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BLUE JAY VOCAL BEHAVIOR.

The University of Michigan, Ph.D., 1976
Zoology

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BLUE JAY VOCAL BEHAVIOR

by
Steven Michael Cohen

A dissertation submimitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Zoology)
in The University of Michigan
1977

Doctoral Committee:

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ACKNOWLEDGMENTS

I wish to thank Paul Shelbe and David Bay for their photographic assistance and Dr. Francis Evans for generously making the facilities of the E. S. George Reserve available to me. Dr. R. Alexander, W. Stebbins, R. Storer and B. Hazlett gave me advice and encouragement when I most needed it.

Above all, I owe thanks to my wife Kate.

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I. INTRODUCTION

The Blue Jay (Cyanocitta cristata) is a common and aurally conspicuous member of the avifauna in the eastern portion of the United States. Throughout the year single individuals and small flocks of jays call loudly. Thus, they are an attractive subject for the study of avian vocal communication. This study describes the jays' calls and their behavior when calling. The descriptions are based on field observations of marked individuals. Playback experiments were conducted to test responses to particular calls. Two groups of jays were raised in laboratory conditions to control their exposure to adult vocalizations. The basic assumptions of this study are that calling has evolved because it contributes to the survival and/or reproductive success of the individual, and that the function of each call must always be explained in terms of the advantage the caller derives from drawing attention to itself in the context in which it is calling.

The Blue Jay has been the subject of several studies. Tyler (1946) summarized anecdotes on jay behavior. Arnold (1938) described nestling development, preening behavior and the taxonomic status of the Blue Jay. Hardy (1961) compared the territorial, courtship, and vocal behavior of the Blue Jay to

three other species of jays. He found the Steller's Jay (Cyanocitta stelleri) to be most similar, the Mexican Jay (Aphelocoma ultramarina arizonae) to be least similar and the Scrub Jay (Aphelocoma coerulescens) to be partly similar in characteristics to the Blue Jay. Edwards and Waring (1971) traced the normal development of jay calls in hand-reared individuals which were raised in the presence of wild-caught adults. Conant (1972) provided sonograms of the calls made by her hand-reared captive jays and drawings of their postures. Recently, Wenger (1975) has reviewed some of the confusing features of Blue Jay migratory behavior.

The Steller's Jay is the only congenor of the Blue Jay. It is widely distributed in the western portion of the United States. Brown (1964) described its social organization and vocal behavior in connection with his study of the association between crest erection and agonistic interactions. The vocalizations of the two species appear in many cases to be homologous. These homologies will be mentioned in the appropriate sections. Indeed, hybridization between the two species has recently been reported (Williams and Wheat, 1971).

There is a voluminous literature on the general subject of avian vocal behavior. Major studies of individual species have been done by Nice, 1943; Marler, 1956; Lanyon, 1957; Lemon, 1965; Smith, 1966; Bertram, 1970; Smith, 1972; and Abraham, 1974. In general these studies and many others show that most of the calls in the repertoire of a particular species are restricted to one

context and have one function. Some calls, however, are given in several contexts. The implication is that the call has a different function in each of the contexts in which it is given. But this complication can usually be resolved by considering the relationship between the respondent and the caller. Thus, for example, male song may elicit approach from a prospective mate, withdrawal by a rival and no response from a migrant. The call has a different significance to each class of individuals. The context may or may not reflect this, but does not alter the significance of the call.

Studies of the vocal behavior of individual species have led to insight into some of the general features of avian vocal behavior. Male song, the most intensively described call, is now clearly identified as a major feature of the aggressive behavior which a male uses to keep other males out of his territory, and therefore, away from his mate and/or the resources of his territory. Only conspecific songs elicit strong aggressive responses from the territorial male (Dilger, 1956; Thielke, 1962; Lanyon, 1963; Gill and Lanyon, 1964; Lemon, 1969; Lemon and Herzog, 1969; Thompson, 1969; Emlen, 1972) and the local song dialect is a stronger stimulus than a foreign one (Lemon, 1967; Bertram, 1970; Milligan and Verner, 1971; Harris and Lemon, 1974). Whenever song learning occurs (Poulsen, 1954; Sauer, 1954; Mesmer and Mesmer, 1956; Thorpe, 1958; Marler, Kreith and Tamura, 1962; Marler and Tamura, 1964; Lemon and Scott, 1966; Mulligan, 1966; Dittus and Lemon, 1969; Immelman, 1969; Thielke, 1969;

Marler, 1970) the learning is probably favored because it helps the learner more effectively threaten the individuals who are or will be the learner's greatest potential threats. Thus, the "critical period" for song learning probably coincides with the time when reproductive rivals first meet on the nesting grounds or the first time young males hear their potential rivals (Poulsen, 1954; Lanyon, 1957; Thorpe, 1958; Marler and Tamura, 1964; Dittus and Lemon, 1969; Falls, 1969; Immelman, 1969).

Bird calls are also known to facilitate individual recognition of parent and offspring. For example, the chicks of colonial nesting sea birds distinguish their parents from the hostile adults who are nesting in neighboring territories by the calls which their parents make. The parental calls provide enough auditory information for the chicks to make the appropriate approach or avoidance response (Tinbergen, 1953; Tschanz, 1968; Stevenson et al., 1970). The chicks in turn are recognized by the vocalizations they make (Tinbergen, 1953; Stonehouse, 1960; Davies and Carrick, 1962; Tschanz, 1968).

Individual recognition by call is also known to occur between mated birds (Thorpe, 1963; Tschanz, 1968; Beer, 1970a; White et al., 1970). Female goldfinches (Spinus tristus), for example, recognize their mates by the "flight song" the pair share (Mundinger, 1972) and mated mynah birds (Gracula religiosa) recognize each other by the distinct characteristics of their calls (Bertram, 1970).

Coordination of the onset and flow of biologically significant interactions is a function frequently attributed to particular calls. The calls are correlated with the apparent readiness of the caller to feed or be fed (von Haartman, 1953; Tinbergen, 1953; Collias, 1960; Stokes, 1961; Thorpe, 1961) and to mount or be mounted (Vogt, 1938; Lanyon, 1957; Stokes, 1961; Hartby, 1969; Samuel, 1971).

II. MATERIALS AND METHODS

A. Basic Observation Area

The Edwin S. George Reserve is approximately two square miles in area and lies 25 miles northwest of Ann Arbor, Michigan. It has been fenced and undisturbed since 1930. Field work in the oak-hickory woods on the Reserve occurred between October 1971 and July 1972 and October 1972 and July 1973. Observation and tape-recordings of marked birds (see below) were made between January and July of 1972 and 1973. The observations made during January and February are referred to as winter observations; the observations made in April are characterized as prenesting-period observations; and the observations made in May and June are called nesting-period observations.

The jays were usually found and observed in three wooded areas of the Reserve: 1) the area which extends from the northwest border of the Great Swamp to the old fields in the north central portion of the Reserve; 2) the Southeast Woods; and, 3) Big Island. Jays were frequently found roosting in the red cedar trees (Juniperus virginiana) around Burt Pond and in the bushes Viburnum spp.) east of the main house. Birds were regularly noticed going into and coming from the Big Swamp, but following them into this wet area to observe them there was impractical.

B. Trapping

My trapping efforts were concentrated in the central portion of the George Reserve. There, three feeding stations were stocked with corn, suet, and sunflower seeds. These feeders probably helped maintain the large jay population on the Reserve. Mist nets were strung in front of the perches which jays used on their way to and from one of the feeders. Potter traps were on and under a feeding table. The third feeder was enclosed by a 6' x 6' x 6' (183 x 183 x 183 cm) house trap. Using all of these methods I caught, banded, tagged and released 110 jays.

C. Marking Techniques

Several marking techniques were tested in an effort to facilitate individual identification of jays. Color bands (National Band and Tag Company, Newport, Kentucky) proved unsatisfactory since banded jays were rarely close enough and in good enough light for me to be able to read the bands. Moreover, careful scrutiny of every individual was required just to determine if it were marked. I found that 1½" (3.8 cm) squares of vinyl plastic (Safety Flag Company, Pautuckett, Rhode Island), numbered with vinyl ink (Nazdar Corporation, Detroit, Michigan), and attached to the patagium of each wing with patagial wing clips (National Band and Tag Company), transformed jays into very conspicuous birds. The tags did not appear to interfere with flight. Unfortunately, the upward orientation of the tags when the jays were perched made seeing the numbers difficult. Moreover,

on some birds the tag became hidden from view because it slipped under the wing or because it was obscured by body feathers. I then adopted the practice of hanging a 1½" (3.8 cm) square tag from one leg (Figure 1). An aluminum band (Size 10, National Band and Tag Company) threaded through the two slits in the shank portion of the tag and closed around the bird's tibiotarsus held the tag to the bird. Using a band one size too large allowed the tag to rotate freely on the leg. To prevent the band and tag from slipping or being pulled over the bird's toes, I attached the standard size USFWS band to the same leg under the aluminum band. The only tag loss I observed on 15 captives over a six month period was due to wear between the slits in the shank of the tag.

Leg-tagged birds were easily spotted by eye at distances up to 100 meters. The 1¼" (3.1 cm) high numbers and letters could be read at this distance with a X20 spotting scope (Bausche and Lomb) mounted on a gun stock.

The extent to which the dangling tag interfered with flight, perching or other aspects of behavior is not easy to determine. People expressed concern for the well-being of the tagged jays. But the birds seemed to adapt quickly to the tag and band which together weighed approximately 3 grams. By making the shank of the tag long enough, i.e., approximately 2" (5.1 cm) the tag always hung below the perch. Tags with shorter shanks interfered with perching because they tended to lie over the perch and be stepped on. I saw the tag on a jay get caught in twigs only twice and

Fig. 1--A vinyl leg tag. It is attached to a jay's tibiotarsus with an aluminum band.

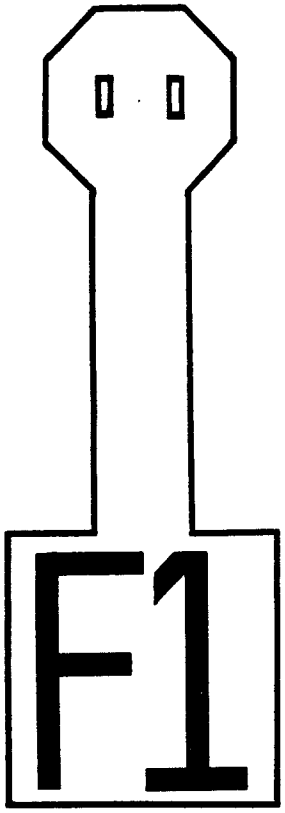


Fig. 1

both times the birds managed to free themselves. During flight the tag either flapped slightly under the bird or was pressed up against its underparts. Once I saw a Cooper's hawk (Accipiter cooperii) unsuccessfully pursue a leg-tagged jay. One jay, #48, is known to have survived at least 1½ years with its leg tag. Only six tags were ever found on the ground in the George Reserve. The feathers nearby indicated that the six birds had been devoured by scavengers. Many tagged jays were never seen again, nor were their tags found on the ground. They probably were not seen because they left the vicinity and not because they died.

Whatever the effect leg-tagging may have had on the survival of tagged jays, wearing the tag did not seem to adversely affect the jay's social interactions. Two pairs of jays which nested on the George Reserve in the Spring, 1973 were composed of individuals who had each been tagged the previous winter. Six other pairs of nesting jays were composed of one tagged and one unmarked jay. Fifty-four fledglings tagged a day or two before they left the nest were all fed by their parents. One brooding female was caught by hand on her nest. After being tagged, she did not desert the nest and her mate continued to feed her. Their brood fledged successfully.

D. Basic Observation and Tape-Recording Techniques

All observations were made in the morning hours, weather permitting, starting about one half hour after sunrise, the time

when jays leave their roost, and ending not more than four hours later. I used both an X20 spotting scope mounted on a gun stock and 7x35 binoculars to look for jays and read their tag numbers. Once I found a marked jay I started a stop watch and tape recorder (Uher Report S with a Uher M15 microphone). All recordings were made at 19.05 cm/sec (7 1/2 ips). I recorded the bird's calls, described every time it hopped, flew, foraged or called, and noted the presence and behavior of other jays or the calls of unseen jays. As soon as I lost sight of the bird, I stopped the watch, noted the duration of the observation and turned off the tape recorder. In this way, i.e., using the "Focal Animal Sampling Technique" (Altmann, 1972: 20) I collected data on only one individual at a time and kept a record of how long each observation lasted. Whenever I had to choose which bird to search for or which one to watch when two or more marked birds were visible simultaneously, I chose the one with the least total observation time to date. Thus, if two marked birds were visible and one was calling while the other was silent, the decision on whom to watch at that juncture depended on the total time each had already been observed and not on their behavior.

I was unable to standardize the duration of each observation because the time a jay stayed in view depended on the time which elapsed before it flew out of sight or disappeared in the canopy or undergrowth. While I couldn't control when the jay terminated the observation, I did have a stopping rule to decide when I

should stop observing a particular individual. If I had watched an individual for a total of ten minutes in one day, either in one straight period or in total from several short encounters, I did not watch that individual again that day. This precaution probably helped avoid watching the most conspicuous individuals and those who were inactive for long periods (Altmann, 1972: 13).

Some jays were, of course, easier to find and watch than others. Clearly, the more vocal a jay was, the more likely I was to notice it. Consequently I was much more likely to find and watch a jay which was calling or had just called than one which was silent. On the other hand, the silent jays which I noticed were usually ones which had attracted my attention by their movement. So I was much more likely to find and watch a silent jay that was hopping or flying than one which was perched. And, since I spent most of my time walking on the established trails and along the edges of the wooded areas, I was much more likely to find and watch jays which were in view from those areas rather than ones which frequented other areas. Thus, the observations were biased toward jays which were calling or moving when I was near them and toward jays which frequented the areas most accessible to me. This may account for the wide differences in the total observation time ammassed for each bird. Those birds which were encountered only rarely had totals of only several minutes while those encountered more frequently had totals of several hours.

I treated these records of varying length in the following way. To analyze the seasonal pattern of calling I used just the first ten minutes of each record. This maximized the number of individuals sampled in each season. It also standardized the observation time used for each individual. To describe differences in calling behavior associated with breeding status, I used the first 90 minutes of observation of each bird. This was the maximum observation time common to all the birds being described, though not the maximum time for every individual. Thus, the duration of the sampling period is standard in this sample too. To describe the behavior of particular individuals, when they were with and without their mates, I used the total observation time available for each individual.

In all, I have records of slightly more than 175 hours of observation of marked birds. These include records on 38 birds observed for a total of 23 hours in the winter, 36 birds observed for a total of 77 hours in the spring, and 25 birds observed for a total of 75 hours near their nests in the summer. I spent 520 hours watching unmarked birds and nearly 3000 hours in the field trapping and searching for them.

E. Other Samples

When observing behavior leading to feeding of females by their mates and feeding of fledglings by their parents, I collected data in a different way. After seeing a female being fed at

one nest, I visited another nest and watched until feeding occurred there. This seemed to be a more efficient strategy than waiting for the next feeding which might be as much as an hour later. Similarly, after seeing each fledgling fed near one nest I went to the next nest, to watch feedings there. Using this procedure I observed 17 females fed four times by their respective mates, 75 feedings of four-week-old fledglings and 50 feedings of five-week-old fledglings.

F. Playback Experiment Areas

From April through July 1974 I did playback experiments on unmarked individuals in the Nichol's Arboretum and the Matthei Botanical Gardens. The Nichol's Arboretum lies along the Huron River within the city limits of Ann Arbor. It has stretches of wooded hilside where jays are abundant year around. The Matthei Botanical Gardens is east of Ann Arbor and has wooded areas in which jays are common in the spring and summer. Both areas have trails through and along the edges of the wooded areas. The experiments were conducted from these trails and edges after a jay was encountered.

G. Playback Experiments

Two types of playback experiments were performed. The first type was designed to compare the behavior of jays during the broadcast of a typical call to their behavior during the broadcast of a control sound. The playback tape contained a call which had been

rerecorded at 9.5 cm/sec (3 3/4 ips) from field tapes. The call was selected for the quality of the original recording and sounded in all ways "typical". The playback tape consisted of 30 repetitions of that call one second apart. This was followed by 30 seconds of silence. The next half of the tape contained 30 beeps of a 2000 Hz tone sounded one second apart and another 30 seconds of silence (Figure 2). The complete two-minute section of the playback tape comprised one trial for one experimental individual. On the next two-minute section of the playback tape the order of presentation of the call and tone was reversed. Thus, the next bird tested heard the tone broadcast first followed by a half minute of silence and then the call played 30 times and another half minute of silence. Similarly the order of presentation of the tone and call was reversed on each succeeding section of tape for each subject tested.

I started a playback test after finding a jay which was perched between 25 and 50 meters from me. I stood still, started the tape recorder and counted the number of calls and movements the bird made during each minute of the tape. I had to lump all hopping and flying under the rubric of "movement" because they were hard to categorize more specifically. Hops blended into hops which included a flap or two of the wings. These in turn differed very little from short flights. The distance of a flight seemed to depend more on the distance between trees rather than the bird's motivation to escape or approach the speaker. In fact,

Fig. 2--Playback procedure. In the type I format, one broadcast was of a prerecorded call and the other was of a control tone. In the type II format, one broadcast was of a prerecorded call and the other was of the subject's call recorded immediately before the experiment began.

PLAYBACK PROCEDURE

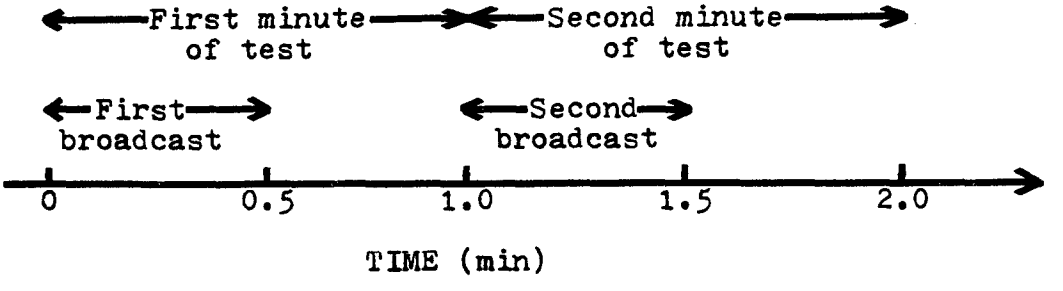


Fig.2

most movements from tree to tree or within the same tree were neither approaches nor withdrawals but tended to maintain the distance between the subject and the sound source, within the restrictions of the available perches, and to change the view or "perspective" the subject had of the sound source. I did record at the end of each minute of playback the change in distance between the bird and the sound source. If the jay moved out of sight before the tape ended, the partial record was discarded and the trial performed again on the next bird encountered.

The second type of playback experiment was designed to compare the behavior of jays during the broadcast of a recording of their own rendition of a call and of the same call given by a different bird. I carried two Uher tape recorders, one to broadcast the prepared tape of the typical call and the other with a blank 3 second loop in it. After locating a bird I recorded its call on this loop. When a satisfactory recording was obtained I was able to initiate the experiment following the same format described for the first type of playback experiment. I broadcast 30 seconds of the bird's own call, waited 30 seconds and then broadcast 30 seconds of the standard call. The test ended 30 seconds later. Again the order of presentation was reversed with each trial. The number of calls and movements during each minute was counted and the change in overall distance in each minute was estimated.

Since the field recording of an individual's call was often made under less than ideal conditions, i.e., planes were overhead,

tractors and trucks were passing by, etc., I was not able to match the volume and quality of the two tapes. These factors may have detracted from the stimulus value of the bird's own call.

H. Tutoring Experiment

I hand-reared two groups of four jays, one group each in 1972 and 1973. The birds were taken from different nests when 5 to 7 days old and color banded for individual identification. They were fed the diet recommended by Lanyon and Lanyon (1969), but "wax worms" (Lloyd Wildt, Bath, Michigan) were substituted for bee pupae. When the jays were able to feed themselves, they were maintained on ad lib amounts of Tasty Dinner With Fruit (8 IN 1 Pet Products, Inc., Brentwood, N. Y. 11717), Gaines Kibbled Dog Food (General Foods Corp., White Plains, N. Y.), sunflower seeds and water.

The four birds in each group were housed as a group indoors, in an acoustic isolation chamber. This chamber consisted of three boxes nested inside each other. The outer box, made of 3/4" (2.9 cm) plywood was insulated from the middle box also of 3/4" plywood by 2" (5.1 cm) of fiber glass. The inner box was made of 1/2" (1.3 cm) homosote board and measured 60x30x50 cm. It had a perch along each side and was illuminated by a 40 watt fluorescent tube. An automatic timer outside the chamber turned the light on and off and was adjusted each month to provide average day length for that month. Air circulation through the chamber was achieved through baffles between the walls on each side. A 4" (10.2 cm)

exhaust fan mounted over the exit port on the outside of the box drew air out of the inner chamber. Fresh air entered through the port on the opposite side. The exhaust fan ran continuously. The door of the chamber had an observation window consisting of two panes of glass; the outer pane was one-way glass. The door frame was lined with felt insulation to insure a snug fit.

Sound attenuation of this acoustic isolation chamber was measured directly using a General Radio Sound Level Meter 1564-A and a Uher tape recorder. The recorder was placed inside the chamber and a tape of jay calls was broadcast. Readings on the C-scale of the meter indicated that when the door of the chamber was closed the sound intensity of the calls being broadcast dropped 25±2 dB measured one foot away from the door. Since the intensity of bird calls made out of doors and heard in the room in which the chamber was kept was never greater than 65 dB, the chamber would have attenuated them to the 40 dB level. These sounds would probably have been masked by the continuous hum of the exhaust fan.

The calls made by each bird were recorded every two weeks until the birds were eight months old. The group raised in 1972 was not tutored. The 1973 group was tutored with eight minutes of typical jay calls once in the morning and once again in the afternoon beginning when they were six weeks old and continuing until they were five months old. The tutoring tape consisted of 60 repetitions of a Jay Call followed by 60 repetitions of the

Squeaky Gate Call, the Bell Call, and the Rattle. The tapes was played on a Sony TC 40 tape recorder placed inside the chamber and removed after the tape ended.

I. Sonograms

All sonograms were made directly from field recordings using a Kay Vibralyzer (7030A) in the frequency range 80-8000 Hz and the wide band setting. The dark band of background noise at the base of the sonogram was reduced by adjusting the print setting rather than by using a band-pass filter. The sensitivity settings in the record and reproduce modes of operation were adjusted to maintain readings in the -5 to 0 Ohms range of the machine's meter.

The sound energy in jay calls is usually between 1000 and 4000 Hz in a series of bands. The lowest band is commonly referred to as the fundamental and the next band up as the second harmonic. When two membranes are vibrating at different frequencies, as is often the case in jay vocalizations (Conant, 1972), two fundamentals and two second harmonics are present. Since these distinctions are not of primary importance in this study the bands are simply referred to by number, starting with the lowest band. The longest and darkest or broadest band in a call is the one used to describe a call which has several bands. Frequency measurements of a band were made at the beginning and end of a sustained call and at the beginning of a short note.

The sonograms used for illustration were selected because they were the ones which, in the set of sonograms illustrating a

point, were least contaminated by extraneous noises like the sound of my voice, the ticking of my watch, the call of another bird, or the roar of an airplane or truck. They were photographed using Kodak Tri X film and printed on Kodal polycontrast RC paper. Some grays were lost in printing. The prints are 3/4 the size of the original sonogram, thus some of the fine details in the original are smaller and somewhat harder to see in the photograph.

III. RESULTS

Blue Jays are monomorphic and momogamous. Only a few behavioral differences distinguish the male member of a pair from the female. For example, only the female Begs and only the male feeds her. While nesting, only the female incubates the eggs and broods the young. The male feeds her on or near the nest. He also brings the food for their young until she starts foraging.

Nesting Blue Jays are generally silent and inconspicuous. The male forages so far from the nest that he often becomes visible to an observer only when returning to the nest with food. When returning he calls very softly or not at all. Similarly, when either member of the pair displaces another jay from the vicinity of the nest, the displacement is always done silently. Nesting jays only call loudly while warding off actual attempts at predation on their eggs or young; though some jays which nest in places where they are repeatedly disturbed by people or cats, resort to calling and defending the nest with very little provocation.

