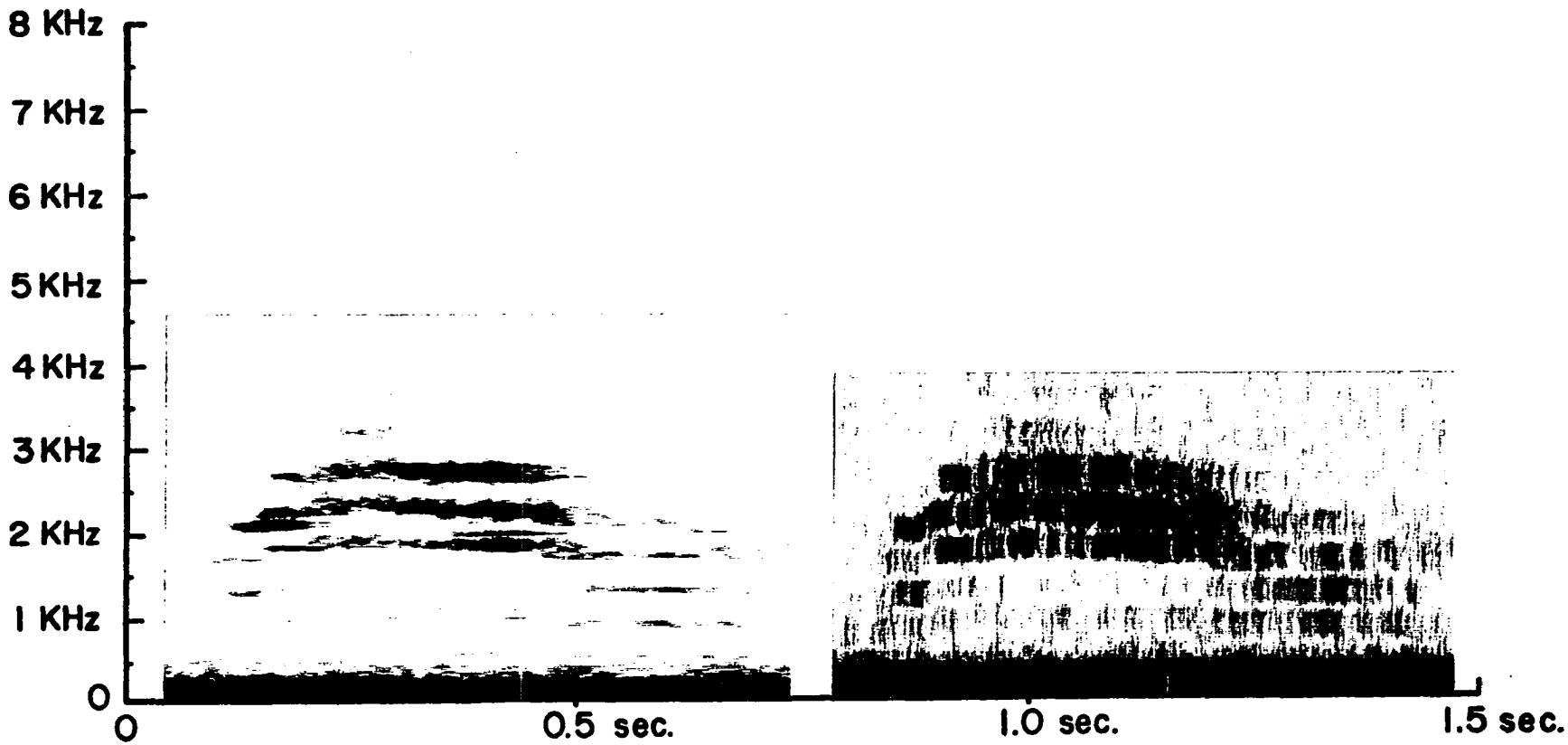
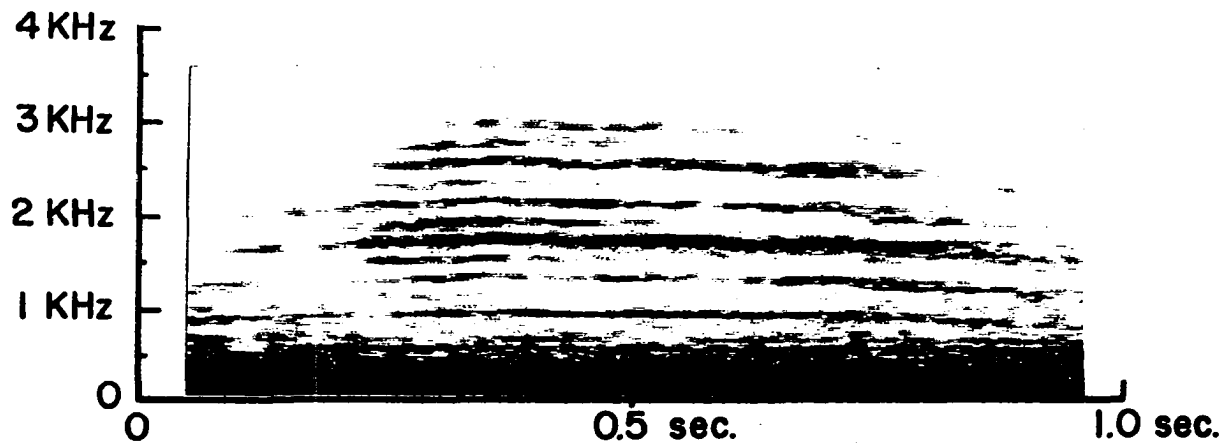

8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.
1.5 sec.

Figure 33. The meow of a cat.


4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.

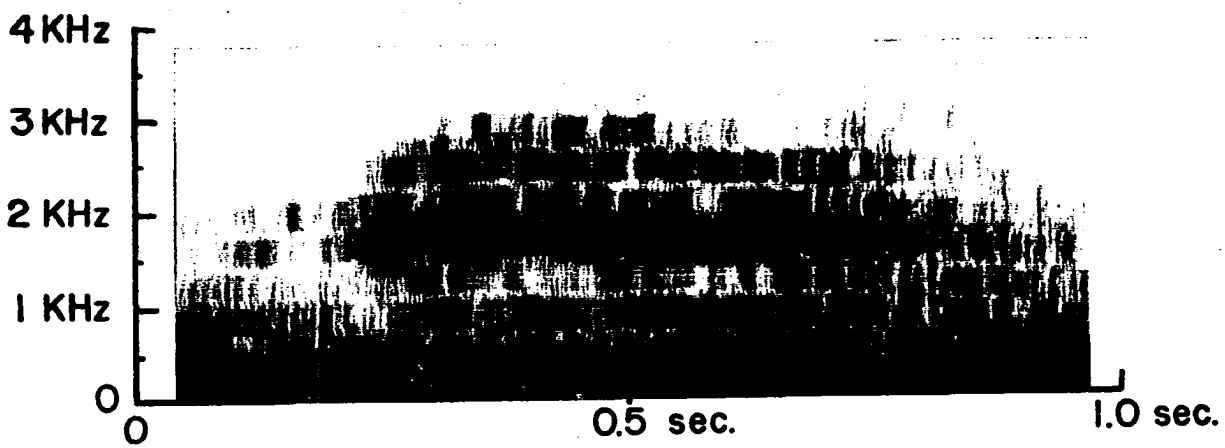

4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.

Table 2.--Physical characteristics of the harmonic spectra calls

Call	SS	F (KHz)	Duration (ms) Mean	SE	CV	No. of Harmonics	Dominant Frequency	FM	Inflection	No. of Calls
DC	1	0.50-1.60	412	153	64	4-11	varies		up then down	3
DC	2	0.70-1.00	275	61	38	0	F	x	down	3
AC	1	0.55-0.65	389	22	15	5-7	H1-H4	x	up then down	7
FC	1	0.40-0.90	431	9	7	5-7	H3,H1,H2	x	none	15
FC	2	0.90-1.80	373	18	28	2	H1 or H2	x	down (terminal)	15
YFC	1	0.75-1.65	438	13	13	0-4	H3,H1	x	none	18
YFC	2	1.85-2.40	443	14	14	2	H1,H2, or F	x	down (terminal)	18
YFB1	1	0.70-1.20	209	20	38	509	H1,H2,H3		down	14
YFB2	1	0.30-2.00	395	54	57	1-10	H1,H2,H4	x	none	16
YFB2	2	0.70-3.30	265	45	44	0	F	x	none	5

