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# COMMUNICATION AND OTHER SOCIAL BEHAVIOR IN *PARUS CAROLINENSIS*

SUSAN T. SMITH

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# COMMUNICATION AND OTHER SOCIAL BEHAVIOR IN *PARUS CAROLINENSIS*

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# COMMUNICATION AND OTHER SOCIAL BEHAVIOR IN *PARUS CAROLINENSIS*

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DEPARTMENT OF BIOLOGY
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# 1

# INTRODUCTION

## Theory and Methods

### *Objectives*

This study of communication in *Parus carolinensis,* the Carolina Chickadee, has as its primary objectives: (1) to identify the specialized signals used by this species and the information encoded in each signal; (2) to begin to understand how the communication pattern helps to mediate the species' social organization; (3) to compare, by means of observations and published reports, the display repertoire of the study population with that of other populations of *P. carolinensis* and with congeneric species; and (4) to compare the information encoded in the display repertoire of this persistently social bird with that encoded by less social species in other avian families and by mammals.

Many interactions between conspecific animals are facilitated by behavior specialized for communication; this study is concerned primarily with such behavior. Although an animal can gain information about another individual by watching any of its activities, only those actions which were evolutionarily developed to be useful primarily in transferring information are considered to be "displays". Chickadee displays are both vocal ("calls" and "songs") and visible (postures, plumage movements, and body movements). The term "signal" is employed here for activities that are displays, or that are probably displays in the case of activities that one cannot be reasonably sure have been evolutionarily specialized for communication.

Most of the studies of parid vocalizations antedate the use of extensive tape recording and of sonagraphic analysis. Researchers had to rely on a sharp ear and even the very best observers must have had trouble sorting out some of the more rapid and complex calls. Further, presentation in the literature was limited to descriptions and phonetic representations, which are sometimes adequate but at other times are unclear or confusing. In addition, most observations on vocalizations were made incidental to other, more ecologically slanted, work rather than during study of social behavior or of communication behavior itself. Many authors commented on only the more conspicuous calls and gathered little information about the accompanying interactions, with the result that information about the behavioral significance of displays is very scanty. The present study is one of the few on parids made with considerable use of sonagraphic analyses of tape recordings

and in which a study of the display repertoire *per se* was a primary goal.

Finally, in this study the vocal and visible signals which were identified were analyzed with an approach developed by W. J. Smith. It was originally applied by him to tyrannid flycatchers but since then he has studied signals of some mammals in the same manner (1966 and 1969; also see below). This study is the first application of his approach to a parid display repertoire.

### *Approach*

For each signal or display an attempt was made to define: (1) the situations in which it was used; (2) the compound message it encodes; and (3) at least some of the meanings of the signal to the recipient bird(s), as judged by their observed responses.

The "message" of a display is "the information encoded in the signal that is descriptive of some aspect(s) of the central nervous state of the communicator" (W. J. Smith, 1966, p. 6). The message is the information about the displaying individual that the recipient of the display would know in the theoretical event in which he received only the display, unaccompanied by information from contextual sources. Messages indicate which behavior, of the communicator's entire behavioral repertoire, he is performing or is likely to perform (see W. J. Smith, 1969, and discussion below).

The message of each display is identified by examining in detail the use of the display and abstracting those features of the communicator's behavior that are common to all of the situations. For example, the communicator may often attack, or give signs (e.g., by orientation and intention movements) that he might attack, when using a certain vocalization but he rarely flees when using it. With another vocalization attack may be rare, intention movements common, and escape more probable. Each display thus encodes not only the specifications of acts that might be performed (in this example, attack and escape) but also the probability of their performance. Each display has, therefore, one constant but compound message.

It is, in fact, possible to find a message statement consistent with all usages for each signal in an animal's repertoire. A spurious message could be derived if too little behavior is sampled to be representative. Even a large sample might omit a category of behavior which occurs rarely but which would alter considerably the interpretation of the message of a display. In practice one can not know when "all" types of situations have been observed, but effort should be made in the field to observe the maximum range of behavior and kinds of situations at all seasons. The message of the display must then be consistent with all observed usages. If the message of a display and the situations in which the display is used are both understood correctly, then the responses of the recipents, i.e., the "meanings", should be appropriate.

In practice it is frequently impossible to determine the appropriateness of a response because, like the communicator, the recipient has a current state, not always known to the observer, as well as a personal history and temperament, all of which affect his response to the display in any particular situation. A response which seems grossly inappropriate, however, would suggest that the display has been misinterpreted, i.e., the message statement is incorrect. Hence, appropriate responses comprise limited but still useful criteria for the accuracy of a message.