Blue Jays form three kinds of flocks. One kind of flock forms around a perched predator, like a hawk or owl. The jays call and dive at the predator until it flies away. Mobbing predators in this way occurs throuthout the year and appears to involve all the jays in an area. Another kind of flock which jays form moves as a loose group, alternately flying and then perching. The jays call repeatedly and remain together for as much as fifteen minutes. This kind of flock forms sporatically in the late winter and more

frequently during the spring. As the season progresses only unmated birds join these flocks. The flocks continue forming, but less frequently during the nesting season. Nesting birds do not interact with these flocks, even when one passes near the nest. In contrast with the two flocks already described, the third kind of flock which jays form is relatively inconspicuous. It is composed of a set of birds which, during the winter, share a common home range, roost together at night, and rest together during the day. The members of these flocks move independently and do not call when together.

The Blue Jay's calls have been described several times (Arnold, 1938; Tyler, 1946; Hardy, 1961, 1964, 1969; Edwards and Waring, 1971; Conant, 1972). Table 1 lists the various onomatopoeic and functional names of jay calls used in the literature. Five calls are regularly identified: the Jay Call, the Squeaky Gate Call, the Bell Call, the Rattle, and the Yurp Call. The first three calls are relatively loud and can be easily heard when the caller is more than 100 meters away. The Rattle Call is not quite so loud. The Yurp Call is the softest of the five. It can be heard with certainty only when the caller is less than 50 meters away. Differences in individual rendition of these calls have not been recognized.

A. Individual Differences in Call Rendition

Jay Call. The Jay call is the call most frequently made by Blue Jays. It accounts for more than half of all the calls made

TABLE 1

NAMES OF BLUE JAY CALLS

Calls	Tyler 1946	Hardy 1961	Conant 1972	Edwards 1972
Jay	Peer, Beer	Jay, Jaay, Jayer	Flight Contact Call, Alarm Call	Jeer Cry
Squeaky Gate	--	Squeaky Gate, Wheedle-ee	Pump Handle	High-low Pump Handle, Monotone Pump Handle, Quiet Pump Handle
Bell Call	Tull-ull Twirl-erl, Teekle, Anvil	Cleop	Bell Song	--
Rattle	R-r-r-rt	Rattle B'r'r'r	Rolling Click	Rattle
Yurp	Kuk	Kut,	Soft Keu	Kueu
Belling Call	--	Female Solici- tation Call, Keu	Begging Keu, Young Fledgling Begging Call	--
Swallowing	--	--	--	--
Squacking	--	--	Distress	--
Chortling	--	--	Song	Random Jabber
Peeping	--	--	--	Peeping
Chucking	--	--	--	Chucking
Chirping	--	--	--	Chirping
Mewing	--	--	--	--
Churring	--	--	--	--
--	--	--	--	Growling
--	--	--	--	Whirring

by Blue Jays in any season (Figure 3). Most Jaying is done while the caller is perched. An individual will often start calling after being perched and silent for a while. It will remain perched while calling, or fly a short distance (e.g., less than 75 meters), then perch and call again. It is not engaged in any obvious activity such as foraging, or in any obvious interaction such as fighting or courting. Jays also give the Jay Call while flying alone, or in flocks, and while mobbing an owl or hawk.

There is considerable variation in rendition of the Jay Call. Hardy (1961) mentions that the Jay Call is sometimes rendered as "jayay" and other times as "jayer" and that "assembly" calls closely resemble "alarm" calls. Conant (1972) provides sonograms of many versions of the Jay Call and attributes slightly different functions to each version. In the field, I heard and recorded many renditions of the Jay Call. But comparison of sonograms reveals that only two versions are given by every jay (Figure 4). One version of the call sounds monotonal and short; the other, ditonal and slightly longer. The tonal differences between versions arises from the fact during the first 0.05 seconds of the ditonal version of the Jay Call there is a 700 Hz rise in the frequency of the call, as measured on the darkest band of the sonogram, usually the fourth. No comparable change in frequency occurs in the darkest band, usually the second, of the monotonal version (Table 2). It is the rapid rise in frequency at the beginning of the ditonal version which gives one the impression

Fig. 3--The distribution of calls given by marked jays in three different seasons.

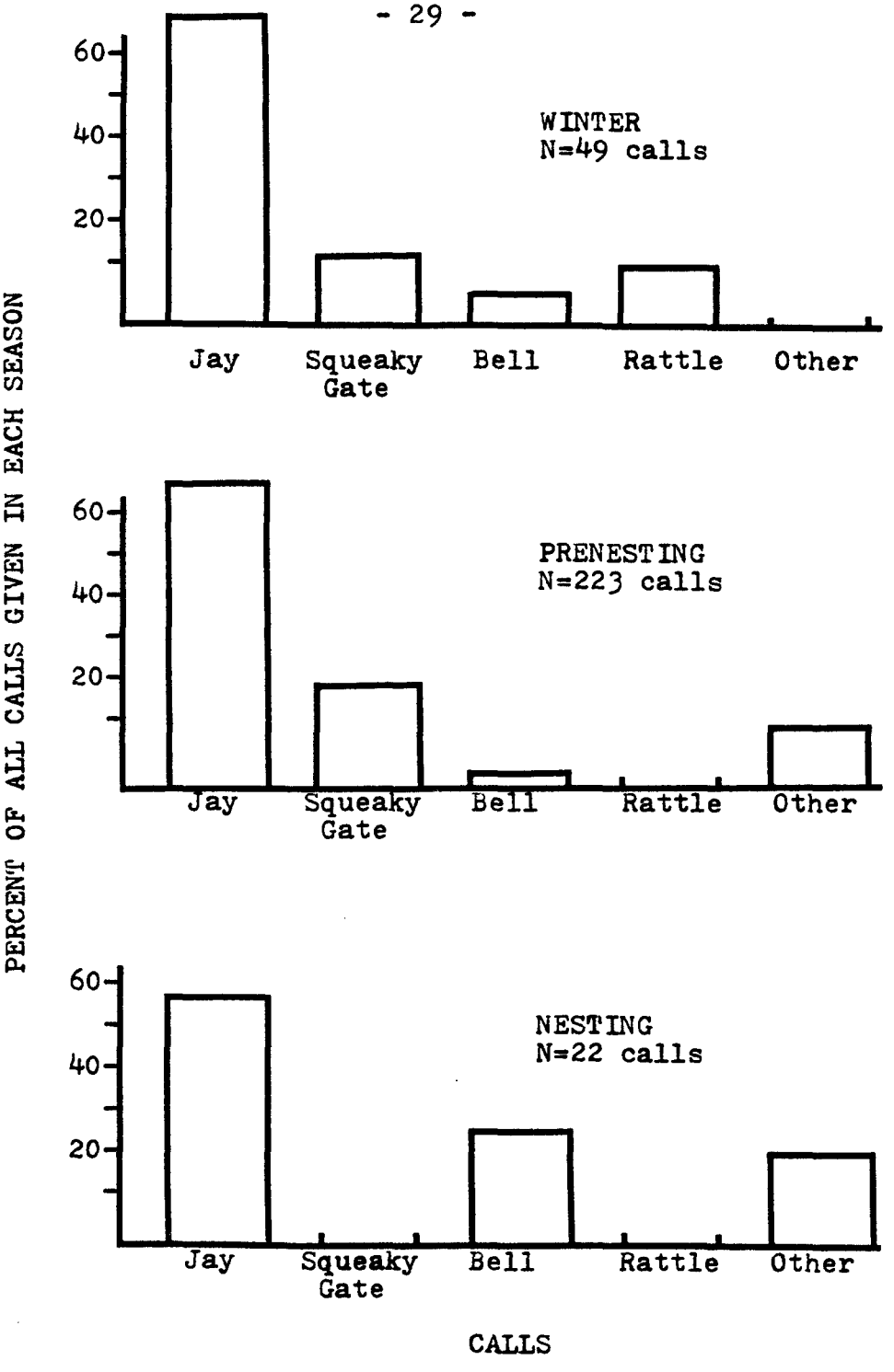

PERCENT OF ALL CALLS GIVEN IN EACH SEASON
60
40
20
WINTER
N=49 calls
Jay
Squeaky Gate
Bell
Rattle
Other
PRENESTING
N=223 calls
NESTING
N=22 calls
CALLS

Fig. 3

Fig. 4--Individual jays give two versions of the Jay Call. Each sonogram in column I represents a different bird's monotonal rendition of the Jay Call; each sonogram in column II represents that bird's other rendition of the Jay Call; this rendition sounds ditonal, though it consists of a single note which is slurred upward initially.

Fig. 4

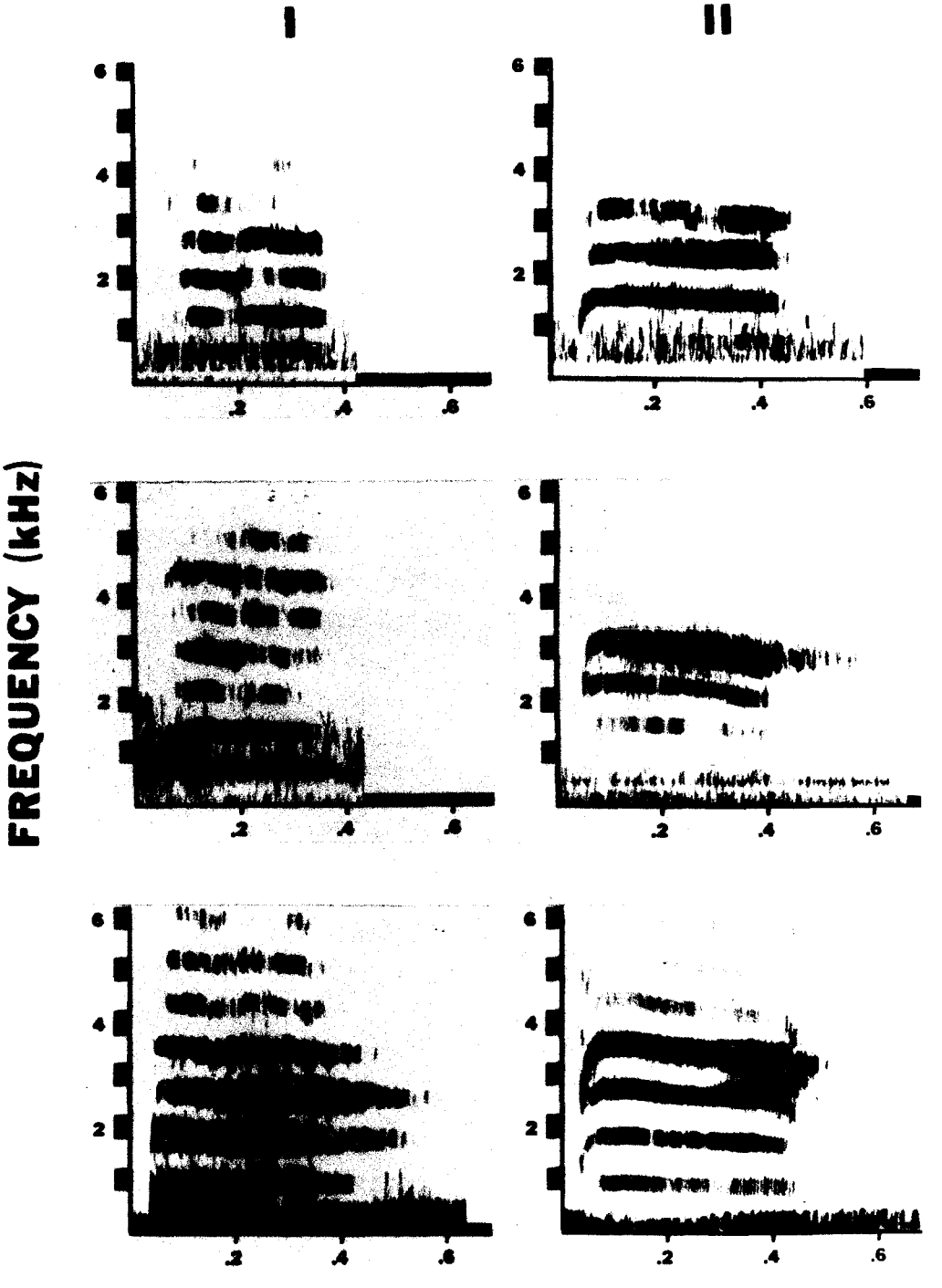


Fig. 4(cont.)

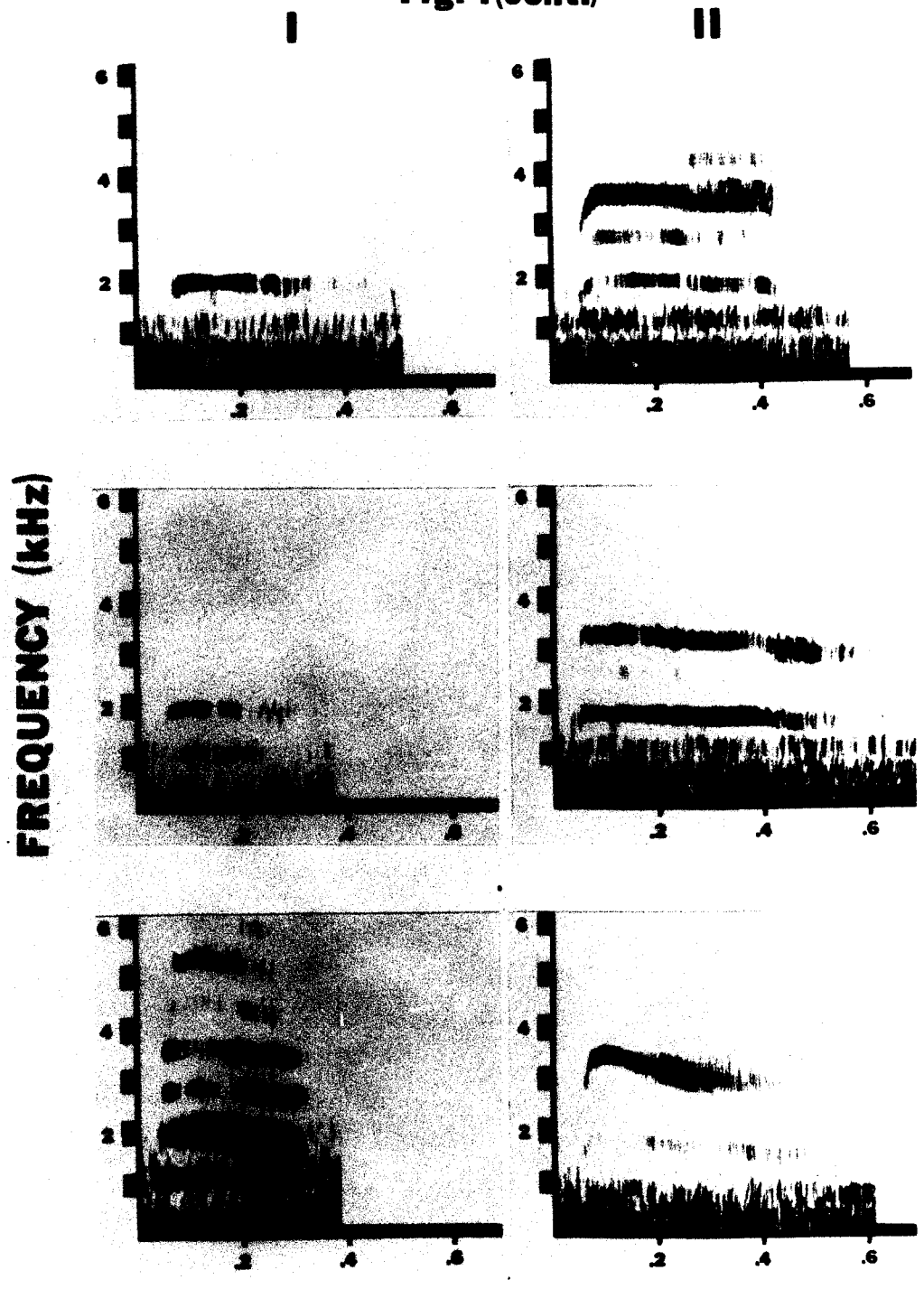


TABLE 2

FREQUENCY MODULATION AT THE BEGINNING OF THE DITONAL JAY CALL BY TWENTY DIFFERENT BLUE JAYS

Frequency (Hz) Initial	High	Δ Frequency (Hz)
2200	3100	900
2100	3300	1200
2900	3400	500
2200	3400	1200
2700	3600	900
2200	3100	900
2500	3100	600
2800	3500	700
3000	3100	100
3100	3300	200
3100	3300	200
3000	3100	100
2800	3900	1100
2600	3400	800
2400	3500	1100
2100	3100	1000
2500	3100	600
2800	3700	900
2200	3100	900
2100	3300	1200
		$\bar{X}$ = 700

that the call is ditonal and that the first tone is of a different pitch than the second even though the call consists of one note which is slurred upward initially. It is interesting to note that my subjective impression was that the first tone was higher than the second when in fact it is the reverse. Several other differences exist between the two versions. There is a slow drop in the frequency of the ditonal version averaging 325 Hz during the major portion of the call, compared to only a 75 Hz drop in the monotonal version (Table 3) ($t = 22.0$, $p < .01$). The average duration of the ditonal version is more than a full tenth of a second greater than the duration of the monotonal version (Table 3) and the difference is significant ($t = 2.10$, $p < .05$). And the frequency band most emphasized in the ditonal version is around 3200 Hz while the band with the most energy in the monotonal version is around 2100 Hz (Table 3).

While there are only two versions of the Jay Call, considerable differences exist between individual renditions of each version. Figure 5 illustrates individual differences in the monotonal version. In the first bird's rendition of the call (Figure 5A) all frequency bands start simultaneously, but in the next bird's call (Figure 5B) the bands at 1200 and 2800 Hz start approximately 0.07 sec earlier than the band at 2100 Hz. They end later too. The reverse occurs in Figure 5C. Delivery of the monotonal version of the Jay Call also varies in the duration and number of silent intervals in the darkest band (Figure 5D-F).

TABLE 3

DIFFERENCES BETWEEN VERSIONS OF THE JAY CALL
GIVEN BY TWENTY DIFFERENT BLUE JAYS

Monotonal Version				Ditonal Version			
Initial Hz	Final Hz	Δf Hz	Duration Sec	Initial Hz	Final Hz	Δf Hz	Duration Sec
1700	1700	0	0.37	3100	3000	100	0.38
1400	1400	0	0.38	3100	3000	100	0.21
2200	2100	100	0.33	3000	2700	300	0.21
2100	2100	0	0.25	3100	2900	200	0.39
3000	2900	100	0.26	3600	3000	600	0.31
1900	1800	100	0.21	3300	3000	300	0.48
3000	2900	100	0.25	3700	3000	700	0.47
3100	3100	0	0.27	3900	3100	800	0.38
1800	1400	400	0.31	3900	3100	800	0.35
2400	2400	0	0.28	1700	1600	100	0.40
2400	2300	100	0.30	3200	3200	0	0.50
1600	1600	0	0.26	3600	3200	400	0.52
1700	1700	0	0.26	3000	3000	0	0.24
1600	1600	0	0.29	3100	2900	200	0.50
1400	1400	0	0.38	3100	3000	100	0.39
3000	2900	100	0.26	3600	3000	600	0.37
2300	2300	0	0.30	3100	2900	200	0.39
1900	1500	400	0.28	3500	3100	400	0.46
2200	2100	100	0.20	3200	3000	200	0.47
1600	1600	0	0.25	3300	2900	400	0.50
$\bar{X}$ =2115	2040	75	0.28	3255	2930	325	0.42

Fig. 5--Individual renditions of the monotonal Jay Call differ in several respects. All three sound bands in A begin about the same time; but the first and third bands in B begin considerably before the second; the same two bands begin after the second in C. There are interruptions in the darkest band of D and E; but none are present in F. And the energy distribution differs in G, H, and I.

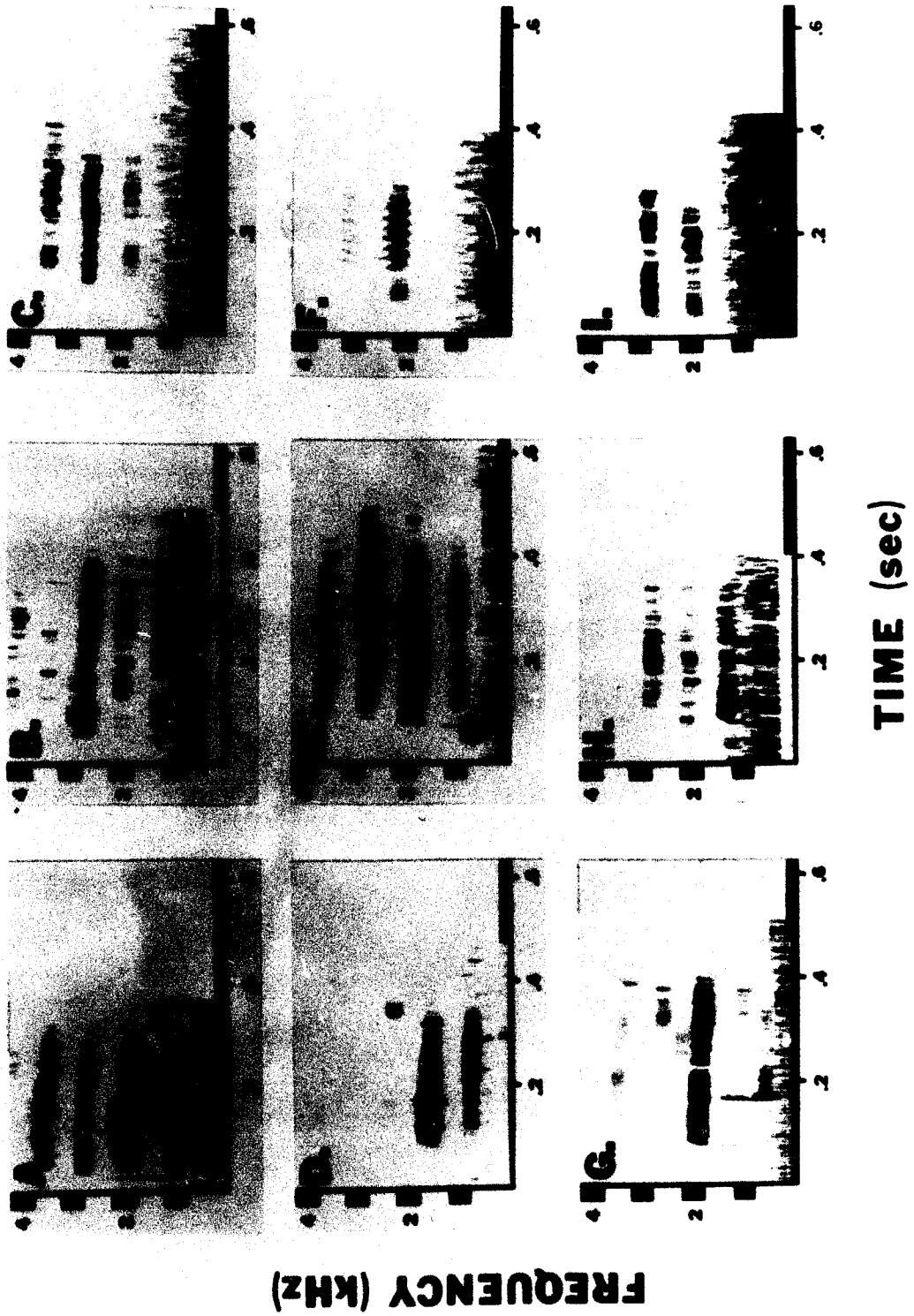


Fig.5

There are two interruptions in Figure 5D; at least three in Figure 5E, and none in Figure 5F. Another way in which the call varies between individuals is in the pattern of energy distribution within the call. Figure 5G illustrates a call in which most sound energy is concentrated in the 2000 Hz band; Figures 5H and 5I illustrate calls with energy in different bands.

Individual renditions of the ditonal version of the Jay Call are more variable than delivery of the monotonal version. For example, every individual gives a short and longer version of the call (Figure 6A) and versions which differ in having or not having a set of frequency bands (Figure 6B). Moreover, many individuals give at least one unusual rendition of the ditonal Jay Call (Figure 7). Figure 8 illustrates three renditions of the ditonal Jay Call from the repertoires of two Blue Jays.