Table 2. Continued

Call	SS	F (KHz)	Duration (ms) Mean	SE	CV	No. of Harmonics	Dominant Frequency	FM	Inflection	No. of Calls
YFB3	1	0.90-2.80	69	8	58	0	H1,H2,H3, etc.	x	up then down or down	20
YFB3	2	2.70-3.90	78	10	51	0	H1	x	up then down or down	14
YFB4	1	3.40-4.00	538	175	47	0	F	x	varies	2
YFB4	2	2.70-3.10	650	50	11	0	F	x	varies	2
BK	1	1.60-1.80	158	22	24	2	H1,F,H2	x	down	3
SK	1	0.60-2.00	193	10	47	2-5	H1, or F	x	none	80
LK	1	1.20-1.50	486	36	19	2-5	H1,F,H2		up then down or down	7
CC	1	0.50-0.70	150	0	0	6-11	H1,F,H2		up then down	10
MC	1	0.40-0.70	871	61	18	3-7	H3,F,H1		up then down	7

Table 3.--Postures and functions associated with calls in the harmonic spectra group

Vocalization	Postures	Functions
DC	crouching, flight, being handled	distress, fright
AC	simple bobbing, mild or intense aggression, neutral	alarm
FC and YFC	neutral, simple bobbing, maintenance	flock contact
YFB1-YFB4	crouching, wing and tail fluttering	food solicitation
BK	crouching, wing and tail fluttering	courtship feeding solicitation
SK	neutral, maintenance, courtship feeding	pair or family contact (proximal)
LK	simple bobbing, wing and tail fluttering	pair or family contact (distance), frustration, hunger
CC	varies	?
MC	varies	?

Pumphandle Calls

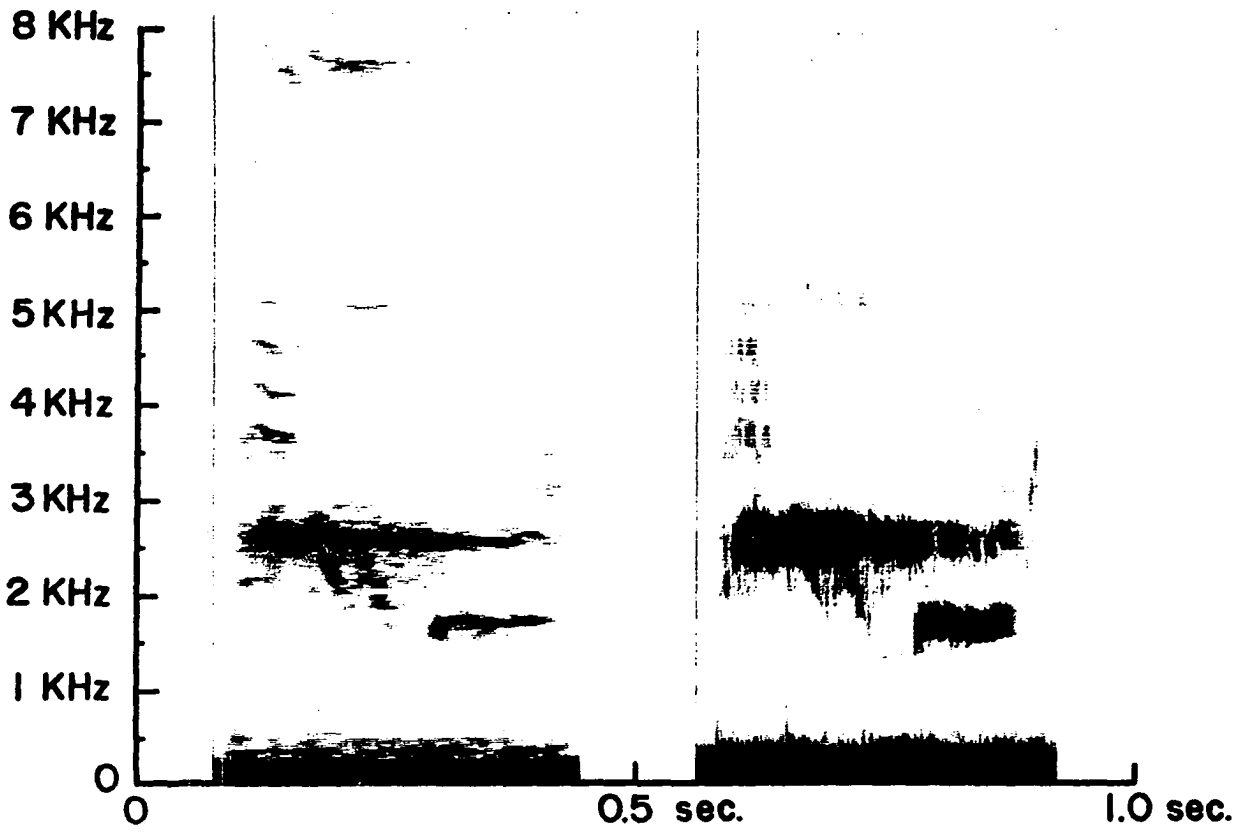
The Bell Song (BS, Fig. 34) is the principal territorial call of the Blue Jay. It also may be given in situations where the bird is excited by a strange object, noise, or animal in or near the cage. In such instances the BS may be given as an "alert signal" by one bird, apparently serving to call attention to something or, on the other hand, it may simply be an expression of the excitement generated by a strange circumstance.

The BS is accompanied by simple bobbing in 28 of 71 cases (40%) for which calls and postures were recorded simultaneously. Calls accompanied by simple bobbing were given in the territorial context. Other postures accompanying this call are the neutral and investigatory postures. The latter posture usually accompanies the BS of a highly excited bird.

BS calls usually have two clear notes, each of which is produced by a different SS. S1 has an F of 2.30 to 2.90 KHz which is rarely inflected up or down. If there is inflection it never exceeds 0.10 KHz. S1 occasionally has one, rarely two, very low intensity harmonics. The F is often modulated about 0.50 KHz above and below the F. The duration of S1 ranges from 250 to 350 ms (avg. = 267).

S2 of the BS begins 175 to 225 ms after S1 at an F of 1.50 to 1.70 KHz and remains at the initial value throughout its duration. There are no harmonics and the duration of S2 ranges from 50 to 200 ms (avg. = 113).

Figure 34. The Bell Song (BS).


8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.

The first attempts of BS of one- to three-month-old Blue Jays differ from adult BS calls in a number of ways. The YBS (Fig. 35) calls have two SS. In general F of YBS S1 is lower than those of BS S1 (1.80 to 2.80 KHz). The F of S1 is usually inflected up from 0.10 to 1.00 KHz and then down 0.10 to 1.80 KHz, but may remain stable. The F is often modulated to the same degree as S1 of BS. Sometimes there are three or four harmonics, but the F is the dominant frequency. YBS S1 are longer than BS S1, ranging from 275 to 600 ms (avg. = 427).

S2 of YBS may begin before, after or simultaneously with S1, and the F ranges from 1.00 to 2.90 KHz. S2 often has up to three harmonics with the F being dominant. Modulation of YBS S2 is similar to that of BS S2. The S2 is quite long, lasting from 125 to 550 ms (avg. = 406).

The Wheedle Bell Song (WBS, Fig. 36) sounds similar to the BS, but is quite different in structure. It is given by mildly excited birds and also by birds which appear to be in situations which involve uncertainty, possibly because of a conflict of drives exists. For example, a captive jay may be quite hungry but reluctant to approach a feeding station, perhaps because there is a strange human (a person other than the author) in the cage. The WBS is often given by a bird in such circumstances. In situations of uncertainty the WBS is usually unaccompanied by neutral or investigatory postures, whereas when the WBS is an apparent expression of excitement

Figure 35. The Bell Song of young Blue Jays (YBS).