Superimposed on the variability in call rendition described above for both versions of the Jay Call is the variability in the tempo at which the Jay Call is given. Both versions of the Jay Call are commonly given singly, and in pairs, but occasionally in triplets, and in double and triple pairs. The rate of calling while perched varies from one to ten calls per minute. Jays also give both versions of the Jay Call while participating in spring flocks. In this context they call at rates between 15 and 25 calls per minute. The ditonal version of the Jay Call is also given in rapid succession for only a few seconds at the beginning of flight and also in repeated bouts at rates up to 40 calls per minute for long periods while mobbing.

Fig. 6--Variation in the ditonal Jay Call. Each pair of sonograms is from the repetoire of one bird. A. Variation in duration of the ditonal Jay Call. B. Variation in the number of frequency bands in the ditonal Jay Call.

Fig.6

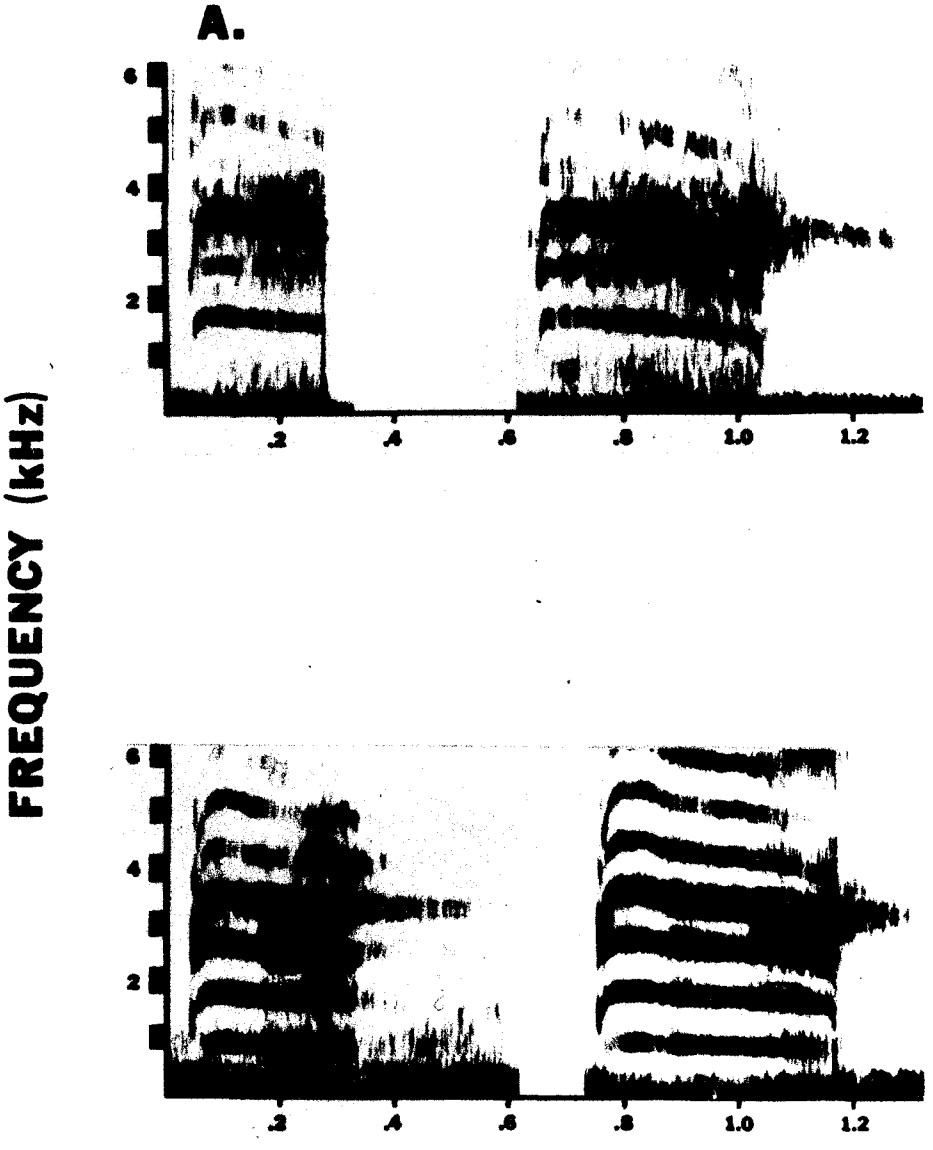


Fig. 6 (cont.)

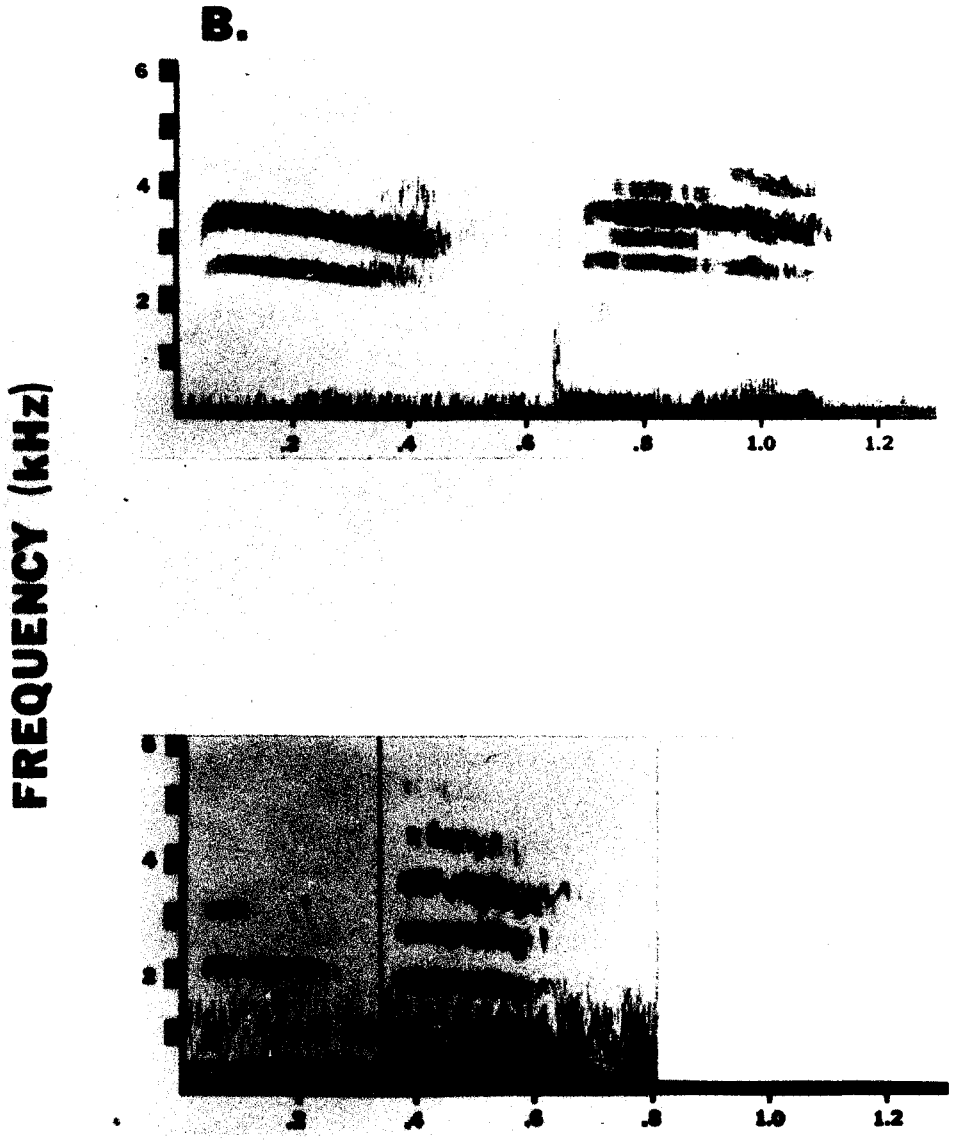


Fig. 7--Unusual renditions of the ditonal Jay Call by different birds.

A-B. The Frequency range of the call broadens toward the end of the call.

C. The beginning of the call is higher rather than lower in frequency than the rest of the call.

D. The beginning of the call is modulated.

E. An interruption occurs in the production of the call.

F. The frequency range of the call broadens in the middle of the call.

Fig.7

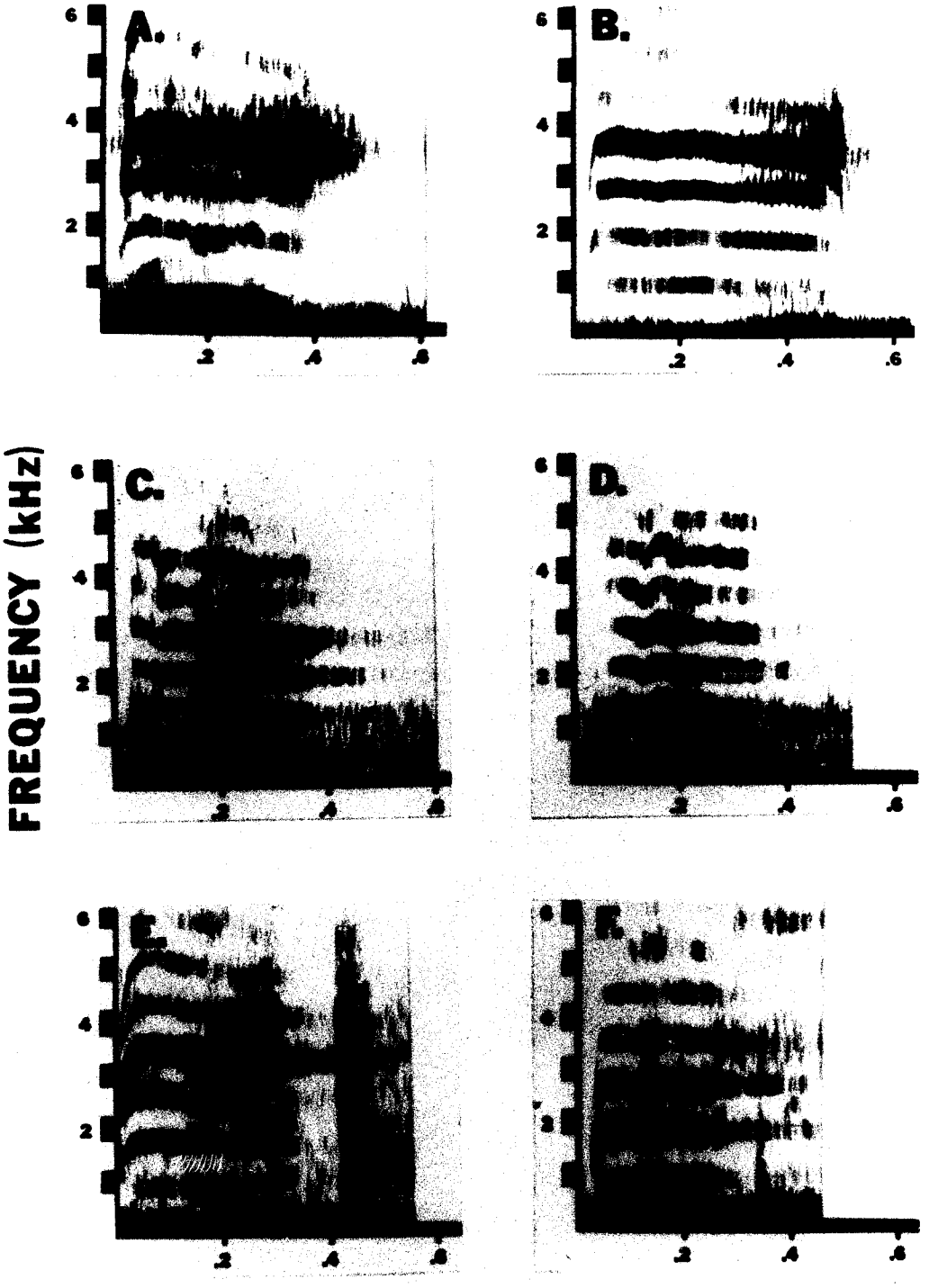
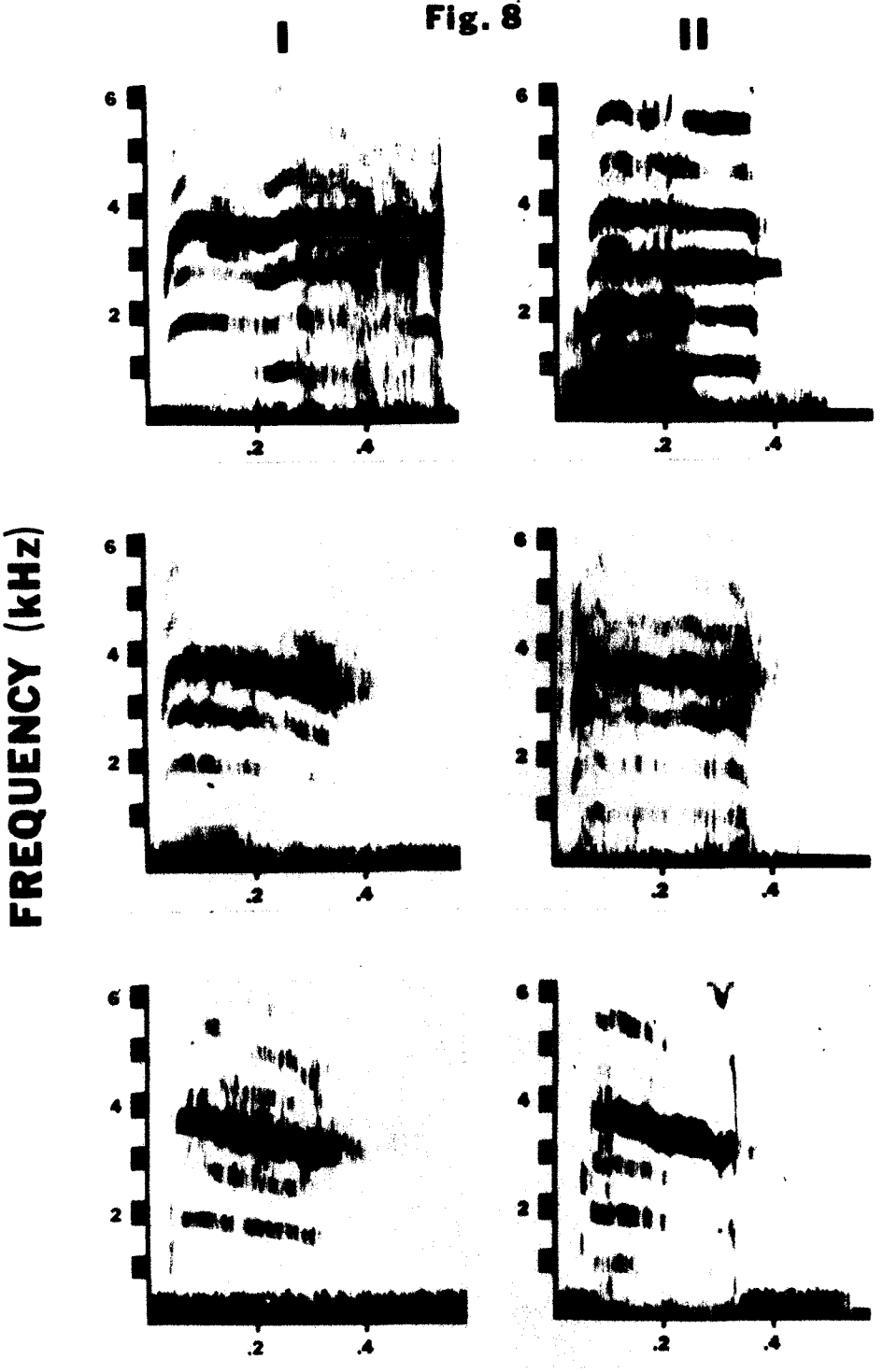


Fig. 8--Some unusual renditions of the ditonal Jay Call from the repetoires of two jays.

I. Calls by jay #B1

II. Calls by jay #K2

Fig. 8



Squeaky Gate Call. The Squeaky Gate Call (Figure 9) is given throughout the year, but most frequently in the prenesting season (Figure 3). Like the Jay Call, a bird giving this call is perched and not interacting with other birds in any obvious way. The Squeaky Gate Call is also given by members of a spring flock.

The Squeaky Gate Call is composed of three notes, the first being slightly higher in frequency and longer in duration than the next two (Table 4). But, again like the Jay Call, there is individual variation in rendition of the Squeaky Gate Call. Each sonogram in Figure 9 represents the Squeaky Gate Call of a different jay. Sonograms 9A-C illustrate differences between individuals in the frequency of the first note. Sonograms 9D-F illustrate differences in the shape of the first note. Sonograms 9G-I illustrate differences in duration of the next two notes. Sonogram 9J illustrates the absence of the first note. Sonogram 9K is a Squeaky Gate Call with an extra note at the end and 9L is a Squeaky Gate Call with an extra note at the beginning of the call. In sonogram 9M the first note is about the same frequency as the next two. In sonogram 9N the call consists of eight notes, the first two being similar to the last three, and the long middle one being slightly higher. In the last sonogram of Figure 9 the third note is higher than the second.

Bell Call. The Bell Call (Figure 10) is given most frequently during the nesting season (Figure 3) especially, but not exclu-

Fig. 9--Individual jays differ in their renditions of the Squeaky Gate Call. See text for analysis.

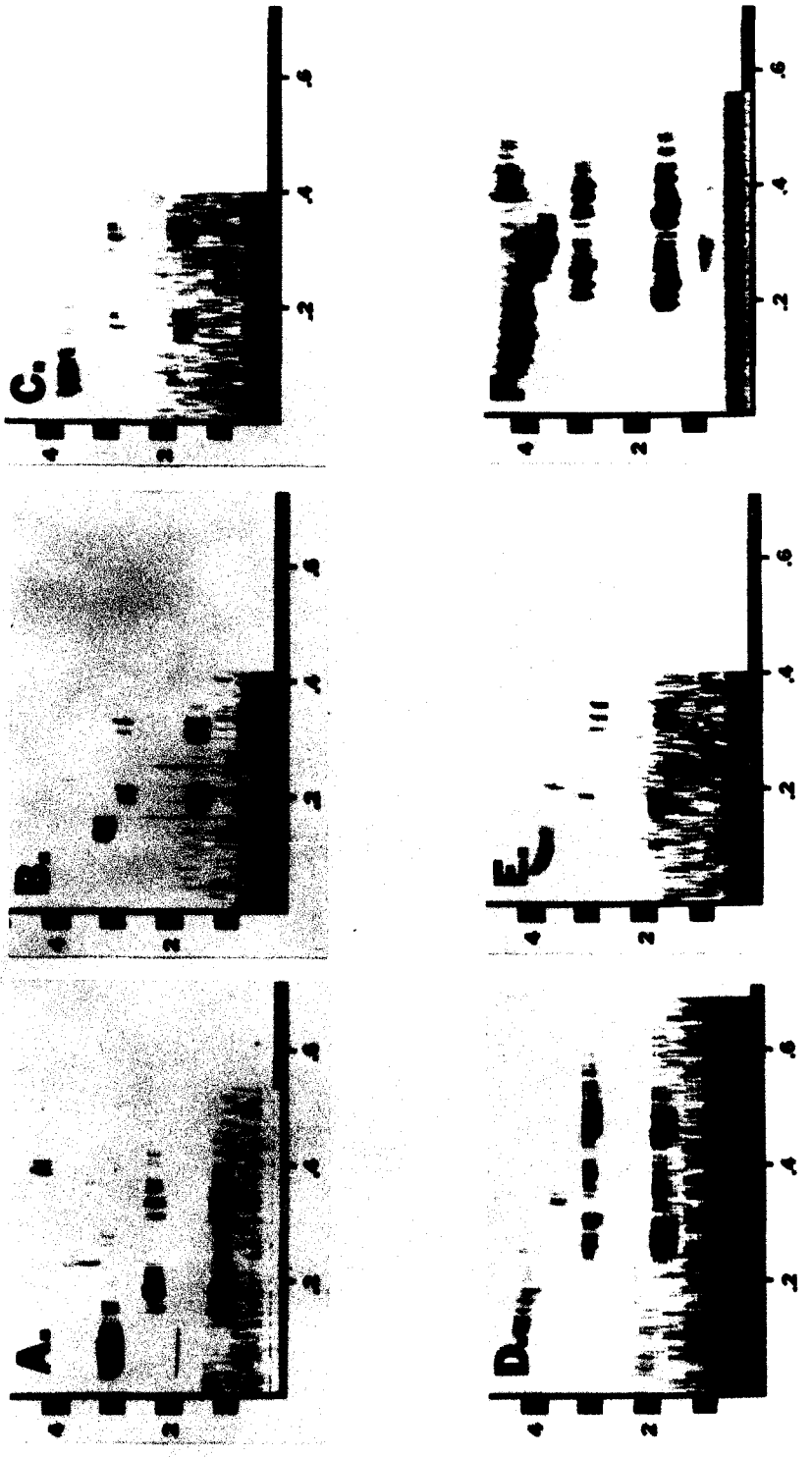


Fig.9

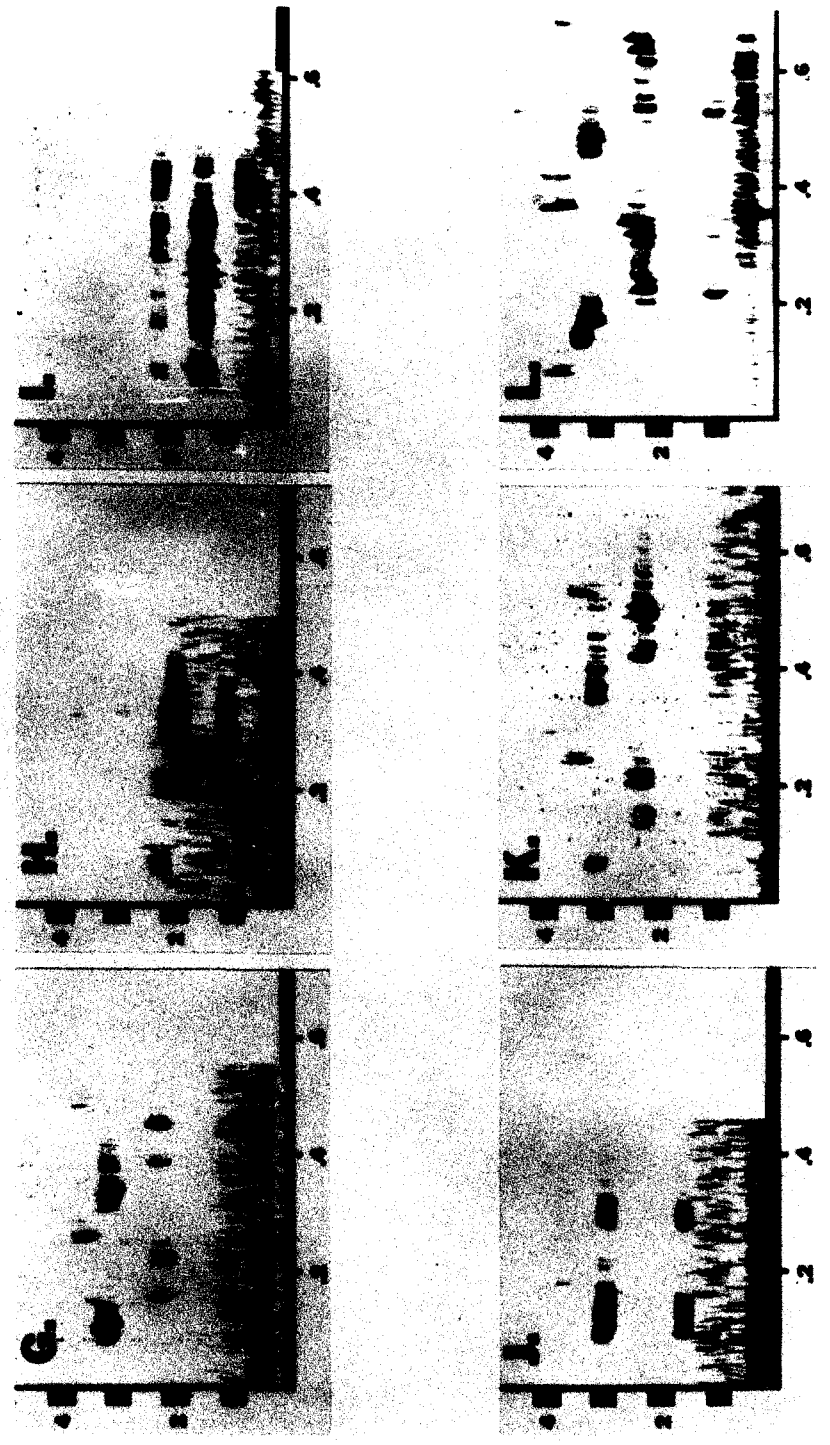


Fig.9(cont.)