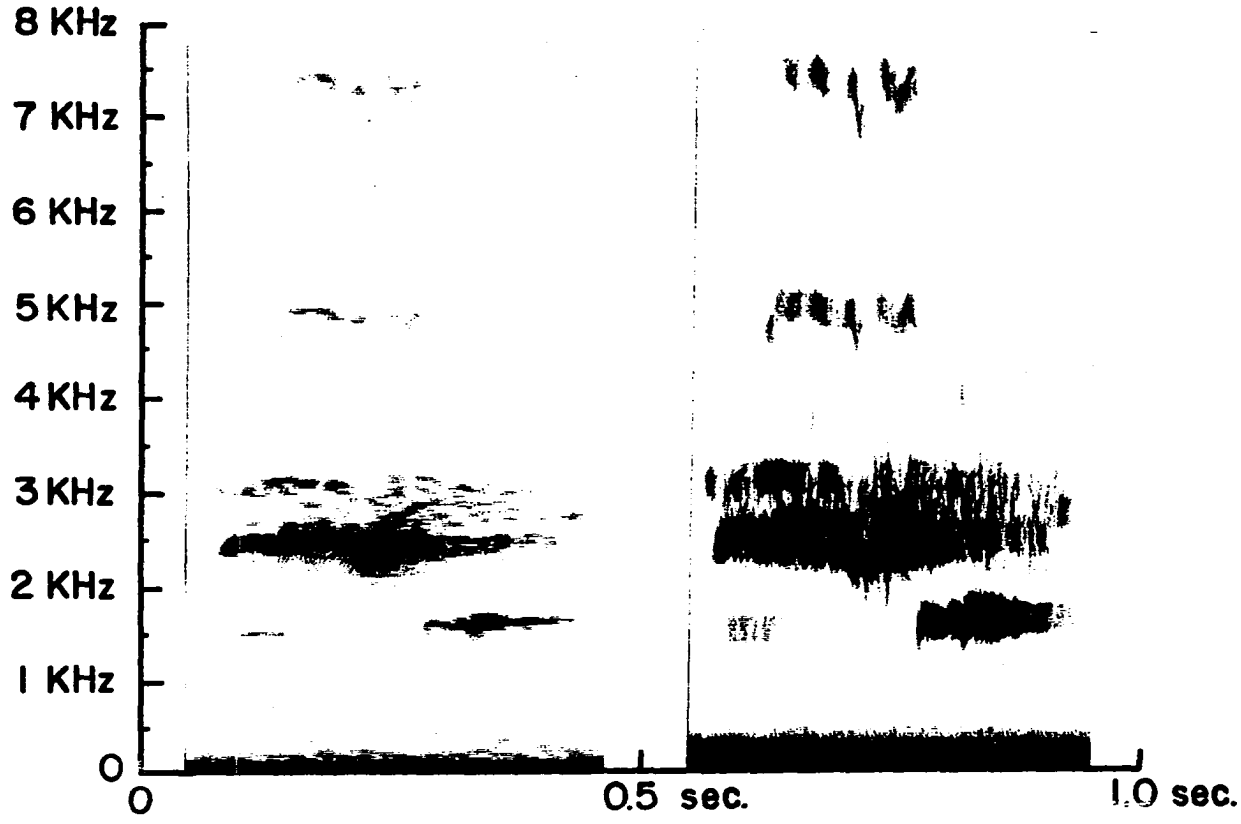
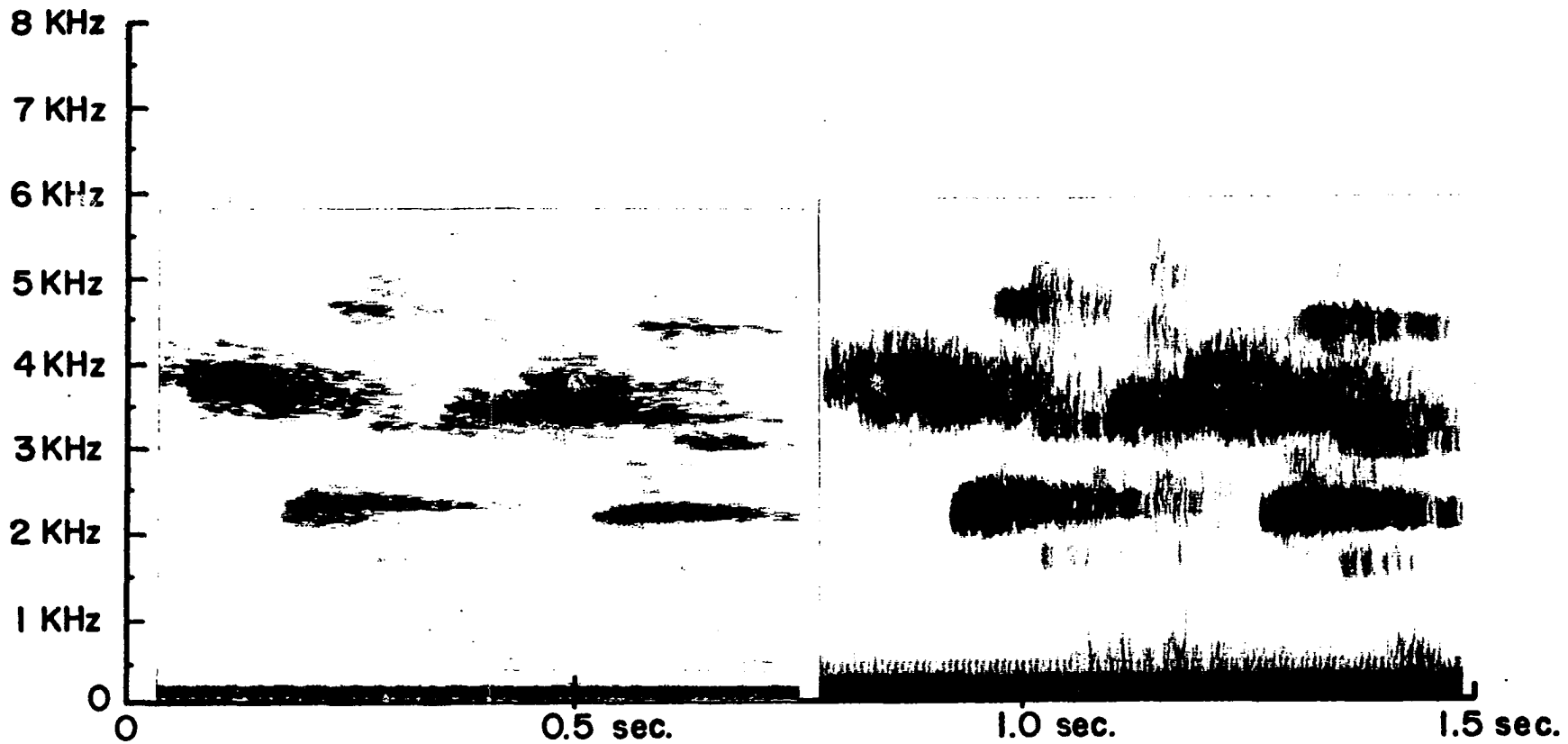

8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.

Figure 36. The Wheedle Bell Song (WBS).


8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.
1.5 sec.

(14 of the 56 call and posture recordings [25%]), it is accompanied by simple bobbing.

The first of the two SS of the WBS has an F of from 3.30 to 3.80 KHz. During the first 100-150 ms, the F may rise 0.10 KHz and thereafter decrease 0.10 to 0.70 KHz. Sometimes the F simply decreases from beginning to end of the call. In most cases S1 is strongly but irregularly frequency modulated. If S1 was harmonics, there is only one and it is less intense than F. The duration range of S1 is 300-450 ms (avg. = 341).

S2 of the WBS begins 100-200 ms after S1 at an F of 2.10 to 3.00 KHz and remains at the initial value until it stops. There are no harmonics, but, as in S1, there is usually substantial but irregular FM. The duration range of S2 is 100 to 300 ms (avg. = 225).

Table 4 lists the physical characteristics and Table 5 lists the functions and postures associated with the pumphandle calls.

Click Calls

The Rolling Click Call (RC, Fig. 37) is always accompanied by simple bobbing (one or two bobs per RC), and, apparently, is exclusively a female vocalization. I have sexed my captive animals behaviorally during the breeding season. The animals observed to give the RC were either unsexed, because they did not mate, or were classed behaviorally as females. The RC indicates excitement

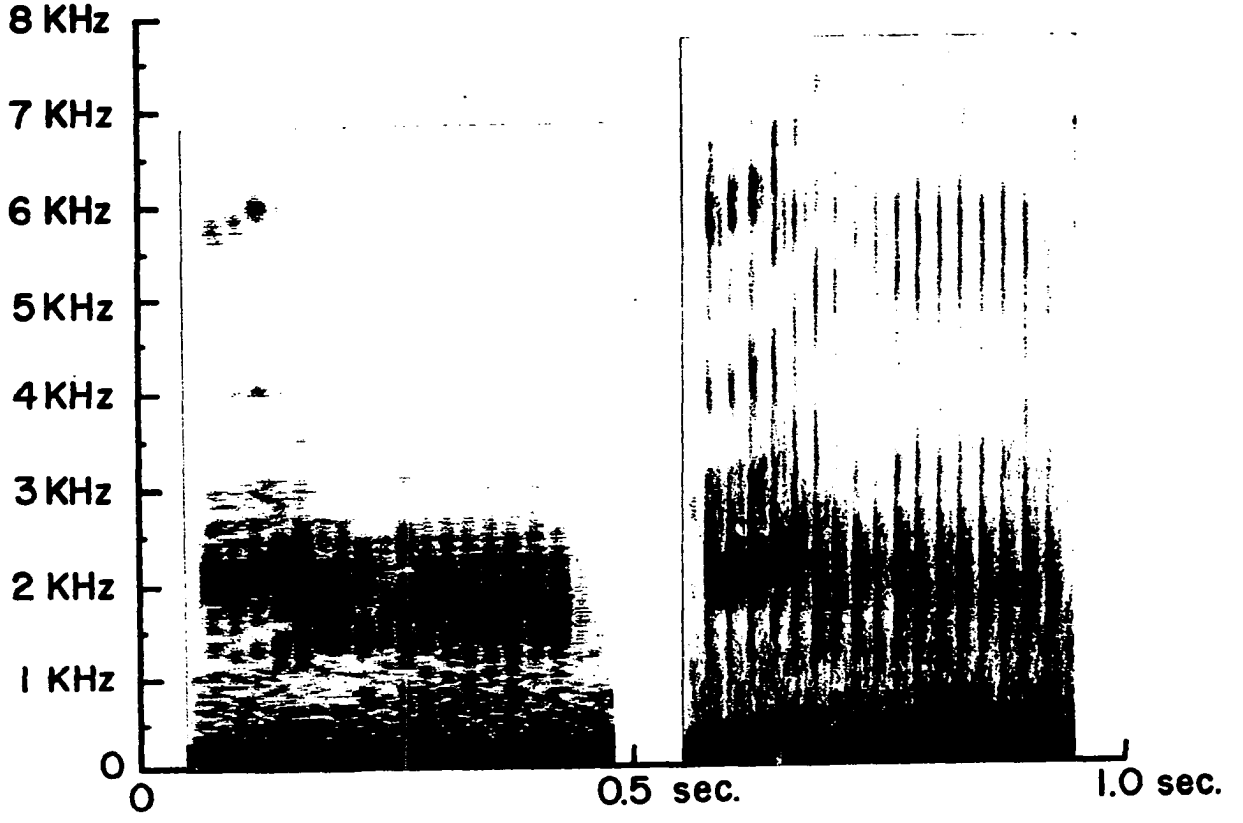
Table 4.--Physical characteristics of the pumphandle calls

Call	SS	F (KHz)	Duration (ms) Mean	SE	CV	No. of Harmonics	Dominant Frequency	FM	Inflection	No. of Calls
BS	1	2.30-2.90	267	7	22	0	F	x	none, up or down	9
BS	2	1.50-1.70	113	17	46	0	F	x	none	9
YBS	1	1.80-2.80	427	26	34	0-4	F	x	up then down	13
YBS	2	1.00-2.90	406	35	38	0-3	F	x	none	13
WBS	1	3.30-3.80	341	21	17	0-1	F	x	down or up then down	8
WBS	2	2.10-3.00	225	26	33	0	F	x	none	8

Table 5.--Postures and functions associated with the pumphandle calls

Vocalization	Postures	Functions
BS and YBS	simple bobbing, neutral, investigatory	territorial, alert, excitement
WBS	simple bobbing, neutral, investigatory	mild excitement, uncertainty

Figure 37. The Rolling Click Call (RC).


8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.

associated with fear. Specifically, it seems to be associated with a thwarted drive to flee. For example, some of the captive female jays were not very tame and usually avoided me. However, when they were confined in small enclosures for special observation, they were unable to maintain much distance between me and themselves. It was in these circumstances that the RC was most often observed. Occasionally, the RC seemed to function as an alert signal in the same fashion as the BS.

The RC is made up of two series of clicks with voiced sound (only one series is shown in Fig. 37). The first series of clicks contains 15 to 17 clicks (avg. = 16.6), 23 ms apart and the second series contains 14-16 (avg. = 15.8) clicks 23 ms apart. The series themselves are from 60 to 210 ms apart (avg. = 87.8), but only one interval was more than 80 ms long. If this aberrant interval is omitted, the avg. is 72.5 ms.

The voiced sound has only one SS whose F is from 1.70 to 1.90 KHz in the first click series and from 1.80 to 2.00 KHz in the second series. The F is inflected down 0.10 to 0.20 KHz over the duration of each series of clicks. This is probably due to the closing of the mouth, which is easily observed. A further indication that the mouth is closed as the call progresses is the shift in intensity of harmonics. The first four clicks always have two harmonics, but, as the F decreases, only one or no harmonic is present.

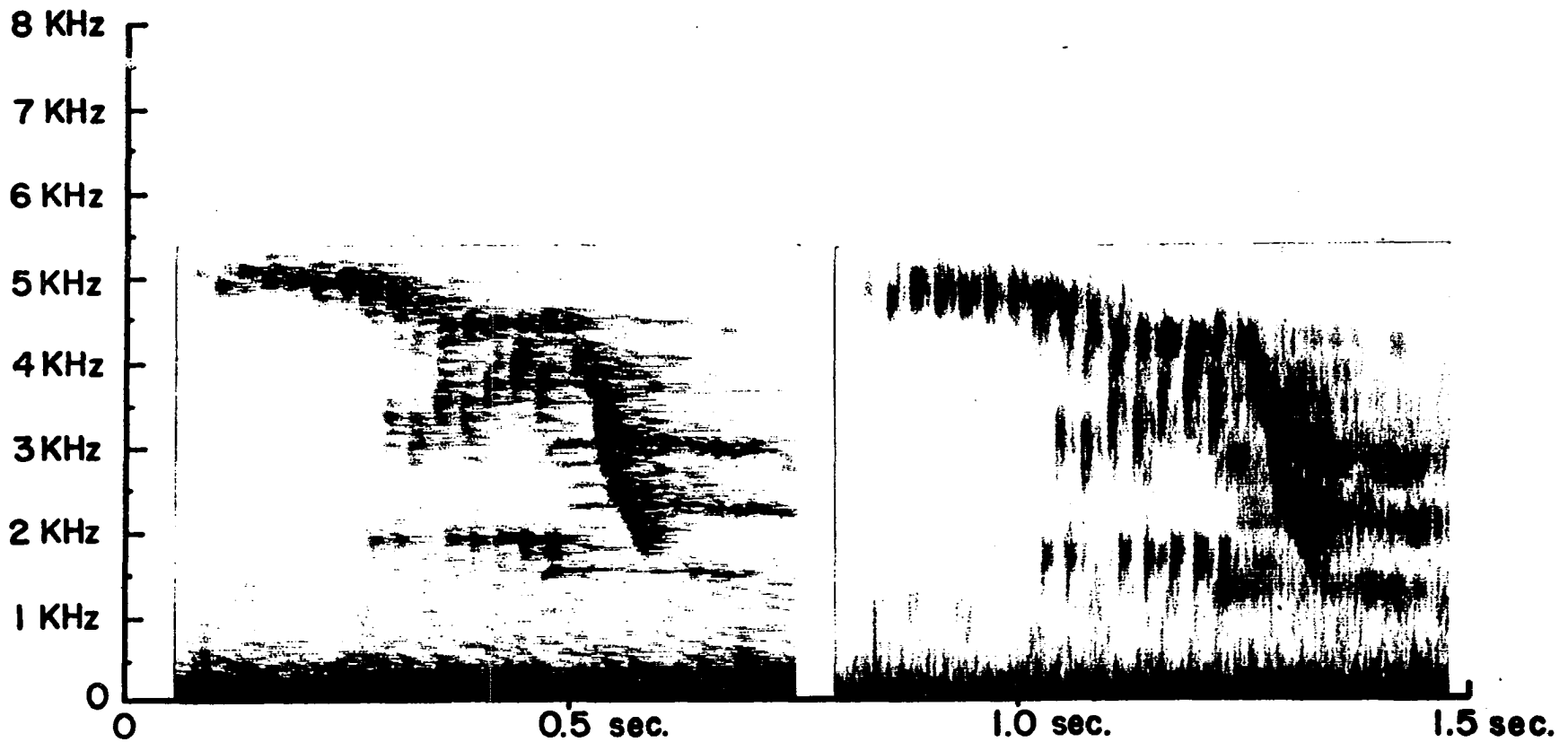
The Descending Whistle (DW, Fig. 38) indicates excitement and, like the RC and BS calls, may serve as an alert note. It is accompanied by simple bobbing 20% of the time it is given and also by neutral and investigatory postures.

The DW contains clicks with voiced sound from two SS. During the first 104 to 115 ms (DW1 in Table 6) the F of S1 starts at 2.40 to 2.70 KHz and drops 0.70 to 1.20 KHz. This part of the call has 17 or 18 clicks, each 27 or 28 ms apart. There is one harmonic, which is much more intense than the F. During the next 50 to 60 ms (DW2 in Table 6) (avg. = 56) of the call there are no clicks and the F drops rapidly 1.40 to 2.60 KHz.