FREQUENCY (kHz)

TIME (sec)

Fig.9(cont.)

TABLE 4

CHARACTERISTICS OF THE SQUEAKY GATE CALL
GIVEN BY TWENTY DIFFERENT BLUE JAYS

First Note		Second Note		Third Note	
Frequency (Hz)	Duration (Sec)	Frequency (Hz)	Duration (Sec)	Frequency (Hz)	Duration (Sec)
3700	0.30	2300	0.07	2300	0.07
4000	0.32	2800	0.11	2800	0.08
3900	0.04	2800	0.02	2800	0.02
3000	0.02	2100	0.01	2100	0.01
3900	0.04	2800	0.10	2800	0.07
3800	0.08	2400	0.04	2400	0.05
3800	0.08	2700	0.01	2700	0.01
3900	0.04	2200	0.03	2200	0.03
2900	0.06	1200	0.05	1200	0.05
3800	0.09	2600	0.15	2600	0.15
2000	0.04	1800	0.09	1800	0.13
----	----	1800	0.07	1800	0.15
----	----	1200	0.06	1200	0.07
----	----	2800	0.10	2800	0.05
2900	0.11	2000	0.07	2000	0.09
4000	0.15	2900	0.14	2900	0.18
3900	0.05	2900	0.10	2900	0.09
3900	0.16	2900	0.10	2900	0.14
2800	0.10	1900	0.10	1900	0.10
2200	0.10	2100	0.09	2700	0.07

sively by males in the vicinity of their nests. The Bell Call is also given by birds participating in spring flocks.

The Bell Call is a whistled call averaging 1900 Hz and is approximately 0.35 seconds long (Table 5). It occasionally has a second note at the end of the call. This note is either slightly higher or lower than the major portion of the call (Figure 10G and H). The Bell Call differs from both the Jay Call and the Squeaky Gate Call in its whistled quality and in the relative difficulty of locating a jay giving this call. The call has a ventriloqual quality unlike the two more common calls and is usually given by a bird which remains perched after calling from high up in a tree. But like the Jay Call and the Squeaky Gate Call, individual variation in rendition of the Bell Call is common. Individual differences occur in the frequency of the Bell Call (Figure 10A and B), in the frequency modulation of the call (Figure 10C-F), and the occasional presence of an overlapping second note toward the end of the call (Figure 10G and H).

Rattle Call. The Rattle Call (Figure 11) is given only by females (Conant, 1972; personal observation) and most frequently in the spring (Figure 3). It is given when the caller is perched and when in spring flocks.

The Rattle Call is a series of rapid clicking sounds. The clicks can be as few as five or six per second (Figure 11A), as many as 40 per second (Figure 11B), or can blend together (Figure 11C). The frequency of each click is centered around 1900 or 2000 Hz, but can be as broad as 1000 or 1500 Hz.

Fig. 10--Individual jays differ in their renditions of the Bell Call. See text for analysis.

Fig. 10

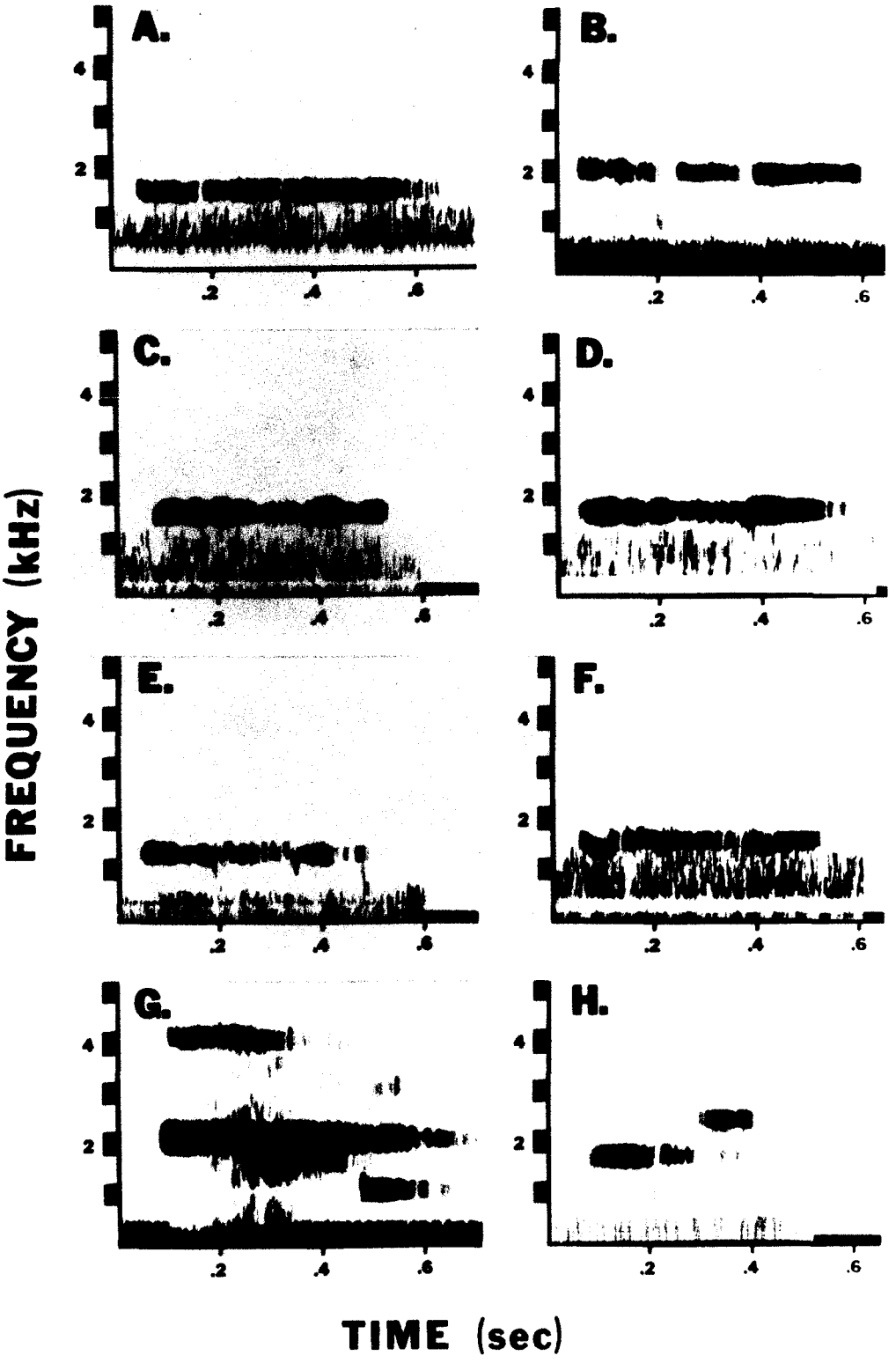


TABLE 5

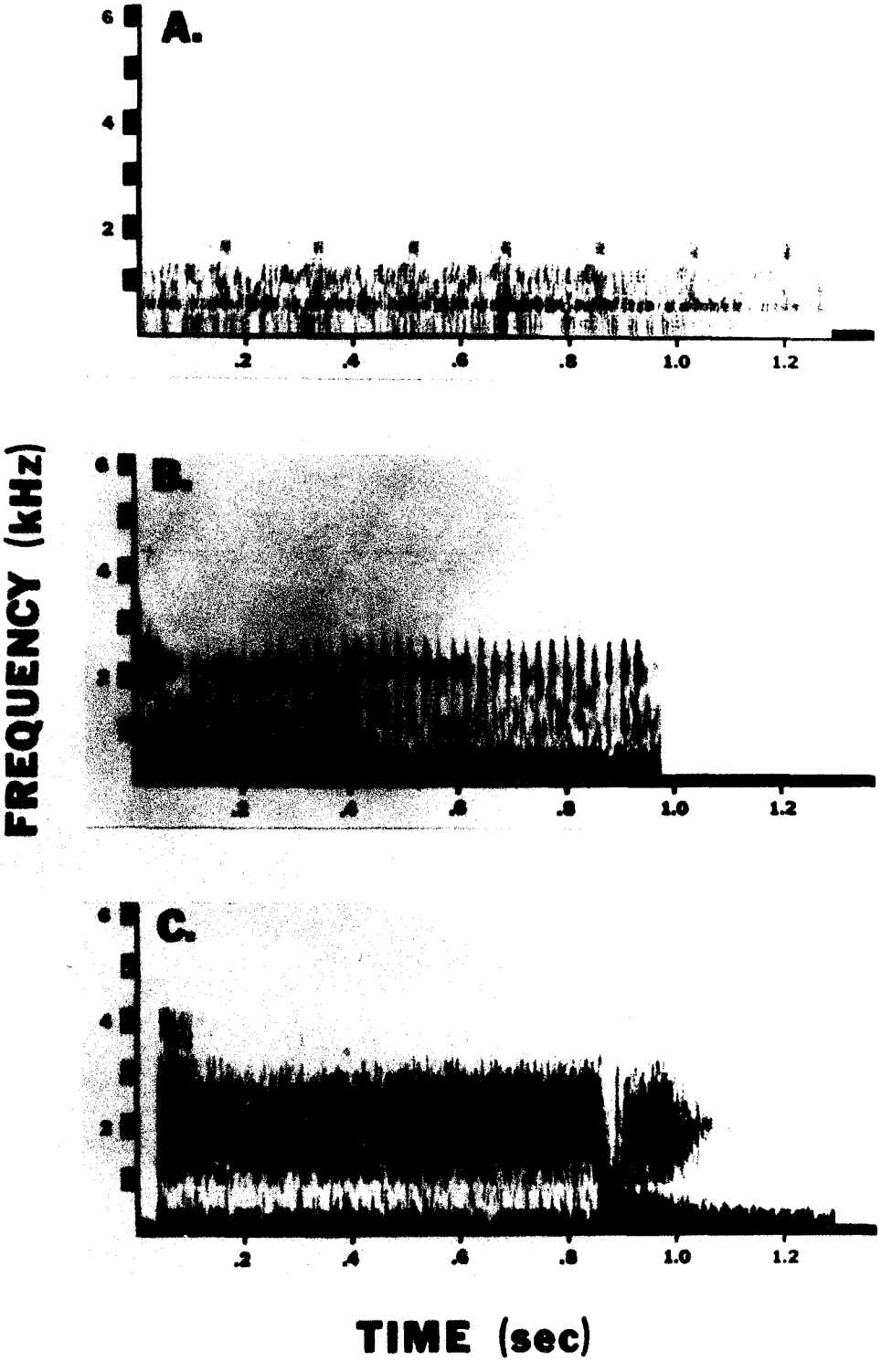
CHARACTERISTICS OF THE BELL CALL GIVEN
BY TWENTY DIFFERENT BLUE JAYS

Frequency (Hz)	Duration (Sec)
2100	0.30
2100	0.28
1900	0.34
2000	0.43
2000	0.30
2000	0.27
2000	0.36
1900	0.30
2100	0.29
1900	0.24
1900	0.64
1950	0.45
1500	0.41
1500	0.47
2100	0.45
1400	0.58
1400	0.23
1800	0.13
2050	0.18
2100	0.26
$r = -0.375$[1]	

[1]Pearson Product-Moment Correlation Coefficient

Fig. 11--The Rattle Call by three different female jays.

Fig. 11



Yurp Call. The Yurp Call (Figure 12) is given throughout the year. It is given in flight by birds which are going to their nests or foraging for nest material. It is often heard being given by a bird which is foraging alone or with its mate. During the nesting season, jays Yurp when approaching their mates.

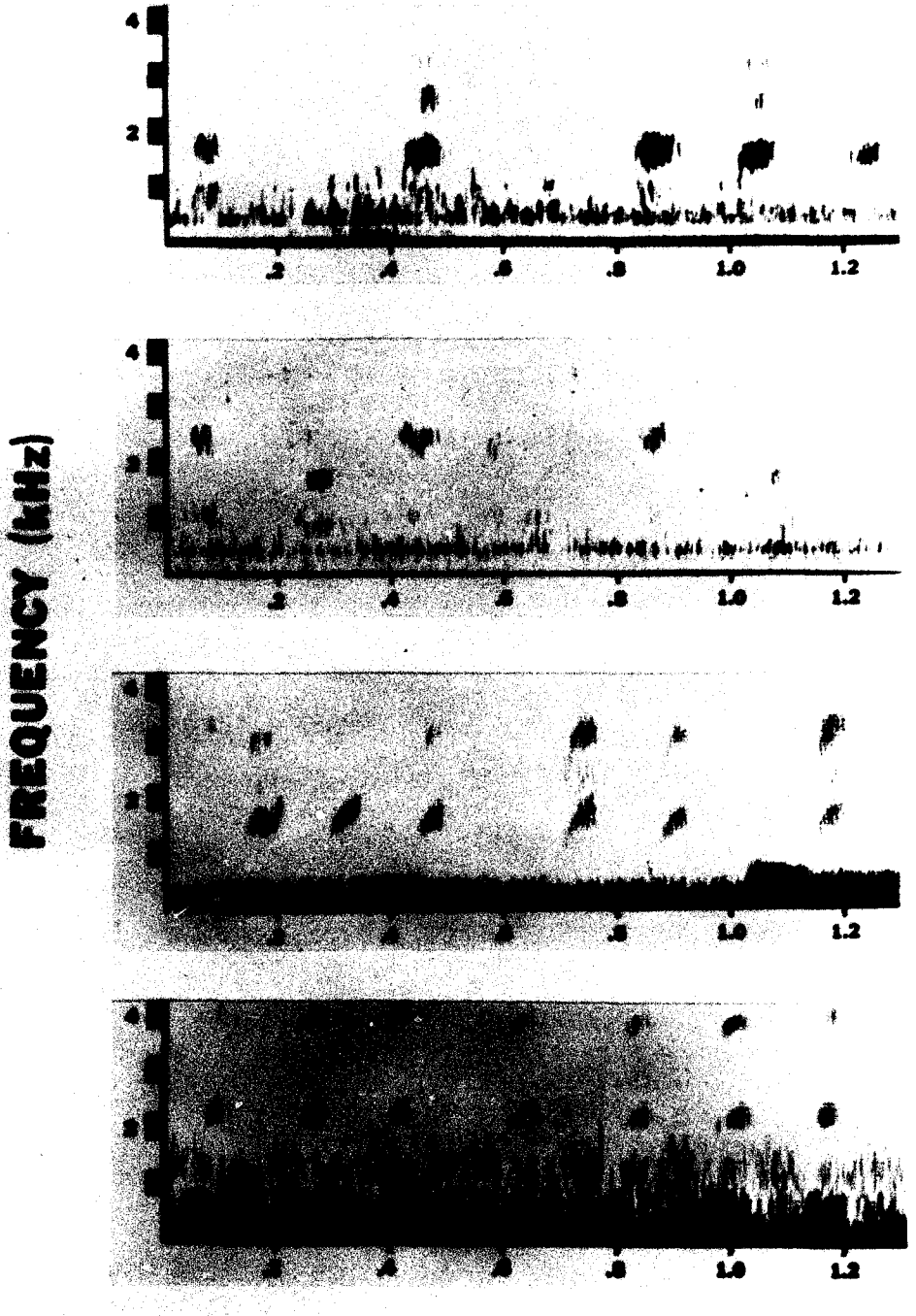
The Yurp Call is not as loud as any of the calls described above. It consists of individual notes in the 1500 to 2500 Hz range. Each note is from 0.03 to 0.05 seconds in duration. The notes are given at variable rates up to 20 per second. Individuals may differ somewhat in the frequency modulation and overall shape of their Yurp Call notes (Figure 12). I was not able to record enough individuals to document this.

B. Social Organization and Vocal Behavior in the Prenesting Season

Calling rates. In general, seasonal variation in avian vocal behavior is correlated with their breeding activities. For example, Steller's Jays call most frequently in the early part of the breeding season (Brown, 1964). But Conant (1972: 80) reports that Blue Jays call most frequently in the nonbreeding season. I counted the calls made by marked individuals during ten-minute observation periods in the nonbreeding season (January-February), the prenesting season (April), and the nesting season (May-June). Yurp Calls were not included in these counts becasue the birds were often observed at distances too great to hear these low intensity calls. All observations were made within three hours of

Fig. 12--The Yurp Call by four different jays.

Fig. 12



sunrise and each bird was alone throughout the observation. The jays called most frequently in the prenesting season (Table 6).

During this period (i.e., late March and all of April) pairs of jays were already formed. Perhaps these are individuals who were mated in the previous year. The pairs are easily recognized because the mates forage together, often less than ten meters apart. While foraging they make short flights and Yurp softly. On occasion, the male approaches the female and feeds her as she Begs vigorously. By mid-April males are feeding their mates at least once an hour in the morning. In contrast, unmated jays always forage alone and never engage in courtship feeding bouts with other jays.

If the high rate of calling in the prenesting season is related to pair-formation, then one would expect to find that unmated individuals are calling more frequently than mated ones. Observations in April totaling 90 minutes per bird revealed very significant differences in calling rates between mated and unmated birds (Table 7). The higher rates recorded for unmated individuals whoud have been much greater had the unmated birds been observed while they were participating in spring flocks.

Call mimicry. A spring flock is a temporary association of 3 to 15 jays which fly from tree to tree calling loudly and frequently. Beginning in late February and continuing through March and April, these flocks form, disintegrate and reform several times each morning and again in the late afternoon. The most conspicuous feature of spring flock behavior is the uniformity

TABLE 6

CALLING RATES IN DIFFERENT SEASONS

Season	N[1]	Total calls[2]	$\bar{X}$ calls per 10 min	Range	s.d.	$\bar{X}$ calls per hour
Winter (Jan.-Feb.)	38	49	1.3	0-8	±1.9	7.7
Prenesting (April)	36	223	6.2	0-35	±7.9	37.1
Nesting (May-June)	25[3]	22	0.9	0-6	±1.7	4.2

[1]Number of jays observed ten minutes each.

[2]Call-counts did not include Yurp Calls

[3]Incubating females only.

TABLE 7

NUMBER OF CALLS MADE BY MATED AND UNMATED BLUE JAYS DURING THE OBSERVATION OF EACH BIRD FOR NINETY MINUTES IN APRIL

Bird	Sex[1]	No. of calls[2]	Breeding status[3]	
B3	female	44	mated	
37	female	331	"	
A5	male	348	"	
48	male	361	"	
WT	female	503	"	
C6	male	577	unmated	
39	male	649	"	
50	male	891	"	
64	male	926	"	$t=2.52$
A1	male	2128	"	$p<0.05$

[1]Sex was determined behaviorally: if the bird Rattled or Begged, it was classified as female.

[2]Call counts did not include the Yurp Call.

[3]No change in breeding status occurred during April for any of these birds.

with which calls are rendered by the participants. The Jay Call is the call most frequently given by members of a spring flock. But despite the number of versions and renditions each jay is capable of making (Figures 6-8), all the members of a flock will give the same rendition at the same time. Figure 13 illustrates two renditions of the Jay Call given by one spring flock just a few minutes apart. In one case (Figure 13B) the call is relatively long, about 0.44 seconds in duration; in the other case (13A) the call is only 0.29 seconds long. As far as could be determined, no particular rendition is associated with a particular behavior pattern; nevertheless, flocks switch from one rendition of the Jay Call to another.

Squeaky Gate Calls and Bell Calls are also given by birds in a spring flock. Again, despite the individual variation in rendition of these calls (Figures 9 and 10), all the birds in the flock give the same rendition of the call at the same time. Figure 14 illustrates two renditions of the Squeaky Gate Call by one flock. In Figure 14B the first note in each call (indicated by an arrow) is slurred down, whereas in Figure 14A that note is missing. My impression is that call mimicry in spring flocks occurs with most of the birds most of the time. It is difficult to illustrate this with sonograms because the overlap of sound bands from two or more jays calling at once makes distinguishing one call from another almost impossible. The sonograms used to illustrate mimicry in Figures 13 and 14 were selected because the

Fig. 13--Similarity in rendition of the Jay Call by members of a spring flock. Each arrow indicates the duration of one bird's Jay Call.

Fig.13

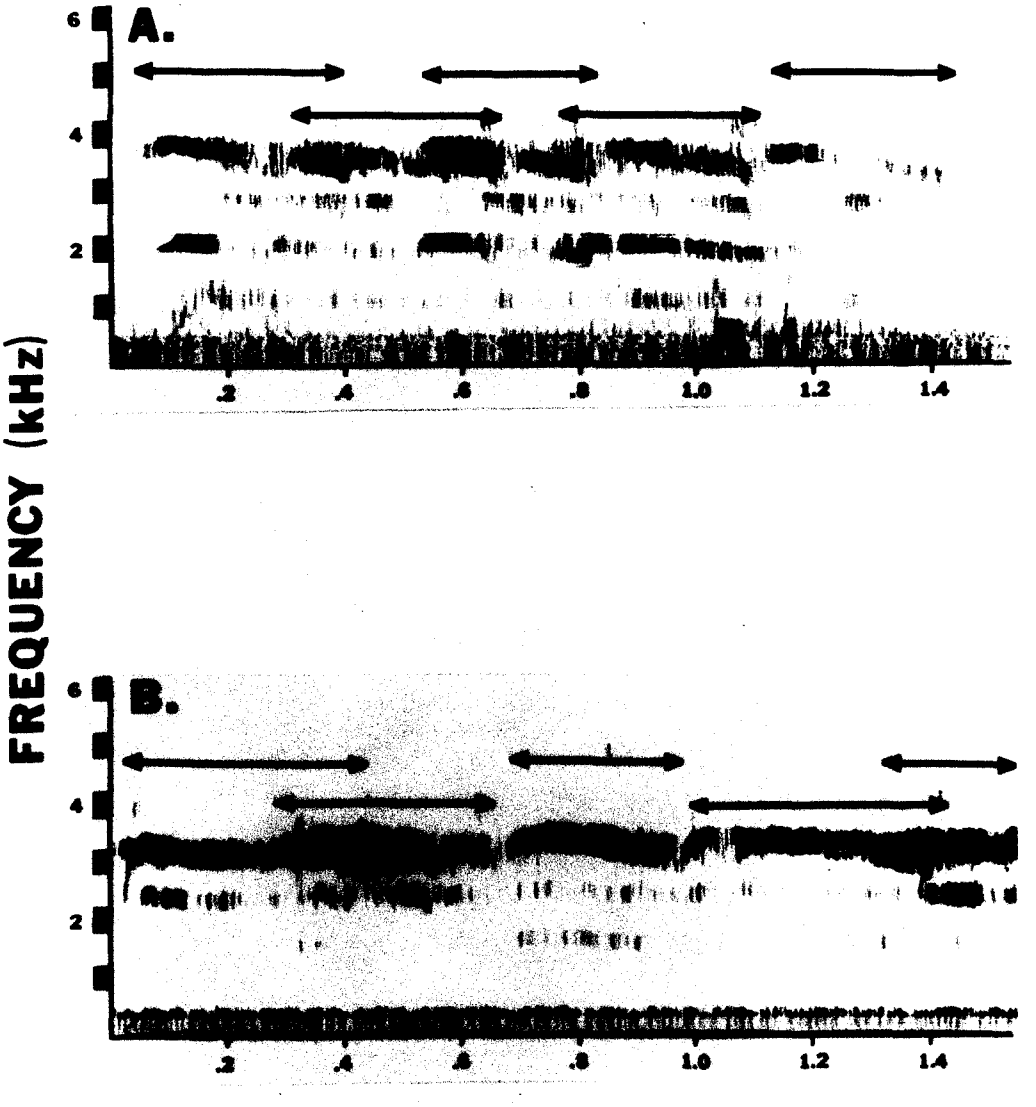


Fig. 14--Similarity in rendition of the Squeaky Gate Call by members of a spring flock.

A. Arrows indicate the first note of one rendition of the Squeaky Gate Call given by each member of a spring flock.

B. Arrows indicate the first note of another rendition of the Squeaky Gate Call given by the same birds a few minutes later.