S2 usually begins about 25 to 28 ms after S1 and has three to nine clicks (avg. = 6.6) 25 to 35 (avg. = 28) ms apart. The F is 3.30 to 4.00 KHz and usually drops 0.10 to 0.60 KHz and then rises 0.20 to 0.60 KHz. There are no harmonics. The average duration of S2 is 56 ms.

The Growl (GR, Fig. 39), to which I have not been able to assign a function, is accompanied by neutral or maintenance postures. There are one or two SS, the first of which has an F of 0.70 to 1.80 KHz. The F is inflected up sharply 0.50 to 3.40 KHz during the first 150 to 250 ms of the call. During the next part of the call the F remains fairly stable and then drops rapidly 0.60 to 3.30 KHz over a period of 50 to 150 ms. There are 5 to 14 clicks (avg. = 7.9) in S1 from 20 to 50 ms (avg. = 25) apart. Harmonics are

Figure 38. The Descending Whistle (DW).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7 KHz
6 KHz
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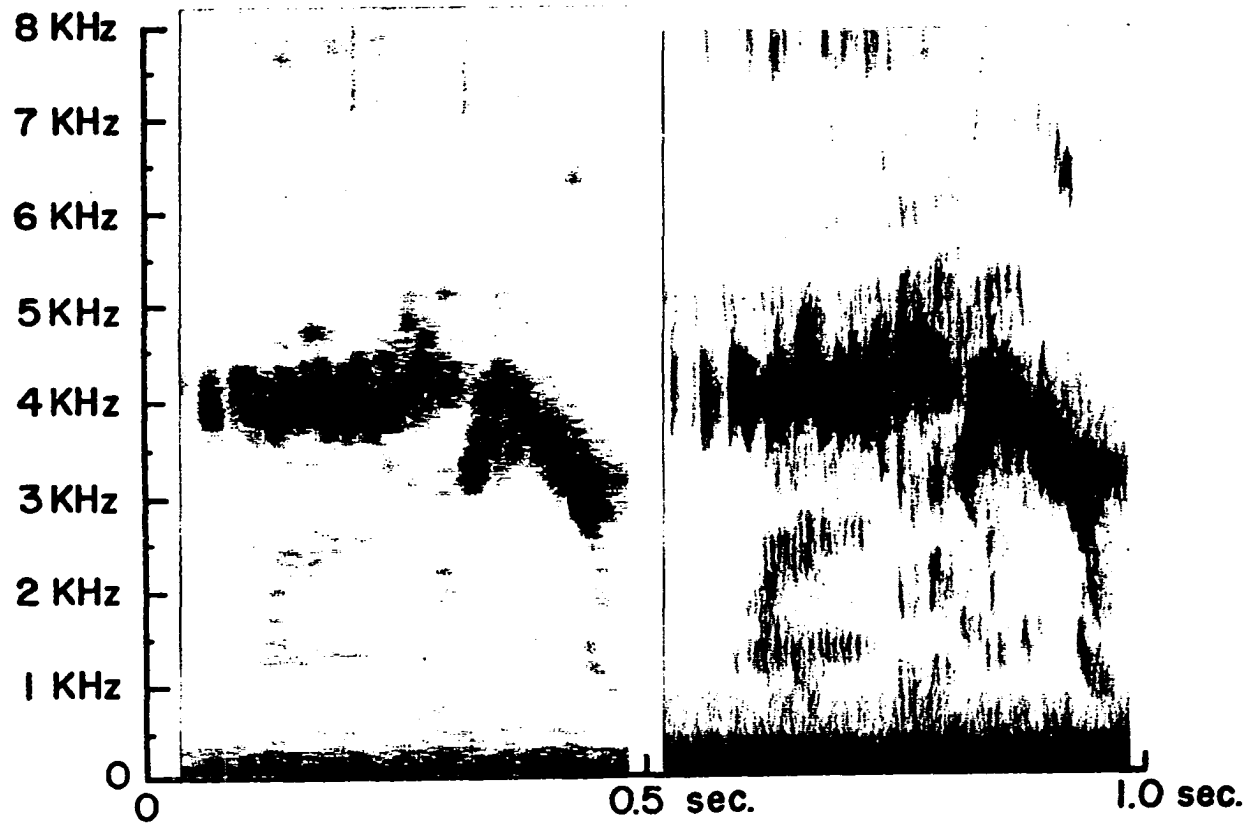
0.5 sec.
1.0 sec.
1.5 sec.

Figure 39. The Growl (GR).


8 KHz
7 KHz
6 KHz
5 KHz
4 KHz
3 KHz
2 KHz
1 KHz
0
0
0.5 sec.
1.0 sec.

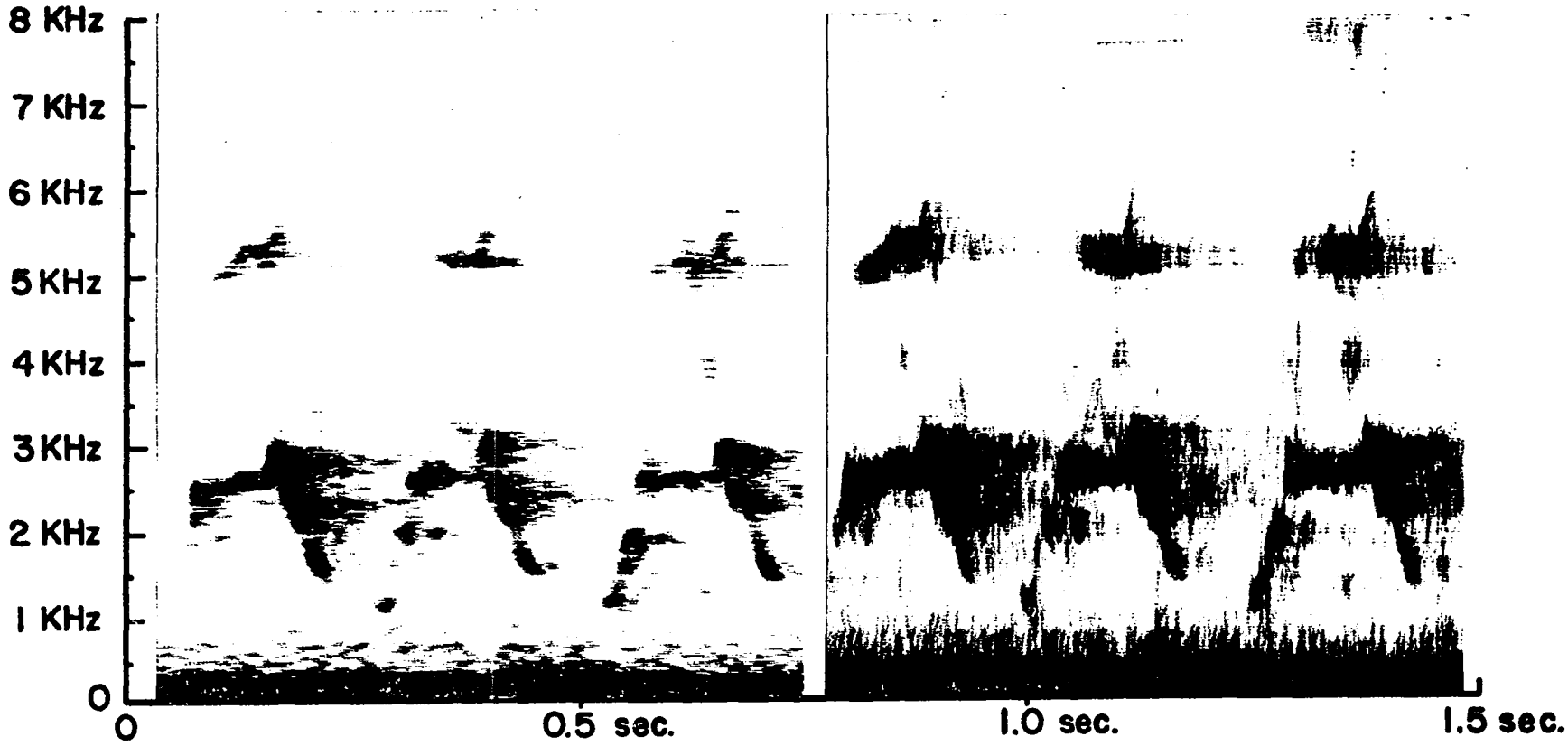
not present. The duration of S1 ranges from 125 to 450 ms (avg. = 230).

S2, when it is present, has an F of 0.60 to 1.80 KHz, which remains stable with respect to overall inflection, but which is frequency modulated through about 0.40 KHz. There are from 9 to 13 clicks (avg. = 11.0) 20 to 40 ms (avg. = 29) apart. The duration of S2 ranges from 75 to 575 ms (avg. = 300).

The Triple Descending Whistle (TDW, Fig. 40) functions as a territorial call, an alert call or as an "announcement of victory" occasionally given by the winner of an aggressive encounter. When the TDW serves as an alert call it is accompanied by neutral posture or, infrequently, simple bobbing, whereas, when it is a territorial call or victory announcement, it is usually accompanied by simple bobbing or neutral posture.

The TDW is actually a series of three short whistles originating from only one SS. Clicks are irregularly present in most TDW. The TDW usually has four distinct notes. The first note, when present (42% of TDW analyzed), is 10 to 20 ms long (avg. = 18) and its F is from 1.00 to 1.60 KHz. It has no harmonics. The second note, 15 to 28 ms (avg. = 22), has an F of 1.50 to 2.10 KHz. It is present in all TDW analyzed and has no harmonics. The third note is rather long, lasting 75 to 95 ms (avg. = 82) with an F of 1.90 to 2.90 KHz, which remains constant except in a few cases, when it is

Figure 40. The Triple Descending Whistle (TDW).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1.0 sec.
1.5 sec.

inflected upward 0.10 to 0.20 KHz. This note usually has two harmonics and the order of dominance of the frequencies is F, H1, H2. The last note is also long, ranging in duration from 55 to 90 ms (avg. = 69), and the F, which begins at 2.50 to 3.20 KHz, drops sharply 1.30 to 2.70 KHz. The harmonic spectra and dominant frequencies are the same as in the third note.

Tables 6 and 7 list physical and behavioral parameters of the click calls.

Song

Song in the Blue Jay is given by both sexes and usually consists of a long series of phrases, the characteristics of which include all of those present in the other three call groups. Most of the vocalizations in those groups are included verbatum in song, along with many series of short whistled notes. Blue Jay songs are very long in duration, frequently lasting over two minutes. Because songs are so long and because they are, essentially, a conglomeration of all the previously described vocalizations, I have not included a sonagram of this vocalization.

Song in the Blue Jay, as I have called it, is a type of primary song (Berger, 1961). Specifically, it is a signal song, that is, one that is used to coordinate the activities of a pair. It is given by the male during courtship bobbing, but never functions as an advertising or territorial song. Song is also given when a bird is relaxed, perching, or

Table 6.--Physical characteristics of the click calls

Call	SS	F (KHz)	Duration (ms) Mean	SE	CV	No. of Harmonics
RC1[a]	1	1.70-1.90	358	11	7	0-2
RC2[a]	1	1.80-2.00	335	9	6	0-2
DW1[b]	1	2.40-2.70	27	1	5	1
DW1[b]	2	3.30-4.00	56	1	8	0
DW2[b]	1	1.20-2.00	28	2	4	0
GR	1	0.70-1.80	230	35	44	0
GR	2	0.60-1.80	300	85		0
TDW1[c]	1	1.00-1.60	18	1	21	0
TDW2[c]	1	1.50-2.10	22	1	17	0
TDW3[c]	1	1.90-2.90	82	1	7	0-2
TDW4[c]	1	2.50-3.20	69	2	15	0-2

[a]RC1 and RC2 represent the first and second series of clicks in each call.

[b]DW1 and DW2 represent the first and second parts of the DW.

[c]TDW1 - TDW4 represent the 4 notes of TDW calls as discussed in the text.

Table 6. Continued

Dominant Frequency	FM	Inflection	No. of clicks	Interval between clicks (ms)	No. of calls
F		down	15-17	23	7
F		down	14-16	23	7
H1		down	17-18	27	6
F		down	3-9	28	6
F		down	0	0	6
F		up then down	5-14	26	10
F		none	9-13	29	10
F		none	variable	variable	10
F		none or up	variable	variable	21
F,H1,H2		none or up	variable	variable	27
F,H1,H2		down	variable	variable	25

Table 7.--Postures and functions associated with the click calls

Vocalization	Postures	Functions
RC	simple bobbing by female	alert, excitement (fear) thwarted drive to flee
DW	simple bobbing, investigatory, neutral	alert, excitement
GR	neutral, maintenance	?
TDW	simple bobbing, neutral	territorial, alert victory announcement

moving about. In these cases it has no apparent function other than that it is an indication that the bird is in a calm behavioral state.

CHAPTER III

DISCUSSION AND CONCLUSIONS

Origin and Significance of Postures and Displays

The functions of visual communication signals of Blue Jays involve a number of components, including fixed and moving aspects of the head, body, wings, legs, and plumage. In birds movement of conspicuous parts of the entire body, as well as the plumage may be important in displays (Tinbergen, 1948), and in addition, the position and degree of piloerection of various parts of the plumage may have specific communicative significance (Morris, 1956). Many of the visual displays of the Blue Jay have the same physical characteristics as functionally similar displays that have been described in other avian species (Armstrong, 1947).

Maintenance Postures

Blue Jays engaged in such maintenance activities as feeding and resting keep the plumage relaxed and the body in a neutral position or one suited to the activity at hand. During water and sun bathing the feathers are ruffled to facilitate wetting or warming (by the sun). Maintenance

postures require little comment, as they are essentially identical to those described for most species of birds.

Agonistic Postures and Displays

Postures and displays of Blue Jays involved in aggressive or sexual activities have many features in common. Most of the aggressive and sexual signals involve some degree of piloerection, especially of the crest. Erection of plumage effectively increases the size of the displaying bird (Dilger, 1956). Erection of the crest alone does not signal a threat; however, when it is combined with a lowering of the head and/or partial opening of the mandibles, aggression is signified. As the degree of aggression increases, other components are brought into play. The degree of piloerection increases, the wings and tail are held open or flicked open and closed and the body is tiptoed. These components further increase the conspicuousness of the bird because they involve motion, increase in effective size, and display of conspicuous markings.

The posture of a highly aggressive bird (Fig. 6) is very similar to that of a sexually excited bird (Figs. 10, 11 and 12), suggesting a common origin for the two types of display. Fanning of the wings and tail and raising of the tail are thought to have been derived from the flight intention movement (Daanje, 1950). Erection of the plumage during courtship is probably derived from aggressive displays;

however, it serves a similar function, increasing the effective size of the bird.

There are distinct differences between intense aggression postures and courtship displays that probably clarify their meaning to the bird at which the display is directed. First, during courtship, the bill is closed and held parallel to the female, whereas in aggressive displays and fighting the open bill is directed toward the object of aggression. In addition, courtship display is accompanied by song, whereas the only acoustic signal that occasionally accompanies aggressive displays is bill snapping.

While sexual displays share many of the components of aggressive displays, they also contain elements characteristic of submissive displays. In avoidance posture the bill is held parallel to or away from the dominant bird, just as the male directs the bill away from the courted female. During courtship bobbing, the male's bill, at the top of a bob is directed upward. This is reminiscent of the bill-up position of a bird in appeasement posture (Fig. 15). At the same time, the head of the male is above that of the female and his throat and belly are exposed. This exposure of vulnerable parts is also seen in appeasement posture and in the posture of the loser of an aggressive encounter.

It is evident, then, that Blue Jay courtship display, like courtship display in many other avian species (Armstrong, 1947), combines elements of both aggressive

and submissive displays. The elements of aggressive displays that serve to make the bird conspicuous are present and the elements of submissive displays included signify that the courting bird does not intend to attack the object of his display. The incorporation of aspects of aggressive and submissive displays into courtship displays indicates that courtship behavior is highly evolved behavior, derived from simpler movements. It is also, in most species, including the Blue Jay, quite stereotyped, supporting the hypothesis that it develops later than other types of agonistic displays (Armstrong, 1947). Further evidence supporting this hypothesis with respect to Blue Jay courtship is the accompaniment of courtship bobbing by song, the most complex vocalization.

Simple bobbing is a puzzling display to which function is assigned only with difficulty. The most notable feature of simple bobbing is the degree of motion involved. I would like to suggest that the lack of specific components that might signify aggression, submission or sexual excitement, indicates that the most important function of bobbing is to lend visual emphasis to vocal displays. As I have mentioned, bobbing is rarely unaccompanied by vocalization and appears to be specifically important in distance communication where gross movement of the body would be the only recognizable feature of the display. That bobbing is given with a wide variety of vocalizations, which, themselves, have distinctly

different functions, is further evidence that the simple bob is a non-specific signal.