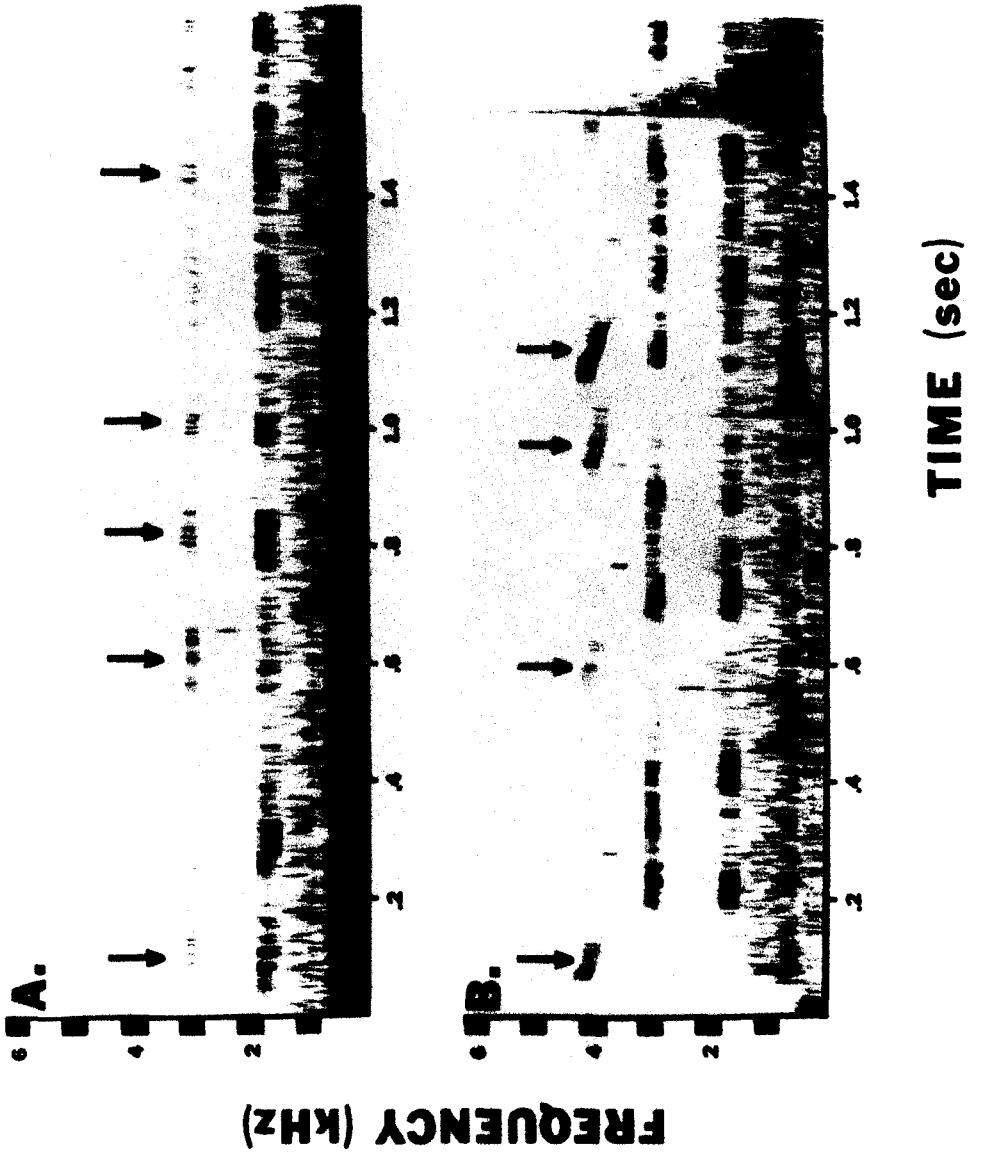


Fig. 14

calls do not overlap as much as they do in many others. Brown (1964: 246) reports a similar sort of matching of calls by male Steller's Jays in the spring.

Both Tyler (1946: 34) and Hardy (1961: 19-20) think jays are engaged in courtship behavior when participating in spring flocks. They suggest that spring flocks are composed of a group of males and a single female. The males are said to be vying for a position closest to the female. I have observed no consistent pattern of following or clustering around a female while watching marked individuals participate in spring flocks. Moreover, I have noted the presence of two or three females in such flocks.

If members of a spring flock are courting, the steps in pair-formation are not obvious. I have never seen courtship feeding, for example, in a spring flock. Moreover, mated pairs participated in spring flocks, at least in late March and early April. Since call mimicry is such a conspicuous feature of spring flock behavior, it may be that learning to mimic others is the first step in jay pair-formation (cf. Mundinger, 1970).

If call mimicry is related to the process of pair-formation then one might expect to also see call mimicry between jays which are mated. The complete repertoires of each member of a pair are not easily obtained, but a review of the available recordings revealed that when both members of a pair were calling, each one's rendition of the call was very similar. Figure 15 illustrates calls made by six different pairs. In each case, the first call

in the sonogram was given by one bird, the second by its mate and the third call, if present, by the first bird again. Both individuals were marked and visible to me when the recordings were made. In no case illustrated is the second bird's call identical to that of its mate. There are small differences in frequency, duration, and frequency modulation between individuals. But the similarity between call renditions of these mated pairs is striking in view of the variability between individuals which was noted earlier and the fact that non-mated birds of the same flock do not call in this way (Figure 15).

If mated jays do mimic each other, they might do so when apart or when together. I did not observe responses to the calling of mated individuals when they were apart, i.e., those observation periods in which I was unaware of their mate's presence. But, I did observe, in the two males and one female for whom I had adequate samples, that the calling rates of mated birds were higher when their mates were not with them (Table 8). Bertram (1970) reports a similar pattern of calling in mated Hill Mynas (Gracula religiosa).

Responses to call mimicry. Since I did not see any overt responses to the calls of the birds I was watching, I decided to test the jay's response to being mimicked. Mimicry is well documented in avian vocal behavior (Borror and Reese, 1956; Nicolai, 1959, 1964, 1973; Immelman, 1969; Bertram, 1970; Mundinger, 1970). Using the type two playback format I compared the behavior of

Fig. 15--Similarity in call rendition by mated pairs. In lines A-F, the first call on each line was made by one bird (m = male, f = female) and the second call was made very shortly afterwards by its mate. (The third call, where present, was made by the first bird again.) In lines G-J, the first call on each line was made by a mated jay and the second call was made by another jay (labeled j_1, j_2, j_3 or j_4). This other jay was not the first bird's mate, and it called less than six seconds after the mated bird.

Fig. 15

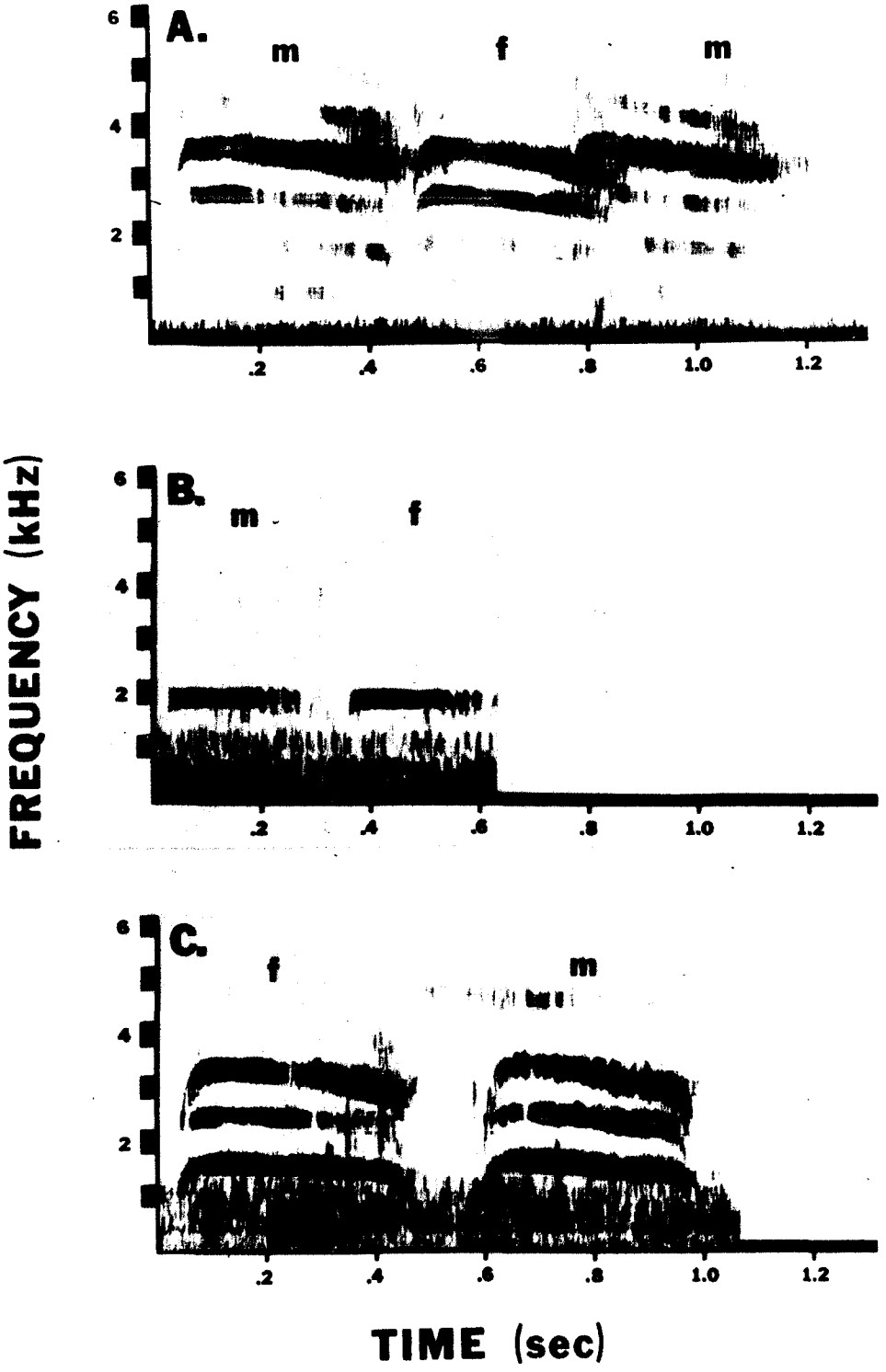


Fig. 15(cont.)

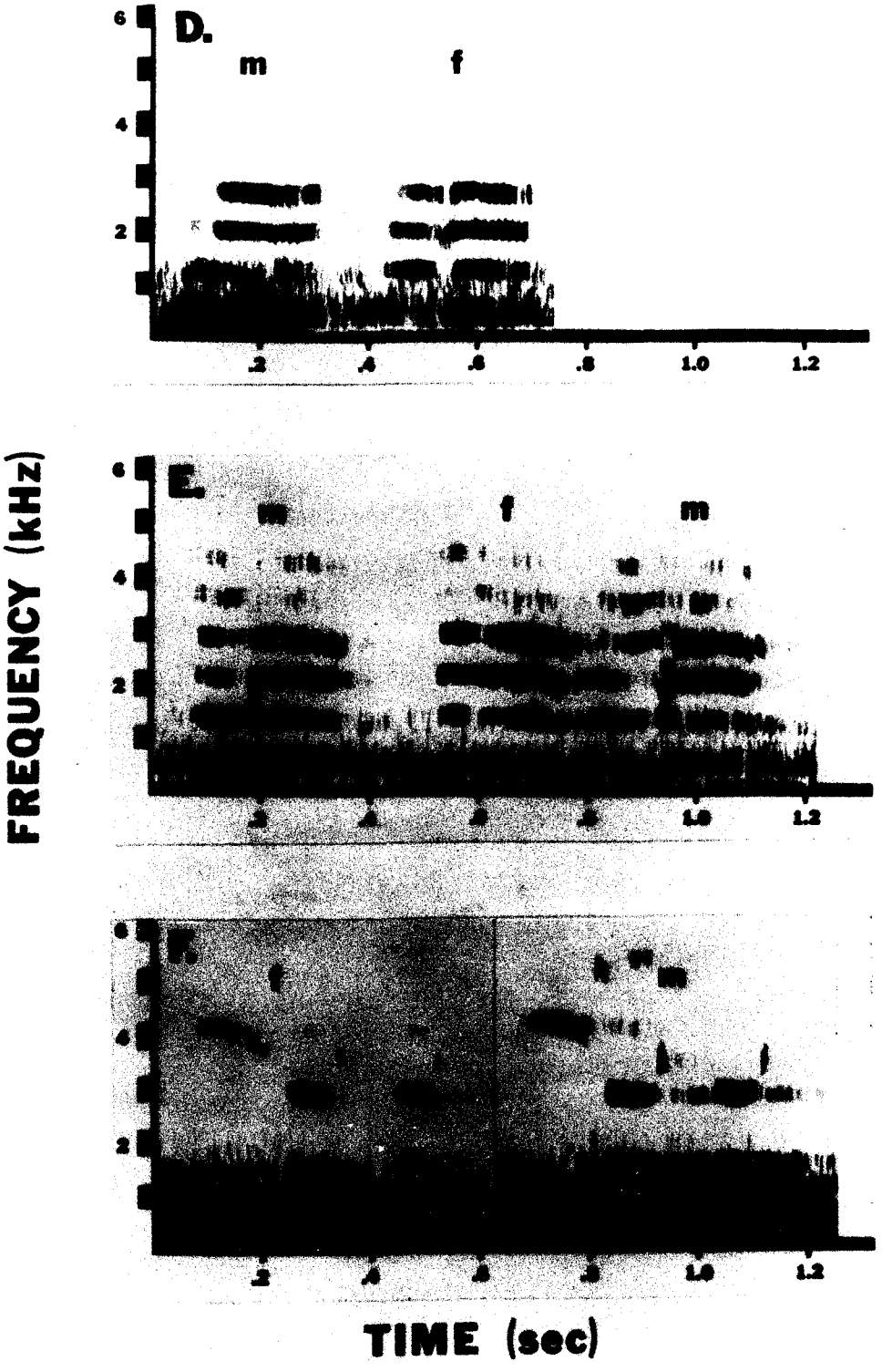


Fig. 15(cont.)

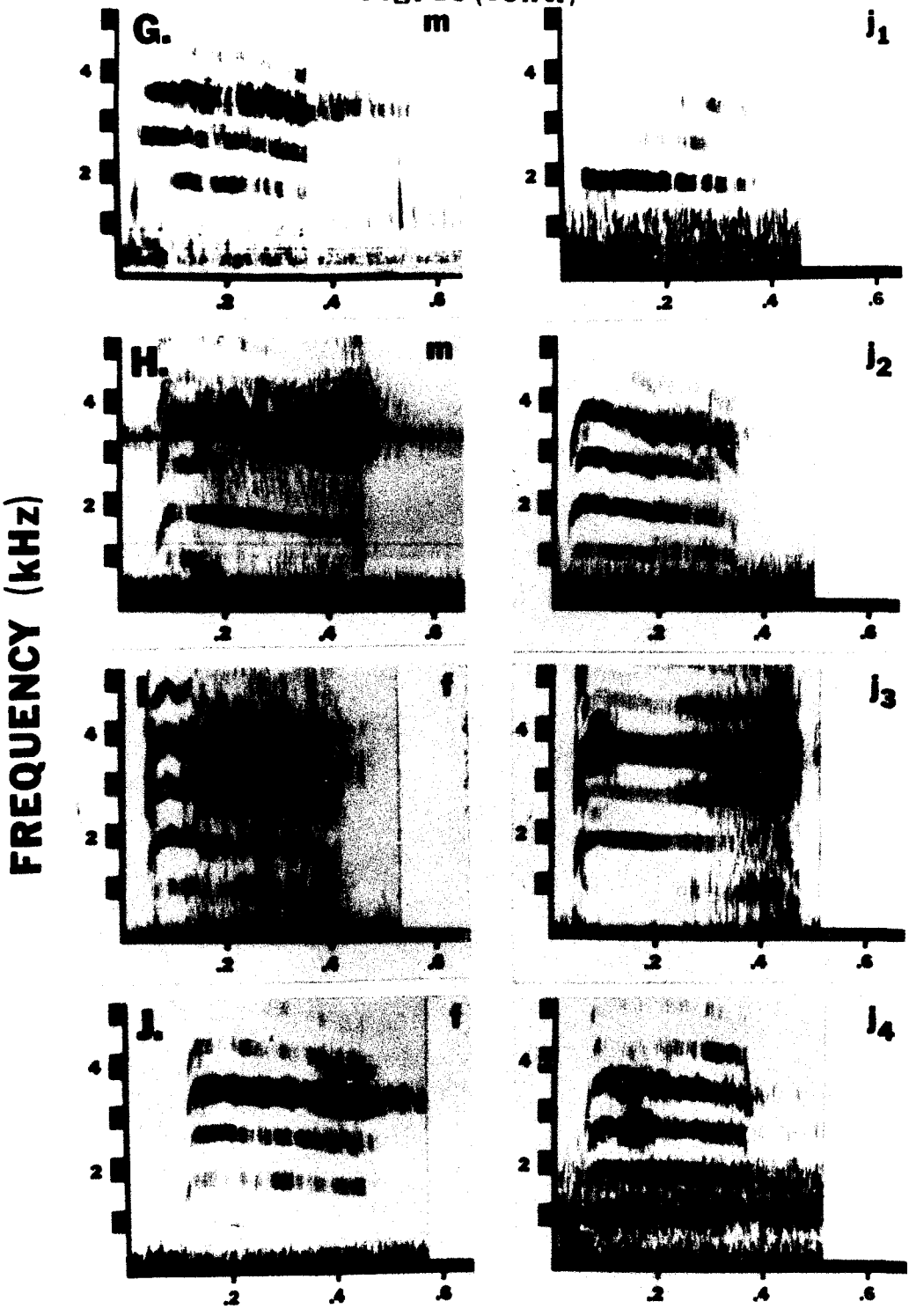


TABLE 8

CALLING IN TWO SOCIAL SITUATIONS BY MATED BIRDS

	#48 (Male)		#A5 (Male)		#37 (Female)	
	Alone (78 min)	With Mate (40 min)	Alone (80 min)	With Mate (57 min)	Alone (34 min)	With Mate (45 min)
Observed	552	161	350	44	323	140
Expected[1]	472	242	230	164	199	263
	x^2=40.6		x^2=145		x^2=135	
	p<.001		p<.001		p<.001	

[1]The expected value was computed using each bird's average calling rate over the entire sampling period. The average rates were: 6.05 calls/min for #48; 2.87 calls/min for #A5; and 5.86 calls/min for #37.

unmated birds during broadcast of the call version they were giving to their behavior during broadcast of the same call given by another individual. Stronger responses to their own calls would support the hypothesis that call mimicry plays a role in jay social interactions.

The differences in behavior of unmated jays during broadcast of their own and another's version of the ditonal Jay Call were clear cut. Despite the fact that the quality of the tape loop was usually *not* equivalent to the prepared ditonal Jay Call, the jays tested called more frequently and moved more frequently during the period in which the "mimetic" tape was broadcast (Table 9). Responses were different to the Squeaky Gate Call. The jays called more frequently during playback of their own call, as they had to the Jay Call, but with the Squeaky Gate Call they did not move more than during playback of the other version of the call (Table 10). Both the Jay Call and the Squeaky Gate Call are the calls most commonly given and heard by jays. It appears then, that unmated jays respond to mimicry of their calls and that mimicry of their Jay Call elicits calling and movement from them while mimicry of their Squeaky Gate Call just elicits more calling.

I tested mated birds' responses to the type two playback (see pages 15-19) of their own and an unrelated jay's version of the ditonal Jay Call and the Squeaky Gate Call. It was difficult to obtain a large sample of mated birds' calls since they are usually silent when together. But again both calling and movement were greater during their own version of the Jay Call than during

TABLE 9

BEHAVIOR OF UNMATED JAYS DURING PLAYBACK OF THEIR OWN AND ANOTHER'S VERSION OF THE DITONAL JAY CALL

Bird	No. of Calls[1] Given During		No. of Moves Made During	
	Another's version	Own version	Another's version	Own version
1	2	10	4	2
2	6	6	1	2
3	5	10	3	4
4	8	8	7	5
5	14	28	4	2
6	3	7	5	8
7	13	7	0	4
8	14	15	1	3
9	4	15	1	3
10	2	4	3	5
11	10	25	2	3
12	15	14	4	2
13	8	16	2	4
14	5	5	4	2
15	10	2	0	3
16	6	2	0	0
17	9	23	1	2
18	3	12	1	5
19	1	9	3	7
20	7	7	2	4
21	4	11	5	4
22	2	12	3	4
23	10	10	2	1
24	14	8	1	4
25	8	6	1	6
	183	272	60	87
	N = 20		N = 24	
	T = 40		T = 70.5	
	$p < .01$[2]		$p < .05$[2]	

[1] Yurp Call not included in call counts.

[2] Wilcoxon Matched-pairs Signed-ranks Test.

TABLE 10

BEHAVIOR OF UNMATED JAYS DURING PLAYBACK OF THEIR OWN AND ANOTHER'S VERSION OF THE SQUEAKY GATE CALL

Bird	No. of Calls[1] Given During		No. of Moves Made During	
	Another's version	Own version	Another's version	Own version
1	6	16	1	0
2	12	13	0	0
3	8	18	0	0
4	6	6	3	2
6	10	7	0	0
7	7	15	2	1
8	6	12	1	0
9	8	14	0	0
10	10	8	3	0
11	9	16	2	2
12	7	9	0	1
13	10	5	0	0
14	5	11	0	2
15	11	8	4	0
16	0	9	1	3
17	9	14	1	1
18	5	15	0	0
19	8	8	2	1
20	4	5	0	3
21	9	17	0	2
22	3	16	1	0
23	8	7	0	0
	163	259	23	20
	N = 21 T = 26 $p < .01$[2]		N = 13 T = 42 $p > .05$[2]	

[1]Yurp Call not included in call counts.

[2]Wilcoxon Matched-pairs Signed-ranks Test.

the control version (Table 11). And only calling increased when their Squeaky Gate Call was played (Table 12). As with unmated jays, the mimetic Jay Call elicits calling and movement whereas the Squeaky Gate Call elicits only calling. It may be that one call helps individuals get together while the other just helps to establish the position of the mate.

The type two experiments reported above show that Blue Jays, regardless of their breeding status, respond strongly to a matching version of the call they are or have been making. How exact the match must be to elicit a response is not clear; judging from the strong positive response to recordings which were often of poor quality and low volume, the "mimicry" need not be perfect. In any case, it appears that matching call versions with another jay is a fundamental feature of Blue Jay vocal interactions.

Is the response which jays give to call mimicry related to territorial behavior or to pair-formation? Hardy (1961: 45-46) reported "true territoriality" in the Blue Jay and Conant (1972) refers to jays as being territorial. But many of the behavior patterns typically associated with type B territoriality (Hinde, 1956) are not seen in the Blue Jay. Male jays, for example, do not sing, nor do they patrol the area around their nests. They do not forage in the vicinity of the nest and they do not restrict their movements to that area. Moreover, neither member of a nesting pair is consistent about excluding other jays from the vicinity of the nest. To be sure, nesting jays do displace other

TABLE 11

BEHAVIOR OF MATED JAYS DURING PLAYBACK OF THEIR OWN AND ANOTHER'S VERSION OF THE DITONAL JAY CALL

	No. of Calls[1] Given During		No. of Moves Made During	
Bird	Another's version	Own version	Another's version	Own version
1	0	1	3	2
2	1	3	4	8
3	0	4	0	3
4	2	0	3	4
5	0	2	2	3
6	0	2	3	5
7	0	4	2	3
8	1	2	2	3
	4	18	19	31
	N = 8		N = 8	
	T = 4.5		T = 3	
	p < .05 (one-tailed)[2]		p < .05 (one-tailed)[2]	

[1]Yurp Calls not included in call counts.

[2]Wilcoxon Matched-pairs Signed-ranks Test.

TABLE 12

BEHAVIOR OF MATED JAYS DURING PLAYBACK OF THEIR OWN AND ANOTHER'S VERSION OF THE SQUEAKY GATE CALL

Bird	No. of Calls[1] Given During		No. of Moves Made During	
	Another's version	Own version	Another's version	Own version
1	3	3	2	0
2	1	6	2	0
3	5	1	1	1
4	3	7	1	2
5	0	2	1	1
6	2	8	0	2
7	1	2	0	0
8	2	8	0	1
9	0	1	2	1
10	5	8	1	3
11	0	5	3	1
12	2	4	0	0
13	1	5	3	2
14	0	3	1	1
	25	63	17	15
	N = 13 T = 8 p < .01[2]		N = 9 T = 19 p > .05[2]	

[1]Yurp Call not included in call counts.