Submissive and Solicitative Postures and Displays

The submissive displays, as a group, are characterized by relaxed or sleeked plumage, upward or horizontal bill point away from the dominant or aggressive bird. The submissive bird usually assumes a position that exposes the throat and belly if the aggressor or dominant is in close proximity. The hunched position of the body, evident in the nestling alarm freeze (Fig. 14), and, to a lesser degree, in avoidance posture (Fig. 13), and sleeked plumage, seen in all of the submissive postures are, in many respects the opposite of the upright stance, ruffled plumage, bill forward threat displays. The turning away of the body and bill from the aggressor is thought to represent the ritualization of the flight intention movements (Tinbergen, 1959), and probably serves to remove the sign stimuli for aggression.

The solicitative displays are characterized by crouched body position, lowered head, widely opened bill and the fluttering of wings and tail. These types of displays develop first in very young birds, where they serve to elicit provision of food by the parents. Later in life adult birds, especially females, revert to this type of juvenile behavior in courtship feeding and copulation solicitation. Appearance

of juvenile solicitative behaviors in adult birds is common in many species (Armstrong, 1947; Andrew, 1961). Such displays apparently serve two functions: 1) to reduce aggressive tendencies in the male, and 2) to signal to the male that the female is receptive to courtship feeding and copulation.

Courtship feeding in the Blue Jay serves to establish a male-feeding-female routine. This is particularly adaptive in that it allows the female to spend more time incubating the eggs (a strictly female activity), relieving her of the need to forage for food. Courtship feeding is also important in the maintenance of the pair bond in Blue Jays. Many of the captive jays that established pair bonds during their first breeding season remained paired during the non-breeding season and into the next breeding season. In these birds there was considerable reduction or complete absence of the ritualized male courtship display in the second breeding season. In addition, birds with well-established pair bonds were ready to nest earlier in their second breeding season. Thus, courtship feeding is an integral part of the breeding cycle that permits reproductive activity to be carried out with maximum efficiency because it reduces the amount of energy that would otherwise be spent in such activities as foraging by the female during incubation and renewed courtship by the male at the onset of each breeding season.

It should be noted that adult solicitative displays

are accompanied by vocalizations (BK, SK, LK) that resemble food-begging calls of the young (YFB1, YFB2).

The Blue Jay's repertoire of visual communication signals has a limited number of components that may be combined in different ways to serve different functions. Similar combinations of components (for example, young food-begging and female courtship feeding solicitation) may have other cues that lend them distinctiveness. Thus, two similar visual displays may elicit different responses due to the presence of additional vocal or contextual cues.

Structure, Function and Evolution of Acoustic Signals

Although the vocal repertoire of the Blue Jay contains only about 20 distinct types of calls, the actual number of meaningful signals is greater because, as with visual displays, a single vocalization may be used to communicate a number of different concepts if it is accompanied by different postures or if it is given in different contexts.

Harmonic Spectra Calls

The harmonic spectra calls are characterized by numerous harmonics, dominant frequencies of high value, and long durations. They function as signals of extreme excitement associated with fear and as contact or location notes.

The Distress Call (DC) has the characteristics of a sound that can be located only with difficulty (Marler, 1955,

Bremond, 1963), that is, it is long, begins and ends imperceptibly, and its dominant frequencies are rather high and stable throughout the call. The DC can be said to be a warning of imminent danger in that the bird giving the call has already been caught or is being closely pursued. It probably elicits a flight response in other jays, although I have not been able to test this hypothesis to my satisfaction. A similar DC in the European Jay has been described (Bremond, 1963).

The Alarm Call (AC) is also a signal of imminent danger, although its abrupt changes in frequency at the beginning and end make it somewhat easier to locate. However, it is a long call with a dominant frequency that is rather high. Hardy (1961) and Edwards (1971) have both described this call and suggested that it serves as an alarm call, and Brown (1964) describes an alarm call in Steller's Jay that is similar in structure to the Blue Jay AC.

The Flock Contact Call (FC) has only one characteristic that would make its source easily locatable--the presence of very pronounced frequency modulation (FM) at its end. However, the FC is repeated very frequently and this probably accounts for its function as a contact note. It is also accompanied by simply bobbing, which lends visual conspicuousness to the caller. Edwards (1971) concurs that this call, to which he gives the name "monotone waa" call, serves as a flocking call.

Type 1 and Type 3 Young Food-begging Calls (YFB1, YFB3) are easily locatable calls due to short durations, abrupt changes in frequency, and/or low values of dominant frequencies. On the other hand, YFB2 and YFB4 provide few cues for location in that they are of long duration and end indefinitely. YFB1 and YFB2 are given by nestlings or very young fledglings, while YFB3 and YFB4 are given by older nestlings and fledglings. Thus, although the calls given change with age, there are calls that can be located both with and without ease used by a young bird of any age. I have not ascertained how young birds might decide which type of call to use, but it seems likely that they may take cues from the behavior of their parents.

The Keu calls are all different types of contact notes used by pairs and family groups. The Begging Keu Call (BK) and the Soft Keu Call (SK), used as proximal communication signals, are frequently repeated, but the Loud Keu Call (LK) is not. The LK has more pronounced changes in inflection and is usually quite loud, unlike the BK and SK. Thus, all these contact calls provide good location cues, but in different fashions. Goodwin (1952) describes a call similar to the SK in the European Jay that is used by the male to call the female to a nest site he has chosen. Hardy (1961) and Edwards (1971) both suggest the Keu calls to be important vocalizations in communication between members of a pair.

The Crow Call (CC) and the Meow Call (MC) are both examples of vocal mimicry, a phenomenon that has been

described in Blue Jays (Visher, 1912; Edwards, 1971). Whether or not these calls serve any specific functions is unclear at present.

Because the harmonic spectra calls share so many physical and functional similarities and because they are quite similar to the calls of other jays (Hardy, 1969), it seems reasonable to hypothesize that they were all derived from one basic type of call. This call, in its primitive form, was probably rich in harmonics with a low fundamental frequency (F), and little or no inflection. Slight changes in duration, in F, either by inflection or modulation, combined with the additional behavioral cues afforded by combining postures and displays with acoustic signals, may have become stable over time, provided they were adaptive, allowing the development of an increased number of specific signals.

The Pumphandle Calls

The pumphandle calls are higher in frequency and shorter in duration than most of the harmonic spectra calls. They have few harmonics and, unlike harmonic spectra calls, the F is always the dominant frequency. Pumphandle calls function as territorial calls, alert calls and expressions of excitement associated with uncertainty or potentially threatening situations. The harmonic spectra calls function as contact notes and are locatable mainly by virtue of frequency of repetition and by abrupt changes in frequency

over short time periods (slurs). The pumphandle calls, on the other hand, usually involve distance communication and are locatable by appropriate features: purity of tone, abrupt starts and stops, and clear, sharp, unslurred frequency changes.

The Bell Song (BS) is mainly a territorial call, but it is also an alert signal or expression of excitement usually concurrent with the presence of strange, possibly dangerous, objects or organisms in the environment. Of all the calls in the repertoire of the Blue Jay, the BS is the purest in tone. This purity of tone, in combination with a relatively low F and abrupt start, stop and frequency change, account for the fact that it carries well over long distances (Bremond, 1963). As a territorial call the BS is often accompanied by simple bobbing from a conspicuous location (treetops, etc.), affording a visual cue to facilitate location of the caller. As an alert call the BS is often given with the investigatory posture, which is actually more an expression of the behavioral state of the bird that can be interpreted as such by a proximal observer, than it is a distance location cue. Hardy (1961) and Edwards (1971) have described the BS as a territorial call and Brown (1964) described the structurally similar "musical call" of the Steller's Jay as a territorial call.

The Wheedle Bell Song (WBS) functions mainly as an expression of uncertainty. The start and stop portions of

the call are less abrupt than those of the BS and the WBS is usually given at a slightly lower volume. Thus it is somewhat more difficult to locate; however, it is often given when birds are in groups and may be accompanied by simple bobbing or investigatory posture, both of which lend it some visual conspicuousness.

The Click Calls

The click calls are usually intermediate between harmonic spectra calls and pumphandle calls with respect to dominant frequency values. They have few harmonics, pronounced changes in inflection over relatively long time spans and, of course, clicks. The click calls are usually given at rather low volume, but are easily locatable by virtue of their structure. All of the calls may serve as alert notes. They may also express excitement associated simultaneously with fear and frustration. One call, the Triple Descending Whistle (TDW), is sometimes a territorial or victory announcement call.

I observed the Rolling Click (RC) to be given only by females as did Amadon (1944) and Edwards (1971); however, Hardy (1961) reported that he heard this call from both sexes. Because the call is probably limited to females, one would expect it to be given in sexual contexts or, at least, in relation to a specifically female activity. While Edwards (1971) reported this to be true, I have not. When the RC was not given as an alert call, it seemed to indicate frustration

due to a thwarted drive to flee. Edwards (1971) mentioned that females giving the RC in a sexual context may have been in conflict situations, specifically a conflict between drives to flee from or attack the male as he approached. These circumstances show some similarity to those in which I observed the RC.