[2]Wilcoxon Matched-pairs Signed-ranks Test.

jays. I observed 23 displacements during 51 hours of observation at 17 different nests. But there were 17 occasions during the same observation period when an "intruder" was simply ignored even though it was apparently in the nesting jay's visual field. Not once was there a vocal interaction between the nesting jay and the intruder. I assume jays are not aggressive when foraging or resting when they are away from the nest.

Hardy (1961: 45-46) qualified his description of jays being territorial by saying that the "...territory is not defended at any time against other jays which are not in the same general phase of the breeding cycle as the resident pair." He reports, for example, than an incubating female watched a pair of jays and their young as they passed through her territory and perched in her nest tree. I have seen a pair of nesting jays quietly watch a spring flock of six jays perch in the nest tree and call repeatedly. Hardy (1961: 23) also reports that mated pairs tolerate the presence of a "bystander" jay in their territory and even during bouts of courtship feeding and copulation. I too have also seen "bystanders" tolerated. Indeed, once a bystander seemed to interrupt a copulation. There followed an exchange of Rattles from the mated female and the "bystander". Since only females Rattle, the "bystander" could not have been a male rival as Hardy (1961: 23) suggests. It was probably one of the pair's offspring from the previous year (see Lasky, 1958). Taken together, these incidents show that jays are not territorial in the strict sense and that call mimicry

is not a feature of the agonistic interactions which do occur around the nest. Thus, a jay's response to call mimicry is probably not related to territoriality. Steller's Jays are more typically territorial. They live as pairs on their territories all year and are conspicuously aggressive to other jays which pass by. They vocalize when being aggressive. But, like the Blue Jay, the Steller's Jay does not consistently exclude intruders from the vicinity of the nest, nor does a pair restrict its movements to its own territory (Brown, 1964).

Call learning. If call mimicry is a feature of jay vocal behavior related to pair-formation and individual recognition of the mate, then jays must be able to learn the details of the calls they make. This is known to occur in other species (Poulsen, 1954; Sauer, 1954; Mesmer and Mesmer, 1956; Lanyon, 1957; Marler and Tamura, 1964; Immelman, 1965; Dittus and Lemon, 1970; Marler et al., 1972). In order to see if Blue Jays can indeed learn the details of their calls I raised two groups of nestling jays in an acoustic isolation chamber. Having a single chamber necessitated raising one group in 1972 and the other in 1973. The second group was tutored with jay calls selected from field recordings whereas the first group was not tutored. If jays learn the details of their calls, the tutored birds would be expected to give calls more similar to the ones they heard than the untutored birds.

Figures 16-19 illustrate the calls made by tutored and untutored birds when they were eight months old. In general,

tutored birds gave calls similar to the model calls they were exposed to, even when models themselves were unusual renditions of typical calls. Untutored birds failed to give any calls resembling the Squeaky Gate Call and their renditions of all other call types, though clearly recognizable, differed markedly from normal calls and from the calls made by the tutored birds.

Figure 16 illustrates the Jay Calls given by tutored and untutored birds. The model call (Figure 16M) was 0.60 sec in duration, had the first band of sound around 700 Hz and its broadest band was the fourth which ranged from 3100 to 2850 Hz. Figures 16D-F are typical Jay Calls made by tutored birds. None have first bands as low as the model call. Two of the calls (Figures 16D and E) have a fourth band which is the broadest in the call and which is either the same frequency or slightly higher than the model. The third tutored bird made a call (Figure 16E) much more like those of the untutored birds. The untutored birds all produced Jay Calls with three rather than four strong bands of sound energy. The first band of sound in their calls is about 500 Hz higher than the model call. Their second band is the broadest and is in the same frequency range as the broadest band in the model. The calls of untutored birds sound much hoarser and noisier than normal Jay Calls and resemble a fledgling's Begging Call (see below).

Figure 17 represents the Squeaky Gate Calls given by tutored birds. Untutored birds made no calls which resembled a Squeaky

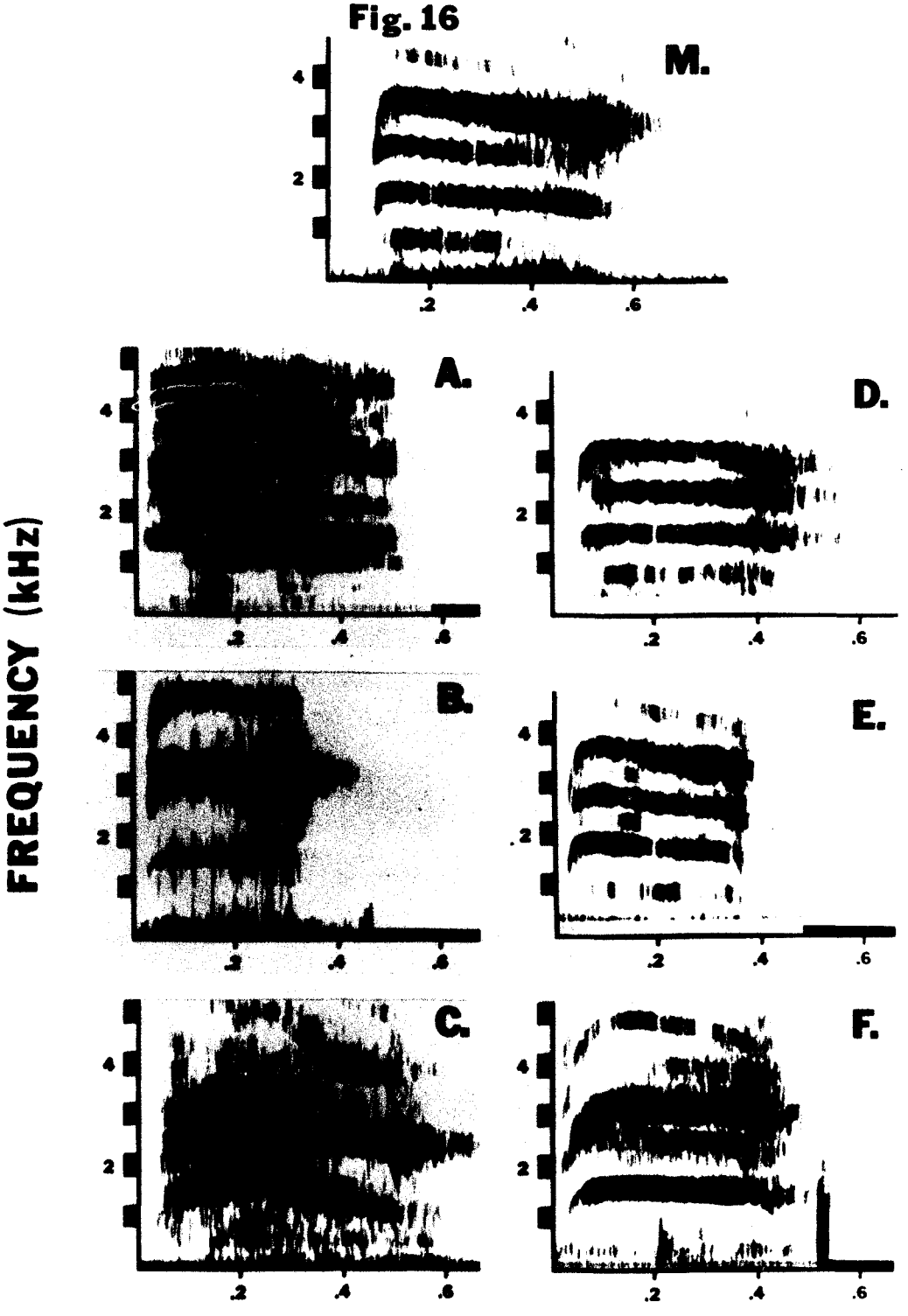
Fig. 16--Jay calls by tutored and untutored birds:

M. Model Call.

A-C. Calls by untutored birds.

D-F. Calls by tutored birds.

Fig. 16



Gate Call. The model call (Figure 17M) is an unusual version of the Squeaky Gate Call in that the first high note is given three times during the course of the call instead of just once (see Figure 12). Two of the four tutored birds gave the high notes in the same way (Figure 17A and B), and the third bird gave two high notes and an extra low note (Figure 17C). The fourth bird gave a relatively crude version of the Squeaky Gate Call (Figure 17D).

The Rattle Calls made by tutored and untutored birds are shown in Figure 18. The model call (Figure 18M) had clicks at the rate of 41 per second. The energy in the model call centered around 2100 Hz and ranged between 1000 and 2200 Hz. The tutored birds (two females) Rattled at approximately the same rate as the model, or slightly faster (Figure 18A and B). The energy in their calls centered around the same frequency as the model but ranged up to 3000 Hz. Untutored birds Rattled much more slowly than the model, i.e., approximately 17 clicks per second (Figure 18C and D). The sound energy of their calls ranged from about 500 to 5500 Hz. This was considerably greater than the range of the model, of normal Rattles which are 1000-1500 Hz wide (see Figure 11), and of the tutored birds' calls.

The rendition of the Bell Call used as a model is depicted in Figure 18M. The call is composed of three notes, the first being the major component of the call. It is 0.68 sec long and has a frequency of 2100 Hz. The second note is not as clearly defined as the first and the third notes. It begins 0.14 sec

Fig. 17--Squeaky Gate Calls by tutored birds. See text for analysis.

M. Model Call

A-D. Calls by tutored birds.

Fig.17

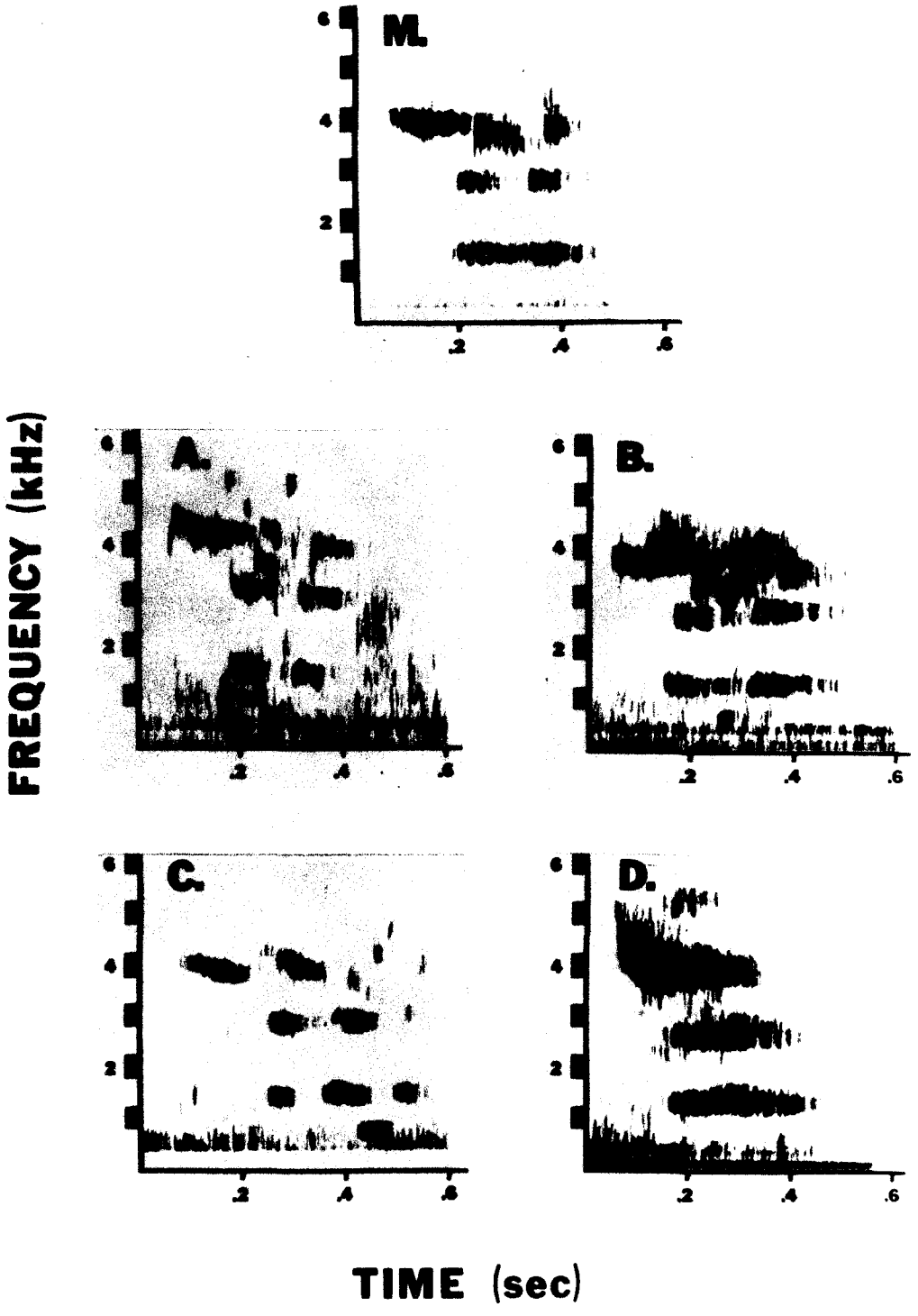


Fig. 18--Rattle Calls by tutored and untutored birds. See text for analysis.

M. Model Call.

A-B. Calls by tutored birds.

C-D. Calls by untutored birds.

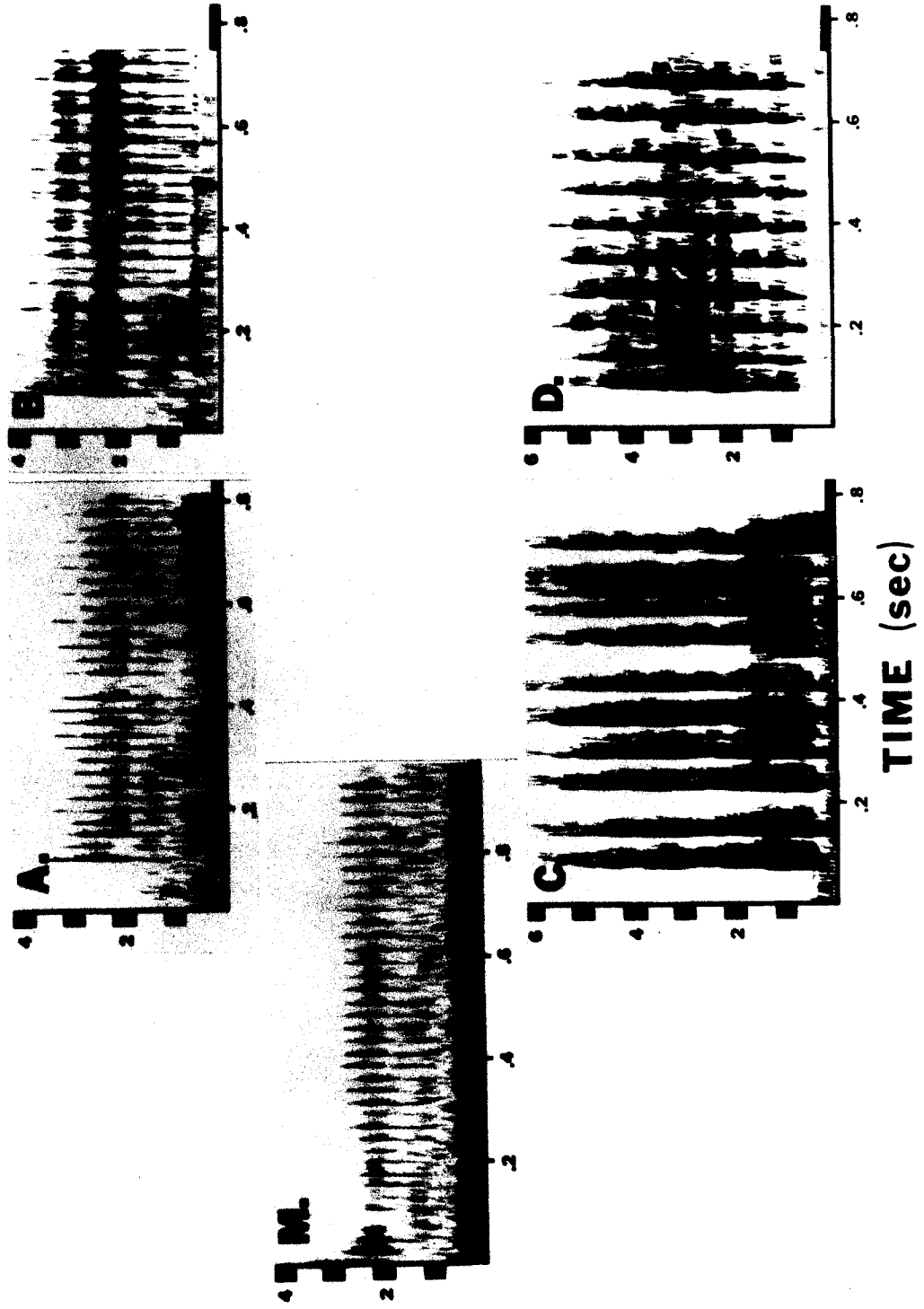


Fig.18

Fig. 19--Bell Calls by tutored and untutored birds. See text for analysis.

M. Model call.

A-B. Calls by tutored birds.

C-D. Calls by untutored birds.

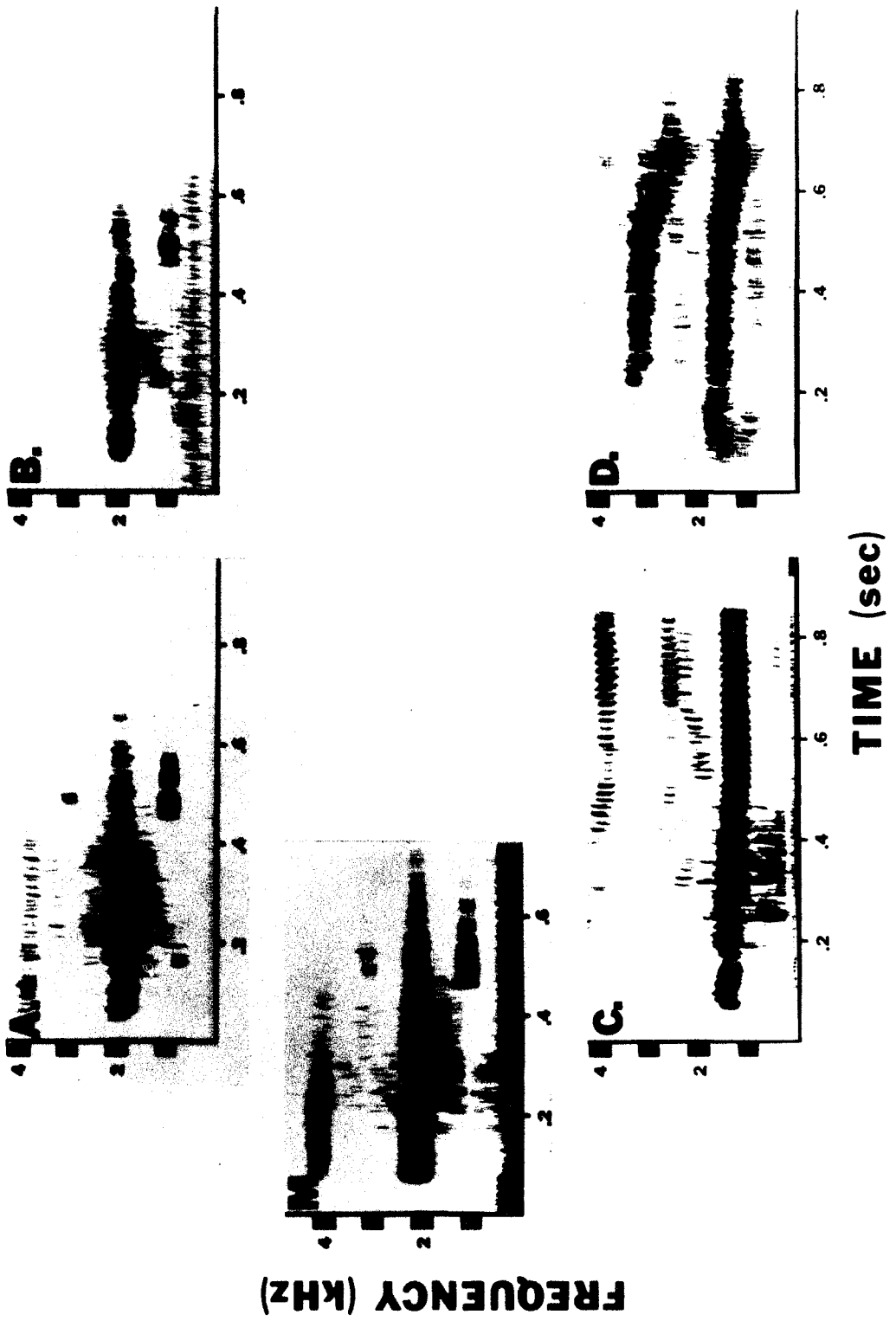


Fig.19

after the first note and lasts for 0.25 sec. It is upwardly inflected starting around 1100 Hz and ending 200 Hz higher. After an interval of 0.02 sec the third note begins. It is about 1000 Hz, lasts for 0.19 sec and ends 0.05 sec before the first note ends. Both renditions of the Bell Call given by tutored birds (Figure 19A and B) are 200-300 Hz lower than the model call and have more highly inflected second notes. The untutored birds gave calls which resemble the Bell Call in duration and structure (Figure 19C and D). But the frequency of their calls was ayproximately 600-700 Hz lower than the model call and they gave no second or third notes comparable to those in the model call and given by the tutored birds.

It appears, therefore, that jays are able to modify the details of the calls they make after hearing other jays. This supports the hypothesis that call mimicry is a feature of jay vocal interactions. Blue Jays probably retain the ability to learn new calls or to modify old calls throughout their lives although the evidence for this remains circumstantial.

C. Vocalizations and Behavior in the Nesting Season

Calling rates. Once incubation has begun, both parental jays are silent in the vicinity of the nest. I observed 17 incubating females 3 hours each. They called 251 times (not counting Yurping, Begging and Swallowing Calls). But three-fourths of these calls (182 out of 251) were given by the females while they were being harassed by Common Grackles (Quiscalus quiscula). Thus undis-

turbed, incubating female jays called at an average rate of 1.3 calls per hour; their mates, who were in view about ten percent of the observation time (5.2 out of 51 hours) averaged 1.0 calls per hour 50 calls in 51 hours). Earlier, in the prenesting season, Blue Jays call at an average rate of 38.1 calls per hour (Table 6).

Yurp Call. Pairs of jays begin foraging together in late February and early March. By the beginning of April they are together most of the day and roost together at night. When foraging together they are very likely to give the Yurp Call. Of the 44 times I was close enough to pairs of birds (N = 17) which were foraging in the vicinity of their nests, before incubation began, I heard Yurping on all but three occasions. In this context the Yurp Call appears to function as a short distance contact call (Conant, 1972). Steller's Jays give Gutteral Notes in the same context (Brown, 1964: 272).

Courtship-feeding calls. Three calls are regularly associated with courtship-feeding. The interaction begins when one of the birds increases the rate at which it is Yurping. Then as the birds approach each other the Yurping becomes more intense. Of the 68 feedings I saw in the vicinity of 17 different nests, all but 7 were immediately preceded by the Yurp Call. Thus, the Yurp Call in this context appears to signal the caller's readiness to feed or be fed by its mate.

Just prior to the actual transfer of food, the female's Yurp Call changes to the Begging Call (Figure 20). In structure this

call is strikingly similar to the monotonal Jay Call (see Figure 5). The chief difference between the two types of calls is the more frequent punctuation of the Begging Call with very short periods of silence. While giving the Begging Call females usually gape, flick their wings, and crouch, though some females perform these movements at very low intensities.

The Swallowing Call (Figure 20) is given during the actual transfer of food i.e., while the male is pushing food deep into the female's throat. The Swallowing Call is a modulated version of the Begging Call. The call is only given when the female is swallowing something that her mate has pushed into her throat. The call is never given when the female is swallowing something that she has found herself; nor is it given on the many occasions that she passes on to the nestlings food which she has received from the male.

Begging and Swallowing Calls of young birds. Nestlings and fledglings give the Begging Call (Figure 21) before being fed. They always gape, flick their wings and crouch while Begging. Adults do not offer food to young birds which are not Begging. While food is being poked down their throats, the young birds give the Swallowing Call (Figure 22).

The Begging Calls given by nestlings about five-days-old are variable in structure and of two general types: one type is a modulated call with energy centered around 4000 Hz (Figure 21A and 21B; also see Conant, 1972); the second type is lower in

Fig. 20--Courtship-feeding calls by a mated female.

A. Begging Call.

B. Swallowing Call

Fig. 20

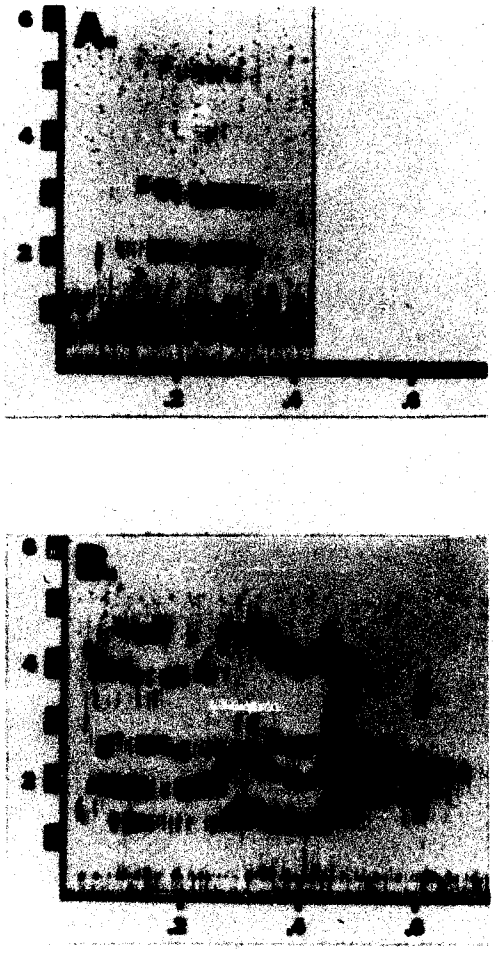


Fig. 21--Begging Calls by nestling jays. See text for analysis.

Fig. 21

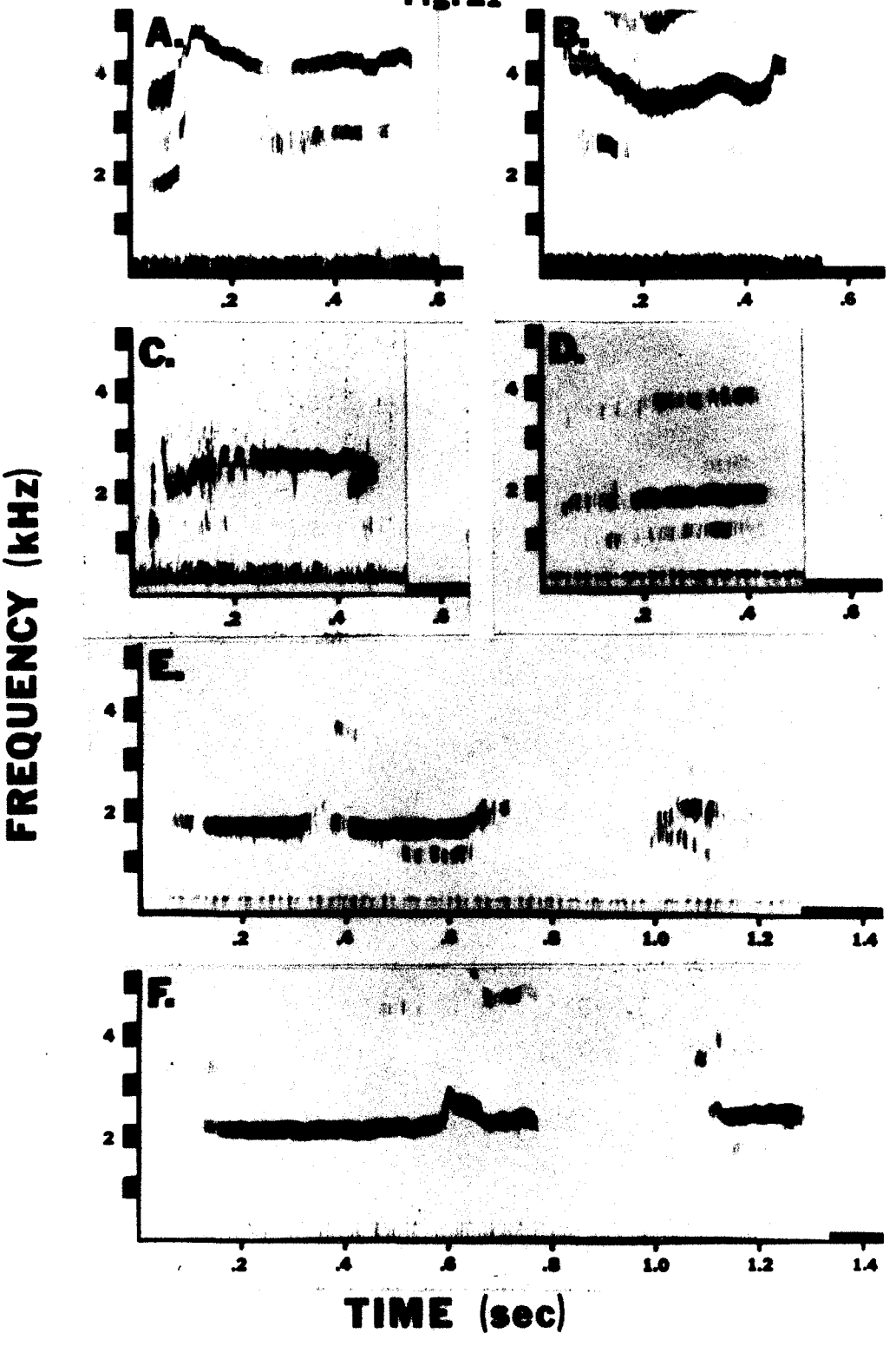
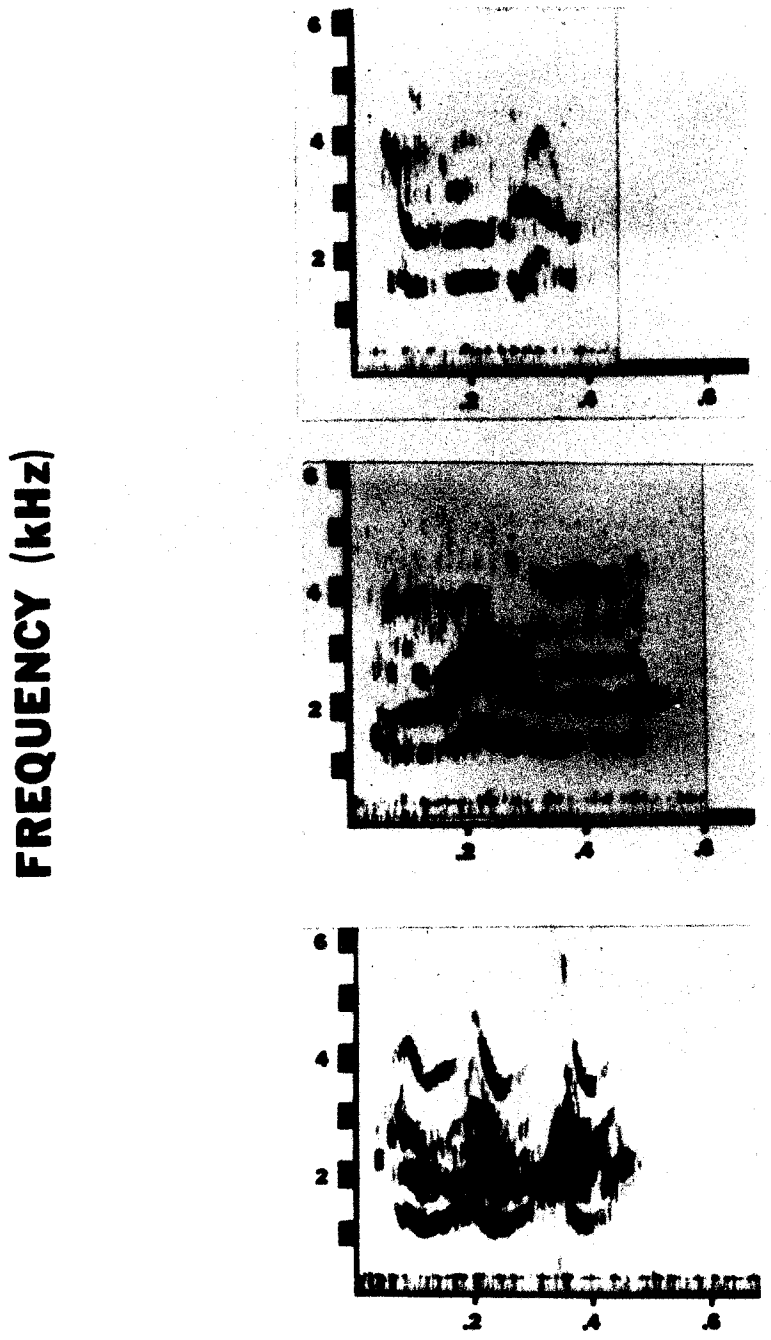


Fig. 22--Swallowing Calls by nestling jays.

Fig. 22



frequency and less modulated (Figure 21C and 21D). By ten-days of age the high-pitched calls are no longer given. The Begging Calls which are given are louder, longer and less variable than before (Figure 21E and 21F). By the time the young have fledged, their Begging Calls have become considerably stronger. Indeed, some renditions of the Begging Call given by fledglings are very similar to typical renditions of the monotonal Jay Call (Figure 5). And it is very likely that the monotonal Jay Call is derived from the fledgling's Begging Call (Figure 23A-C). Brown (1964) asserts that the Begging Call of fledgling Steller's Jays develops into the mature bird's Wah Call and Lanyon (1960) points out that this is a typical developmental pattern in birds.

Fledgling jays seem to Beg whenever they notice the return or approach of an adult. They also Beg and orient toward a sibling after it has begun Begging. For example, when fledglings are very mobile, i.e., more than four-weeks-old, they often forage out of sight of each other. When one is being fed, the Begging and Swallowing Calls it is making appear to stimulate the approach and Begging of other fledglings. At first I thought that each fledgling was using the Begging and Swallowing Calls of its siblings to orient to the parent and then compete for being fed. But I never saw a parent leave the fledgling it was initially feeding to feed the newly arrived one. The approach behavior is probably adaptive to the fledgling in that it makes the parent aware of its position and thereby increases the chance of that

Fig. 23--Possible antecedents of the two Jay Calls.

A. Monotonal Jay Call.

B. Fledgling's rendition of the Jay Call.

C. Nestling's Begging Call.

D. Ditonal Jay Call

E. Fledgling's rendition of the Jay Call.

F. Nestling's Squack Call.

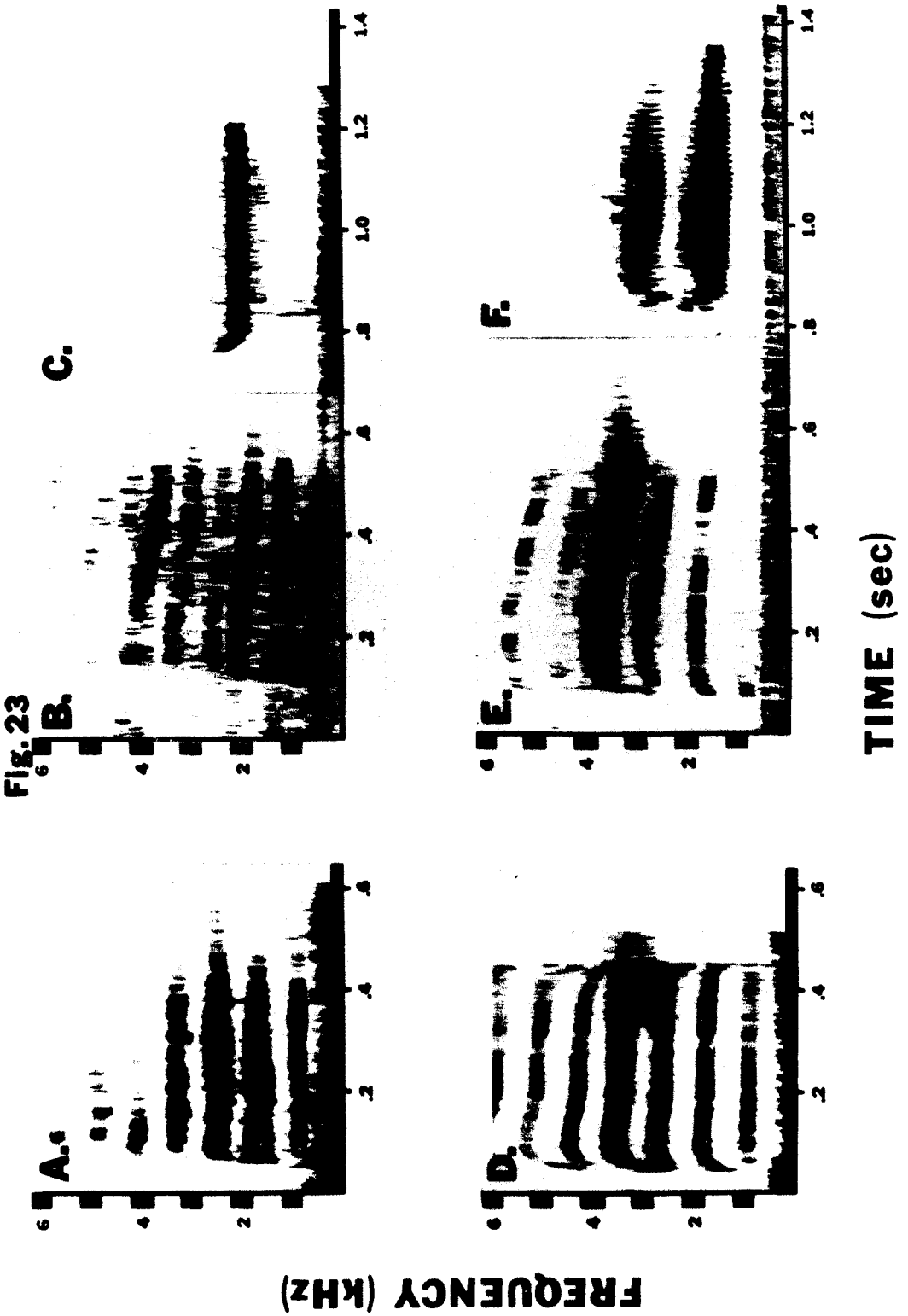


Fig. 23

fledgling being fed next. I was unable to test this hypothesis because the fledglings were often not visible when being fed. It is interesting to note that calling and orienting toward the caller is the same kind of response which the birds give when older to the mature version of the Begging Call.

Behavior of adults when disturbed: Bell Call. Males which are perched in the vicinity of their nests often begin giving the Bell Call when a person passes through the area. Bell Calling in this context is usually done from a high perch. Since the male tends to remain perched between bouts of the Bell Call, he, in effect, withholds visual clues to his whereabouts. Brown (1964: 302) reports that the Tee-ar Call of the Steller's Jay is given from concealment and elicited by a man's presence.

I think the Bell Call functions as a warning call when it is given by the male while the female is on the nest. She remains there and he remains perched while calling. Thus, each minimizes the attention it draws to itself and to their nest. I compared the behavior of jays when hearing playbacks of their own and another's version of the Bell Call. The jays moved less and called more during the broadcast of their own version (Table 13). This is exactly what they do normally. The Bell Call is the only call given by jays which inhibits the movement of another individual.

Hardy (1961:21) describes the Bell Call as being given during "low intensity phases of predator intimidation". Indeed, there is an element of aggressive behavior associated with this call for

TABLE 13

BEHAVIOR OF MATED JAYS DURING PLAYBACK OF THEIR OWN AND ANOTHER'S VERSION OF THE BELL CALL

	No. of calls given during		No. of moves made during	
Bird	Another's version	Own version	Another's version	Own version
1	0	3	1	0
2	0	5	0	1
3	4	1	1	1
4	1	2	1	2
5	2	2	0	1
6	3	4	0	0
7	1	3	2	1
8	1	5	0	3
9	2	3	0	1
10	2	4	1	0
11	0	0	1	0
12	0	0	0	0
13	3	4	1	1
14	0	7	1	0
15	2	2	1	0
16	0	5	3	1
17	3	0	0	0
18	1	7	1	2
19	0	3	1	0
20	0	3	2	1
	25	63	17	15
	N = 16		N = 15	
	T = 17		T = 47.5	
	p < .01*		p > .05*	

*Wilcoxon Matched-pairs Signed-ranks Test.

between bouts of Bell Calling jays sometimes peck vigorously at the perch. The movement is virtually identical to that used when jays open a sunflower seed held between the toes. But no food object is ever present on these occasions. The behavior seems like "redirected attack pecking" (Moynihan, 1955: 243). Similar behavior has been noted by Brown (1964: 247) in the Stellar's Jay. But perch-pounding occurs in association with Bell Calling during nest disturbances in which persons are close to the nest and not in the circumstances described above. In the more threatening circumstances alluded to by Hardy the jays are perched low, not high, they are hopping about—not remaining still, they are giving the Jay Call--not just the Bell Call, and they are acting as if trying to distract the observer's attention from the nest—not concealing themselves.

Behavior of adults when disturbed: Jay Call. The behavior of jays varied considerably when I approached and examined their nests. For example, some just flew away silently; others gave one or several Bell Calls or Jay Calls or Squeaky Gate Calls and then left or stayed near by and watched; some pairs actually engaged in a bout of courtship-feeding while I examined their nests. But the most consistent response to my examination of a nest was delivery of the ditonal Jay Call. When Jaying, the birds would sometimes be overtly aggressive. Together with rapid and repeated Jaying the callers would dive at me and sometimes scratch my head. During the dive they often gave a pair of loud, ditonal Jay Calls

just before delivering the scratch. This is the same behavior jays use during predation attempts by cats (Felis domesticus) and squirrels (Sciurus spp.). My personal experience suggests that the coordination of these calls with the occasional delivery of a scratch makes the call a very effective conditioning stimulus to a predator.

I tethered an immature Red-tailed Hawk, (Buteo jamaicensis) less than three meters away from active nests and counted the number of calls and dives made by the nesting pairs during a five-minute period. I positioned myself about the same distance away from five other nests and recorded the same data (Table 14). Clearly the hawk was a much stronger stimulus of nest-defense behavior than I was.

Behavior of the young. Nestlings and fledglings react to the Jaying of adults in ways which appear to be consistent with their stage of development. Nestlings and young fledglings stop Begging and assume the Alarm Freeze posture (see Figure 14 in Conant, 1972: 50) as soon as rapid Jaying begins. When older and more mobile, the fledglings tend to fly up and away from the place where an adult is Jaying. By the age of nine or ten weeks, fledglings join in the calling, but stay farther from the predator than the adults.

Squack Call. Squacking (Figure 24) is only given by birds when they are held or caught. It is repeated frequently until the bird is released. Nestlings and fledglings are more likely to Squack than older birds, though at three different nests a

TABLE 14

BEHAVIOR OF NESTING JAYS DURING FIVE MINUTES OF NEST-DISTURBANCE[1]

	Cause of Nest-Disturbance[2]			
	Man		Hawk[3]	
Behavior	Before Approach	While Present	Before Approach	While Present
Average No. Jay Calls per nest	0.5	9.0	1.2	195.6
Average No. Bell Calls per nest	0.15	4.5	0.4	0
Average No. Diving Attacks per nest	0	0.12	0	59

[1]Data collected when nestlings were 10-15 days-old in each nest.

[2]Five nests in each sample.

[3]Captive Red-tailed Hawk tethered to a branch within three meters of the nest.

[4]Five minute period immediately preceding approach.

[5]Five minute period beginning when observer was within three meters of the nest.

[6]Five minute period beginning after observer had tethered the hawk and retreated 15 meters from the nest.

nearby parent Squacked just after the nestling I was holding began to Squack.

The Squack is a long call lasting at least 0.5 seconds. the structure of the call resembles that of the ditonal Jay Call (Figure 23) but there is more frequency modulation in the Squack Call. The broadest frequency band is between 1000 and 2000 Hz.

Squacking is the loudest call a young jay makes. It probably is effective in attracting the attention and approach of adults who, if a predator is present, would then mob the predator and possibly force it to release the captured young. I tested the reactions of adults to the Squacking Call using a type one playback format (see pages 15-19). But the first broadcast was preceded by five minutes of blank tape. After placing the tape recorder at the base of the nest-tree and turning the machine on, the five minutes of silence allowed me enough time to move away from the tree and allowed the birds enough time to return to the nest and settle down before the first broadcast began. I conducted the test at ten different nests when the nestlings were approximately 15 days old. Neither the Squack Call nor the control tone elicited any response from the birds at two nests. But the jays dove down toward the speaker and gave Jay Calls when the Squack Call was broadcast at the eight other nests. Two responses occurred to the control tone, but these were relatively weak compared to the behavior elicited by the Squack Call.

Chur Call. I heard Churring (no sonogram is available) on several different occasions. Once after inspecting a nest and

Fig. 24--Squacking by nestling jays.

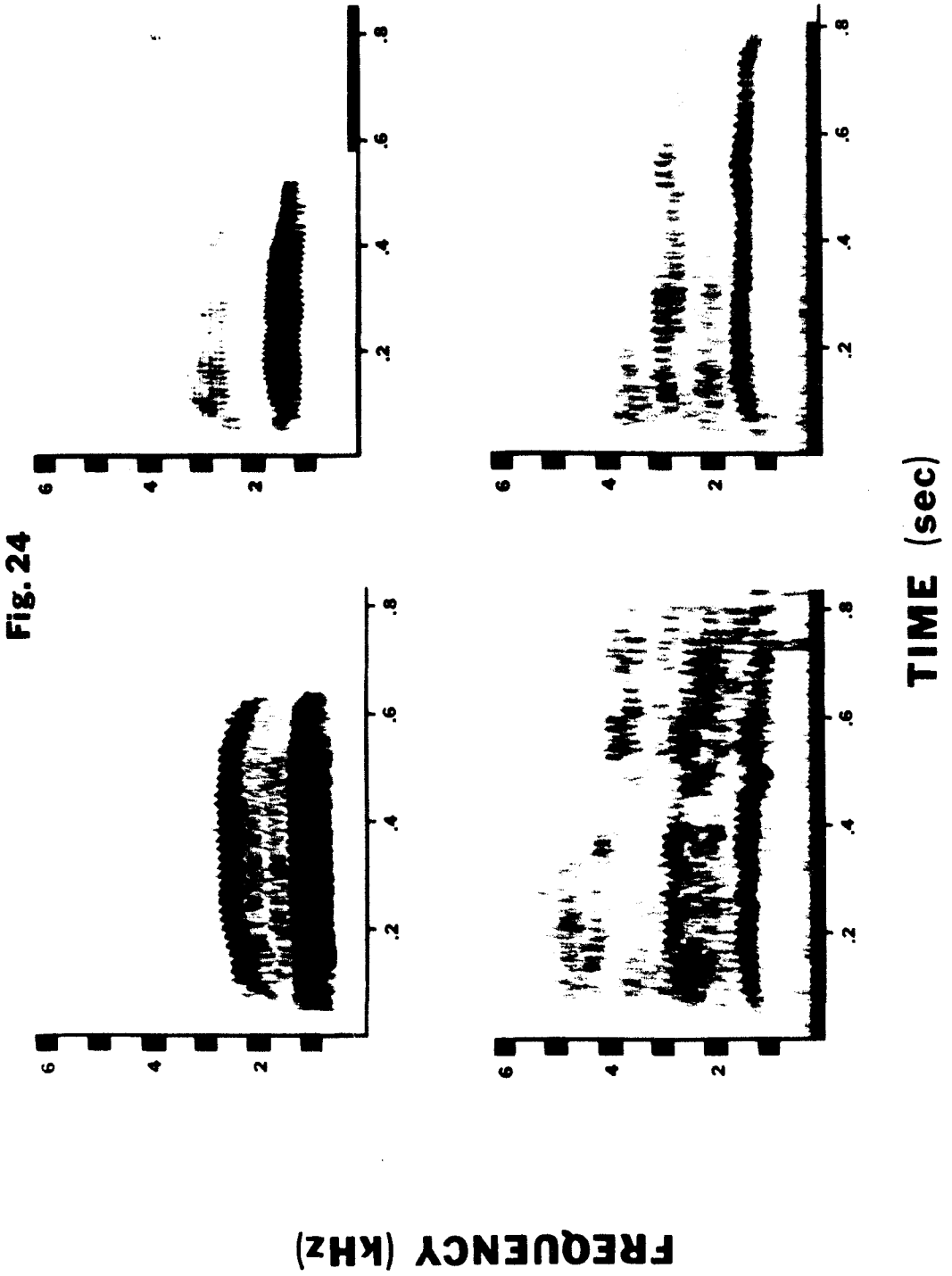


Fig. 24

stepping back the adults began Churring repeatedly while flying back and forth from the nest tree to a wooded area 25 meters away. After ten minutes of this behavior one of the nestlings and then another flew from the nest to the wooded area following the exact path the adults had been plying. The fledglings landed in some shrubs less than two meters above the ground. Then the adults began flying from the fledglings upwards, still Churring continuously. The fledglings eventually began hopping upwards as best they could. On another occasion I heard Churring as I approached the area in which I expected to find some fledglings. They were perched only about three meters high in a sapling and one adult was flying back and forth from them toward higher perches while giving the Chur Call.