The extremely abrupt character of the RC, in addition to its exclusive association with bobbing, make it an obvious, easily locatable signal.

The Descending Whistle (DW) functions mainly as an alert signal or as an expression of excitement generated by the situation which prompts the alert signal. The voiced sound in the DW is more obvious than that in the RC and covers a much wider frequency range. This tends to overpower the abruptness of clicks and the caller is thus less easily located. DW calls, however, are associated with lower levels of excitement.

The function of the Growl (GR) is unclear. It is given randomly by birds in a relaxed behavioral state and perhaps merely serves as an expression of that condition.

The TDW is the only other territorial call besides the BS. It is given at a lower intensity than the BS, but is fairly pure in tone and is characterized by slow, slurry frequency changes. The voiced sound in the TDW overpowers the clicks almost entirely. Because this call is sometimes given by the winner of an aggressive encounter, it may

function as a defense of small, mobile territories such as individual distance, mates, temporary perches and feeding stations rather than territory in the usual sense (nesting territory). The "musical call" of the Steller's Jay (Brown, 1964), which is structurally similar to both the BS and the TDW, is often given during conflicts between males. This same call in the Steller's Jay is also a territorial call similar in function to the BS.

The pumphandle and click calls are more similar to each other in structure and function than they are to the harmonic spectra calls. This suggests that they may have evolved from a single primitive call characterized by purity of tone, absence of harmonics, and abruptness in changes of frequency. Many of the calls in these groups function as alert signals or expressions of mild excitement generated by potential rather than imminent danger. In addition, one call from each group is used as a type of territorial call.

Simple pure tone calls of similar function are found in other New World jays (Hardy, 1969), but the variety of calls seen in the Blue Jay repertoire is not present in most cases. A number of corvids have a rattle call similar to the RC (Amadon, 1944, Hardy, 1961, Sutton and Gilbert, 1942).

I would like to suggest that the calls developed from the primitive pure tone type call (pumphandle and click calls) were enhanced by the combination of clicks with pure tone calls. Thus, there is a spectrum of calls ranging from a

pure tone whistle with no clicks (BS) to a call in which loud, regular clicks dominate the voiced sound (RC).

It is difficult to speculate whether a primitive click call arose independently and was later combined with pure tone calls or whether clicks arose as a "by-product" of increases in abruptness of frequency changes over shorter and shorter time periods.

Song

The principal function of song in the Blue Jay is as an accompaniment to male courtship bobbing. It is very musical in quality and highly variable in structure. Although song is always given at a very low volume, it can be easily heard by the female who is rarely less than a meter away from the male during courtship. Brown (1964) describes a vocalization comprised of whistle-like tones and gutteral sounds that is given by the male Steller's Jay as he circles and sidles up to the female.

Secondarily, song functions as an indicator of an exceedingly relaxed behavioral state. Structurally similar vocalizations have been described in the Mexican Jay (Brown, 1963a), the Gray Jay (Lawrence, 1957), the European Jay and Lanceolated Jay (Garrulus lanceolatus), respectively (Goodwin, 1952). All of these authors report that the vocalization is given randomly by birds in relaxed conditions. Lawrence (1957) suggests that the vocalization, in such a context, constitutes displacement behavior. I do not believe

this is true of Blue Jay song because there is no evidence of drive conflict in the behavior of singing birds.

In conclusion, both the visual and vocal communication signals of the Blue Jay appear to have origins in simple, stereotyped behavior patterns. Most of the visual displays appear to be derived displays, that is, they are ritualized patterns derived from simple fight or flight intention movements.

The vocal displays appear to have arisen from two or three, at most, primitive types of calls. The first type, from which harmonic spectra may have developed, was probably an alarm call rich in harmonics, with a high dominant frequency that showed little change throughout the duration of the call. The second type was probably a territorial call, pure in tone with a low, abruptly changing dominant frequency. Clicks may have arisen as the frequency changes within the call retained their abruptness but occurred in a shorter time span, or they may have been present as a distinct acoustic signal that was later combined with pure tone calls.

Evolution of communication signals in the Blue Jay shows a trend toward variety, rather than complexity. Only one visual display (courtship bobbing) and one vocalization (song) show a high degree of complexity. Instead, a wide variety of vocal and visual signals has developed. The large number of contextually modifiable combinations of both types of signals renders the Blue Jay's repertoire of communication signals quite extensive.

CHAPTER VI

SUMMARY

Visual and acoustic communication signals in the Blue Jay, Cyanocitta cristata, were studied in a population of 25 captive, hand-raised birds and "in the field." Observation, analyses of 16mm films, and sonagraphic analyses of recorded calls were used to elucidate the physical and functional characteristics of signals.

Blue Jays exhibit about 20 distinct visual communication signals. The function of a given signal is determined by the context in which it is given, as well as fixed or moving aspects of "facial expression," head position, body position and piloerection. Movement in general, as well as movement of specific, often visually conspicuous, parts of the body or plumage, probably serves to give visual emphasis to displays, often without changing their meaning, just as an increase in volume might emphasize an acoustic signal.

Visual communication signals may be placed in three groups on the basis of the functional and physical similarities they demonstrate. The first group of postures, which do not appear to function as communicative signals, are

those assumed during maintenance activities. They are characterized by relaxed or fluffed plumage, neutral body position, appressed wings, and closed tail. The second group is characterized functionally as primarily agonistic and is associated with erection of body, and, especially, head plumage and abrupt movements, if any, of wings and tail. The last group of displays functions as submissive or solicitative signals and is associated with sleeking of head and body plumage and fluttering type movements of the wings and tail.

Most of the visual displays appear to be derived displays, that is they are ritualized patterns derived from simple fight or flight intention movements.

Twenty different types of vocalizations in the Blue Jay's acoustic repertoire are described. Analyses revealed that the calls may be placed in four distinct groups on the basis of gross physical characteristics and functional similarities. Within groups the calls differ structurally from each other with respect to the number of sound sources, fundamental and dominant frequencies, inflection, and the occurrence and nature of frequency modulation. The biological significance of a call is determined by its physical structure, the visual displays with which it may be associated, and the behavioral context in which it is given.

The harmonic spectra calls are rich in harmonics, high in dominant frequencies and long in duration. They

function as indicators of alarm, frustration and excitement associated with fear. They are also used as contact notes. The pumphandle calls have few harmonics, strong frequency modulation, and low dominant frequencies. They indicate mild excitement and uncertainty, and they also serve as territorial or alert calls. The click calls have harmonics, clicks, strong and regular frequency modulation, and terminal downward inflection. They express excitement associated with both frustration and fear. Song is highly variable in physical characteristics and is the principal vocalization of the courting male. It is also given randomly by birds in a calm behavioral state.

That vocalizations fall into distinct structural groups, which, within themselves, demonstrate functional cohesiveness, suggests that diversification from two or three primitive call types has occurred. Evolution of communicative signals in the Blue Jay shows a trend toward variety, rather than complexity. The combination of visual with vocal signals enhances the repertoire of communicative signals.

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APPENDIX

Symbols Used in the Dissertation

AC The Alarm Call (Fig. 19).

AM Amplitude modulation--changes in the amplitude of a vocalization.

BK The Begging Keu Call (Fig. 27).

BS The Bell Song (Fig. 33).

CC The Crow Call (Fig. 30).

DC The Distress Call (Fig. 18).

DW The Descending Whistle (Fig. 37).

F The fundamental frequency of a vocalization or one of its sound sources, that is, the frequency with the lowest value.

FC The Flock Contact Call (Fig. 20).

FM Frequency modulation--changes or warbles of the fundamental frequency.

GR The Growl (Fig. 38).

H1, H2, etc. The first harmonic, second harmonic, etc.

LK The Loud Keu Call (Fig. 29).

MC The Meow Call (Fig. 31).

RC The Rolling Click Call (Fig. 36).

S1 One of the sound sources (the first described for each call in the text) of a vocalization.

S2 The second sound source described for a vocalization in the text.

SK The Soft Keu Call (Fig. 28).

SS A sound source--one of two sounds that can be produced by a Blue Jay.

TDW The Triple Descending Whistle (Fig. 39).

WBS The Wheedle Bell Song (Fig. 35).

YBS The Bell Song of young Blue Jays (Fig. 34).

YFB1, YFB2, etc. The Food-begging Call of young Blue Jays, Type 1; Type 2, etc. (Figs. 23 - 26).

YFC The Flock Contact Call of young Blue Jays (Fig. 22).