Churring is sometimes heard in late summer and early fall. Usually the caller is in flight and being followed by one or two silent birds. The ages and relationships of the birds I have seen doing this were never known to me, but it seems reasonable to assume that the caller is an adult and the other birds are its offspring.

Rattle Call. A rattle-like call is reported in two other jays (Cyanocitta stelleri, Brown, 1964 and Garrulus glandarius, Goodwin, 1956) and in the crow (Corvus brachyrhynchus, Chamberlain and Cornwell, 1971). The call is given only by female Blue Jays. It is given in a variety of contexts such as when perched and alone, when another jay is present and silent, when another jay is

present and calling, when another female is Rattling, and when the caller is in a spring flock. On two occasions I saw an unfamiliar jay land on a nest. The female in the nest immediately Rattled and chased the other several hundred meters. This was the only context with a clearly aggressive connotation for the call.

I tested the responses of jays to playback of the Rattle Call using the type one format. Both mated and unmated jays called less and moved more during the Rattle Call than during the control tone (Tables 15 and 16). Surprisingly, not one bird Rattled in response to the playback. This kind of response is consistent with the interpretation of the Rattle Call being a signal which shows aggressive intent. I was unable to perform the type two experiment since it was difficult to find birds Rattling when I was ready to record them.

D. Vocalizations and Behavior in the Nonbreeding Season

Winter flocks. During the winter months I observed that Blue Jays grouped themselves into loosely organized flocks of 5 to 15 individuals. These birds shared a common home range, "rested" together during the day and roosted together at night. But the flock never moved as a unit. Rather, each bird foraged independently or occasionally in association with its mate from the previous year.

Flock membership changes during the winter as some individuals disappear and others join the groups. My impression is that most winter flocks are composed of at least one pair of mated birds

TABLE 15

BEHAVIOR OF MATED JAYS DURING PLAYBACK OF THE RATTLE CALL

Bird	No. of calls made during		No. of moves made during	
	Tone	Rattle Call	Tone	Rattle Call
1	0	0	1	2
2	0	0	1	0
3	2	0	0	1
4	0	0	1	1
5	0	0	1	3
6	0	0	2	5
7	4	0	1	2
8	0	0	1	1
9	1	1	1	2
10	0	0	2	2
11	3	0	2	5
12	0	0	0	1
13	1	0	0	3
14	1	0	3	3
15	0	2	1	4
16	5	0	1	3
17	0	0	3	0
18	0	0	0	1
19	0	0	4	1
20	0	0	0	0
	15	3	25	40
	N = 7		N = 15	
	T = 3		T = 27.5	
	$p > .05$[1]		$P < .02$[1]	

[1]Wilcoxon Matched-pairs Signed-ranks Test.

TABLE 16

BEHAVIOR OF UNMATED JAYS DURING PLAYBACK OF THE RATTLE CALL

Bird	No. of calls made during		No. of moves made during	
	Tone	Rattle Call	Tone	Rattle Call
1	11	9	1	0
2	16	8	2	3
3	14	6	3	2
4	5	3	0	1
5	9	4	1	1
6	13	10	1	2
7	12	5	2	3
8	7	8	4	3
9	0	2	1	4
10	5	6	0	3
11	4	4	0	3
12	15	4	0	2
13	6	10	0	5
14	8	5	1	1
15	7	7	3	1
16	9	11	0	2
17	10	6	0	2
18	15	10	1	3
19	8	3	1	1
20	3	9	0	2
21	9	5	3	1
	186	135	24	45
	N = 19		N = 18	
	T = 37		T = 32.5	
	$p < .02$[1]		$p < .02$[1]	

[1]Wilcoxon Matched-pairs Signed-ranks Test.

and some first-winter individuals. But I do not know to what extent winter flocks are family groups. I was only able to locate nine fledglings of the 55 fledglings I tagged, after they began foraging independently. The nine sightings all occurred in September and within two miles of where the birds were reared. In no case was I able to follow these first-winter birds long enough to see if they were still associating with their parents. One individual was with a sibling. Laskey (1958) saw one color-banded fledgling reappear after being away from its parents all winter. That bird then nested in the area and associated with its parents during its second winter life. Wenger (1975) found from his analysis of United States Fish and Wildlife Service banding records that regardless of age, only seven percent of all Blue Jays migrate.

Jay Call: mobbing. The only coordinated behavior of Blue Jay winter flocks which I observed occurred when they mobbed an owl or hawk. As soon as one bird began giving the ditonal Jay Call rapidly and continuously, the other jays oriented towards and approached the caller. When they saw the predator, they too began Jaying. Jaying and occasional diving attacks normally continued until the predator flew away.

Calling in this context probably reduces the chance of the caller being preyed upon in two ways: 1) calling alerts other individuals to the predator's presence thereby making it less profitable for the predator to hunt in the caller's area; and

2) calling recruits other jays who also mob the predator, thereby reducing the danger to the caller. The group of mobbing jays is not necessarily a social unit acting cooperatively. It can be viewed as an aggregation of individuals each acting in a way which reduces its own chance of being preyed upon. But I never saw jays leave their own home range when mobbing was occurring some distance away, i.e., outside of the home range, though they did often orient toward and approach that area. Twice I saw jays from two neighboring flocks jointly mob a Cooper's Hawk (Accipiter cooperii) when the hawk was perched near a feeding station which was visited by both flocks.

I tested the responses of jays to playback of the ditonal Jay Call at the rate of 30 calls per minute in a type one format. The experiment was performed in April, 1974. All the unmated jays behaved in the expected way: they moved more and called more during the minute which included the Jay Calls than during the minute which included the control tone (Table 17).

Jay Call: alone. I observed Blue Jays call at relatively low rates when alone during the winter. The 38 individuals in the winter sample gave a total of 34 Jay Calls during the entire 380 minute sampling period. This is an average calling of 5.4 Jay Calls per hour.

Conant (1972) characterized the monotonal Jay Call as a Flock Contact Call; Hardy (1961) labelled it an Assembly Call. Both names imply that jays respond to the Jay Call by "answering"

TABLE 17

CALLING BY UNMATED JAYS DURING PLAYBACK OF THE MOBBING CALL

Bird	No. of Calls Made During		No. of Moves Made During	
	Tone	Mobbing Call	Tone	Mobbing Call
1	20	5	2	0
2	24	25	1	4
3	16	21	2	1
4	3	5	0	2
5	10	20	0	2
6	16	12	1	3
7	7	11	1	3
8	7	6	2	5
9	0	9	1	0
10	17	15	1	2
11	13	17	0	0
12	8	15	1	2
13	23	27	2	3
14	12	14	1	3
15	3	6	0	0
16	14	7	1	1
17	20	24	1	4
18	4	10	3	2
19	14	17	1	2
20	17	20	2	1
21	14	22	2	5
22	11	12	2	3
23	8	9	1	2
24	9	10	1	3
25	5	16	0	2
	282	356	29	55
	N = 25		N = 19	
	T = 57		T = 26	
	$p < .005$ (one-tailed)*		$p < .005$ (one-tailed)*	

and/or approaching the caller. One way to test if jays "answer" the Jay Call is to compare the number of calls made by individuals during bouts of calling by other jays to the number of calls these individuals would be expected to make, in the same period of time, at their average rates. A bout of calling for jays is here defined as that period of time in which calls are given less than six seconds apart and includes the six seconds which follow what turns out to be the last call of the bout. During the winter sampling period the bouts of Jaying by other birds totaled 18.3 minutes. The jays under observation called approximately five times more frequently than their average rate during that 18.3 minute period (Table 18). The same relationship holds if one defines a bout of calling to include 30 second intervals between calls. The jays under observation did not move more frequently than average while other jays were calling (Table 18).

No data are available on who "answers" whom in the winter. It is likely that most calling interactions are between members of the same winter flock since those birds are the ones closest to each other. It is also possible that a given jay responds only to the calls of a particular member of its flock, i.e., its mate, its offspring, or its sibling. Since jays do not interact in any obvious way after "answering" the adaptive significance of this behavior in the winter is not clear.

Jay Call: "flying away". A distinctive pattern of Jaying is sometimes given by a jay which has just taken flight (Figure 25).

TABLE 18

BEHAVIOR OF BLUE JAYS IN WINTER WHILE OTHER BIRDS WERE GIVING THE JAY CALL

Interval of silence defining the end of a call bout	Total duration of all call bouts heard[1] (min.)	Calling		Moving	
		No. of Jay Calls given[2]	No. of Jay Calls expected[3]	No. of moves Made[4]	No. of moves expected[5]
6 sec	18.3	12	1.6	16	22[6]
30 sec	27.1	15	2.4	25	32[7]

[1]Calling from distant birds which was barely audible to me was ignored in this sample.

[2]This is the number of Jay Calls given by the birds under observation, not the number given by the birds being heard.

[3]This is computed from the average calling rate of the birds in the entire sampling period. The 38 birds gave 34 Jay Calls during the 380 minutes that they were observed for an average calling rate of 0.089 Jay Calls/minute.

[4]This is the number of moves made by the birds under observation.

[5]During the sample period the birds under observation moved 453 times for an average rate of 1.2 moves/minute.

[6]$X^2 = 1.6$, $p > .05$

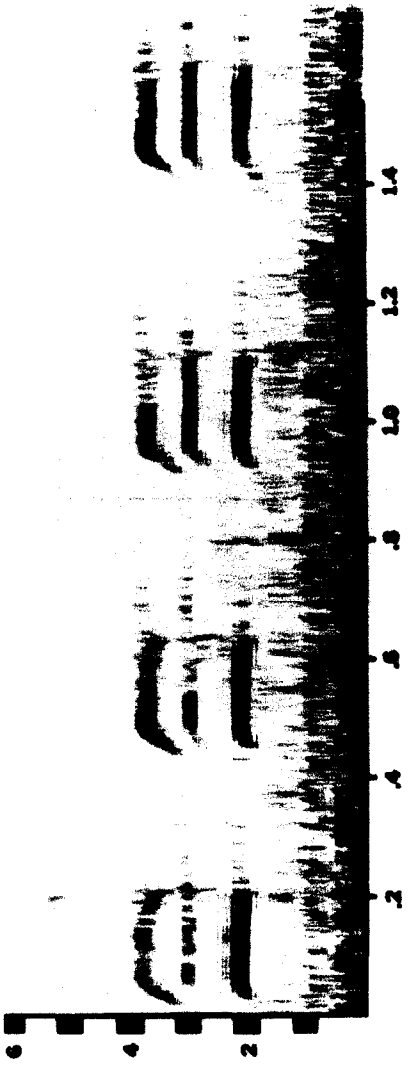
[7]$X^2 = 1.5$, $p > .05$

It is a short rapid burst of five to eight ditonal Jay Calls. This pattern of calling is heard by all who walk in the woods in the winter time. An anecdote among hunters is that the call is a warning to deer. My impression is that the caller is doing its best to get away from something which has startled it. I saw and heard jays call in this explosive manner 117 times. But the stimulus was usually not apparent. Thirty times it seemed likely that I, or another person had startled the jay; five times I noticed that a Cooper's Hawk was in the vicinity when the jay took flight calling in this manner. This is in marked contrast with the continuous Jaying given while mobbing, when an observer can almost always confirm the presence of an avian predator.

Only once did I see more than one bird "fly away" calling this way. Others are probably not present or not noticed because they remain still and silent after the calling. If this kind of Jaying were a "warning" call one would expect the caller to be less easy to locate and that the call would elicit obvious responses from other jays. Since the call is usually given by a solitary jay and the combination of suddenly taking flight and calling loudly makes the caller very conspicuous, I think this call is adaptive in that it informs the predator that the caller is already aware of the predator and, therefore, is a poor candidate for pursuit. When, in fact, a hawk is pursuing a jay, the jay is silent.

Yurp Call. The Yurp Call is the only call given by birds which are foraging. Sometimes Jay Calls precede foraging bouts,

Fig. 25--Ditonal Jaying given by a bird which has just taken flight.



FREQUENCY (kHz)

TIME (sec)

Fig. 25

or occur between bouts of foraging, but no call other than the Yurp Call is given while foraging. I was less than 50 meters away from birds which were foraging in the winter 235 times. I heard Yurping by these birds 61 percent (154 out of 235) of the time.

Yurping birds are occasionally aggressive toward other jays which are foraging near them. Of the few agonistic interactions I saw in the field the most common context in which they occurred was between foraging jays. One jay would stop Yurping and fly directly toward the other; the latter would usually hop or fly away silently. Thus, the Yurp Call may function as a distance-maintanance signal (Marler, 1967) between jays which, when foraging near each other in winter, are in competition for a scarce resource. Playback of the Yurp Call to jays was not attempted because of the difficulty of being close enough to a bird to broadcast the call at normal levels.

IV. DISCUSSION

In this section I will review how other birds call in each of four broad contexts and then describe the Blue Jay's behavior in each context. Where appropriate I will suggest hypotheses about why the jay's behavior is different or unusual.

A. Bird-Predator Calls

Three kinds of calls are commonly reported in association with the presence of a predator—mobbing calls, warning calls, and distress calls. Mobbing calls indicate to both the predator and other birds that the caller is interacting aggressively with the predator (Vogt, 1938; Nice, 1943; Marler, 1956; Stokes, 1961; Marshall, 1964; Ellis and Stokes, 1966; Orians and Christman, 1968; Lemon, 1969; Morse, 1969; Williams, 1969; Chamberlain and Cornwell, 1971; Samuel, 1971). Other birds approach and behave aggressively too. But young birds respond by withdrawing (Kozlowa, 1947; Bendell and Elliot, 1967; Williams, 1969) or becoming silent (Quaintaince, 1941; Marshall, 1964; Bent, 1969: 1273; Morse, 1969). Warning calls, on the other hand, indicate both to the predator and other birds that the caller is taking cover or is ready to take cover if the predator initiates an attack (Smythe, 1970). Again other birds will call and behave in the same way as the

first caller even if they have not seen the predator themselves. Distress calls are usually given by nestlings which have actually been captured by a predator (Marshall, 1965; Ellis and Stokes, 1966; Orians and Christman, 1968; Williams, 1969; Heinz and Bysel, 1970; Chamberlain and Cornwell, 1971; Kok, 1971). The call indicates to the parents what has happened and they respond by approaching and then mobbing the predator (Quaintaince, 1941; Bendell and Elliot, 1967; Orians and Christman, 1968; Williams, 1969; Chamberlain and Cornwell, 1971).

Blue Jays most resemble other species when calling in response to predators. The jay's mobbing call is the ditonal Jay Call repeated rapidly. Other jays, either the members of the caller's winter flock or the other jays which are nesting in the vicinity, approach and mob the predator too. Jays also give a warning call, the Bell Call, during the nesting season. The caller remains perched and relatively inconspicuous. Females remain silent if on their nests or remain perched and give the same call if off the nest. Young Blue Jays give a distress call, the Squack, when captured by a predator. The parents react by quickly approaching the source of a distress call. In addition to these three widely reported kinds of bird calls related to predators, Blue Jays give the ditonal Jay Call when "flying away." This call probably indicates to a predator that the caller is ready to take additional evasive action if the predator initates an attack (Smythe, 1970).

B. Offspring-Parent Calls

The most common call given by a young bird is the Begging Call. It is given when the bird is ready to accept food. The parent responds by approaching and feeding it (Goodwin, 1953; Marler, 1965; Bent, 1968: 725, 1273; Bendell and Elliot, 1969; Williams, 1969). In other species it is the adult who calls after finding or bringing food; in response the young bird approaches or calls and then feeds (Quaintaince, 1941; Nice, 1943; Goodwin, 1953; Marler, 1956; Collias, 1960; Borror, 1961; Stokes, 1961; Ellis and Stokes, 1966; Bendell and Elliot, 1967; Williams, 1969; Heinz and Gysel, 1970; Chamberlain and Cornwell, 1971; Samuel, 1971).

Jays also give the Begging Call in very much the same way that other birds do. The dependent nestlings and fledglings Beg when they are ready to accept food. The adults feed the birds which are Begging. But the Swallowing sounds given by young Blue Jays, Steller's Jays (Brown, 1964), and crows (Chamberlain and Cornwell, 1971) have not been reported in other species. If this call coordinates the release of food by the adult with the young bird's readiness to swallow, it is not clear why only corvids have such a call.

C. Agonistic Calls

Vocal interactions between males are usually associated with aggressive territorial encounters. Males start calling and

approaching after noticing a "trespassing" male (Blanchard, 1941; Quaintaince, 1941; Nice, 1943; Davis, 1958; Borror, 1961; Jenkins, 1961; Stokes, 1961; Morse, 1966, 1967; Bendell and Elliot, 1967; Bent, 1968: 3, 603, 1166; Orians and Christman, 1968; Gladfelter and McBurney, 1970; Gobeil, 1970; Robbins, 1971; Samuel, 1971) or after hearing one on or at the edge of the territory (Blanchard, 1941; Quaintaince, 1941; Nice, 1943; Marler, 1956; Mulligan, 1966; Bent, 1968: 562, 1166; Orians and Christman, 1968; Stokes and Williams, 1968; Gobeil, 1970). Males also call just before chasing or fighting with trespassing males (Davis, 1958; Stokes, 1961; Bendell and Elliot, 1967; Orians and Christman, 1968) and while chasing or fighting (Marshall, 1965; Ellis and Stokes, 1966; Stirling and Bendell, 1966; Bent, 1968: 678, 1166; Lemon, 1969; Williams, 1969; Heinz and Gysel, 1970; Ellison, 1971). The trespassing males may withdraw after seeing or hearing the territorial male (Marler, 1956; Mulligan, 1966; Bent, 1968: 1166; Orians and Christman, 1968; Stokes and Williams, 1968; Gobeil, 1970).

Blue Jays sometimes fight. During a fight jays give the ditonal Jay Call, just as they do in other aggressive contexts, e.g., when mobbing a predator or defending the nest. But fights are rare. This is in sharp contrast with the congeneric Steller's Jay.

Most agonistic interactions between jays are mild and silent involving one jay displacing another. This is seen most fre-

quently during the nesting season when one bird is foraging in the vicinity of another bird's nest. The nesting jay does not call just before or while displacing the other. Rather, it flies silently and directly at the intruding bird which first hops aside and then continues on its way. But surprisingly, nesting jays "ignore" or do not "notice" trespassers almost as often as they displace them. This reduction in aggressive territorial defense by the Blue Jay is probably part of the overall tendency of nesting jays to minimize any conspicuous behavior on their part around the nest: they call less during the nesting season than at any other time; the male forages far from the nest and only returns periodically to deliver food to his mate and their young: and the female remains silently on the nest incubating and brooding the young by herself. The only time nesting jays are noisy is while warding off actual attempts at nest predation. Their inconspicuous behavior around the nest has probably been favored by selection because it gives predators fewer clues for finding the nest.

D. Male-Female Calls

Vocal interactions between males and females during the breeding season are related to courtship and sexual matters. The most common situations in which males call and approach a female are after seeing a prospective mate (Marler, 1956; Ellis and Stokes, 1966; Morse, 1966; Bendell and Elliot, 1967; Orians and

Christman, 1968; Gladfelter and McBurney, 1971; Kolham, 1972), after hearing a prospective mate (Quaintaince, 1941; Marler, 1956; Smith, 1959; Morse, 1966; Bendell and Elliot, 1967; Bent, 1968; Orians and Christman, 1968; Williams et al., 1968; Storer, 1969; Horn, 1970; Samuel, 1971), or after seeing the actual mate (Morse, 1966, 1967, 1969; Ellis and Stokes, 1969; Samuel, 1971) or after hearing her (Stoddard, 1931; Quaintaince, 1941; Marler, 1956; Marshall, 1965; Bent, 1968: 1273; Williams et al., 1968; Storer, 1969; Samuel, 1971; Chamberlain and Cornwell, 1971; Kilham, 1972). Males also call while chasing females (Nice, 1943; Marler, 1956; Borror, 1961; Williams, 1969; Morse, 1970; Gladfelter and McBurney, 1971; Kilham, 1972) and just before copulating (Stokes, 1961; Morse, 1966; Bendell and Elliot, 1967; Storer, 1969; Williams, 1969).

Unmated females in some species approach and call after hearing the calls of conspecific males (Nice, 1937; Kozlowa, 1947; Marler, 1956; Smith, 1959; Stokes, 1961; Ellis and Stokes, 1966; Bent, 1968: 3, 1273; Orians and Christman, 1968; Williams, et al., 1968; Storer, 1969; Horn, 1970; Gladfelter and McBurney, 1971; Payne, 1973). Mated females in some species call just before copulating (Stoddard, 1931; Marshall, 1965; Stirling and Bendell, 1966; Bent, 1968: 562; Storer, 1969; Williams, 1969; Heinz and Gysel, 1970; Horn, 1970; Samuel, 1971).

Calling occurs between mated male and female Blue Jays. When together they give the Yurp Call; when apart one bird calls after

hearing its mate's mimetic call. Each mimetic call elicits a different response from the other member of the pair. The mimetic monotonal Jay Call elicits approach and calling, or following and calling, by the mate. The mimetic Squeaky Gate Call does not elicit movement, but does elicit calling by the mate. The Bell Call, on the other hand, inhibits movement by the mate and elicits calling only when the mate is off the nest.

What is the function of vocal mimicry in the behavior of mated jays? Clearly the mimicry makes the caller more easily recognizable by its mate and it specifies whom the caller is "addressing"; by extension it also specifies with whom the caller is not "willing" to interact. Perhaps this extra information discourages responses by unmated jays to the calls of already mated birds. If this were the case then the rather enigmatic Rattle Call might be given by mated females when unmated jays respond to the mated female's calls.

Calling by males and females also occurs in spring flocks. In this context, the birds fly several hundred meters at a time in a loose group. Most of the time all the birds are calling simultaneously. All are giving not just the same call but the same rendition of the call at the same time, i.e., they are mimicking each other. How this spring flock behavior leads to pair-formation, or even if it does, is not obvious. But what is clear is that, during the prenesting-season, unmated jays are investing much time and energy flying in groups and mimicking each other's calls.

The process of pair-formation in the Blue Jay occurs in the late winter and very early spring. It probably involves two stages, the first being acceptance by the female of the courting male and the second being the learning of each other's calls. Since females must rely heavily on their mates for food during the nesting season they probably accept mates who are able to feed them at precisely the time of year when food is most scarce. At this time, first-year males are probably at a considerable disadvantage having never foraged under these conditions.

The possibility that call mimicry may play a more extensive role in jay social behavior than just between males and females is suggested by the results of all the type two playback experiments. Both mated and unmated jays were consistently more responsive to playback of the mimetic rendition of the call they were giving at the time of testing than to the control rendition of that call. Since each jay has several renditions of each call, it is possible that each rendition is in fact mimetic and specifies a different individual or set of individuals as the "intended" message receiver. If pair-formation involves learning to share renditions of each call with the mate, then the other renditions in each jay's repetoire may have been learned from its parents, other members of its winter flock, and its siblings. These renditions and relationships would not be lost after pair-formation and probably continue after the breeding season ends.

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