Most signals appear to elicit more than one kind of a response (meaning) as a result of being used in various contexts. A recipient of a display has available to him a variety of contextual sources of information. These include the orientation and ongoing activity of the communicator, previous experience of the recipient with the communicator, location of the interaction, presence or absence of other individuals, time of year, genetic predispositions of the recipient, and even the evolutionarily-determined characteristics of the species. Some of the more evident sorts of features can be taken as describing a "type of situation," e.g., the communicator and recipient are confronting one another on a feeding station, or are members of a foraging flock, or are both responding to a predator, etc. In making his response to a display, i.e., the meaning, the recipient acts on the basis of the information about the communicator encoded in the display, as well as on some selection of all the contextual sources of information available to him. Because the latter vary from instant to instant, the response, i.e., the "meaning" of the display to the recipient, also varies. The concept of context has been discussed by W. J. Smith (1965, 1968, and *in press*).

A display may also have more than one function, even simultaneously. Displays have the general function for the communicator of helping to make the recipient respond in a way useful to the communicator. For the recipient they make the communicator's actions more predictable, so that the recipient can adjust his activities suitably. Both short- and long-term functions are achieved. For example, a display may function to help a pair associate amicably and, thus, in the long term strengthen the pair bond and contribute to the likelihood of breeding success. In another situation the same display might function to keep foraging flock members in association, so that in the long term the members gain extra predator protection and access to food sources known to their companions. Many of the functions of a display are learned by stepping outside of the immediate framework of the displaying and receiving animals and taking a longer view of their activities. It requires analysis of data not immediately available in events in which the display is used. Functions of displays are more often inferred than systematically studied; that is true of this project, which was designed primarily to study message, not function.

Further, this project was not designed to study motivations under-

lying the activities of the communicator. In this respect it differs from much of recent ethological research on displays. Although it is impossible to avoid considering motivations, they are not considered in detail in this study. Messages give some indication of what the communicator is likely to do, including how likely he is to act, presumably as a result of aspects of his motivational state and the external situation. More than one motivational state can lead to the same display; the message is common to every use of a display. A statement of a message is, therefore, one step removed from the underlying motivations. The motivational approach has been contrasted with the information content (message) approach by W. J. Smith (*in press*).

### *Comparative Survey of Messages*

Comparative surveys offer further support for the approach which seeks to identify a constant message for each display. Birds of widely differing phylogenies, as well as a variety of mammals, have similar sorts of messages (see discussion in Chapter 4). The following is a list of types of information apparently encoded by those birds and mammals which have been studied with the above approach. The list, together with much condensed explanations, is taken from W. J. Smith (1969, *in press,* and pers. comm.).

1. Identification. The identification message specifies the class(es) to which the communicator belongs and, therefore, the characteristics of the total behavioral repertoire in which he might engage. Identification is encoded in every display, together with other types of information.

2. Location. Every vocalization specifies the location of the communicator. The physical structure of some displays has apparently been modified to make them more or less easily locatable (see W. J. Smith, *in press*).

3. Probability. Each display specifies not only categories of behavior but also some range of probability of their occurrence.

4. Attack. This message is present when an animal accompanies or follows a display with attack or attack intention movements.

5. Escape. This message is present if a display accompanies escape, or escape intention movements and orientation. Escape and Attack frequently are encoded as conflicting behavioral possibilities in the same display.

6. Bond-limited Subset. Some behaviors can occur between animals having a special sort of social relationship, e.g., parents and offspring, or flock members, because of a social convention between them; W. J. Smith (1969) refers to this convention as a "bond." The Bond-limited category includes association, copulation, and play, all of which are sometimes encoded separately in distinct displays.

7. Association. The Association message is encoded in displays typified by persistent association—remaining near without avoidance or contact—between the communicator and one or more other individuals.

8. Copulation. In some species there are displays given only before or during copulation. In chickadees, however, the two vocalizations used at this time also are given in other situations (see below), although one of these calls is used relatively rarely except during copulation. It is very likely that in some other species thought to have displays restricted to copulation further observations will reveal additional circumstances during which the displays are used. It may be exceptional for a species to have a display used solely during copulation. The encoding of broad versus narrow messages is discussed in Chapter 5.

9. Play. Displays associated only with social play are apparently restricted primarily to primates.

10. Locomotion. Some displays are associated with locomotion, its onset, or its termination. Usually the same display encodes another, sometimes unspecified, message of conflicting behavior.

11. Frustration. Some displays are used when an animal is thwarted from performing some behavior by the lack of a suitable opportunity. Types of behavior for which frustration messages are used include escape, attack, association, and probably copulation and play.

12. Social Interaction Hesitance. The communicator is hesitant about accepting in an appropriate manner, or initiating, a social interaction with which he is actually or potentially faced. If the communicator is not interfered with, i.e., is not forced to engage in the social interaction, he will probably continue his ongoing activity. This message has been provisionally recognized only in gorillas and man, and in one avian species (*Myiozetetes similis*), and may not be widespread (W. J. Smith, pers. comm.).

13. General Set. This message apparently refers unselectively to the species' entire behavioral repertoire. This seems like a relatively uninformative type of message, but it is subject to some qualifications. First, no display encoding the General Set has been studied in detail; probably some displays thought to encode the entire set will be found to be narrower. Second, an animal using a General Set display may be more likely to change its behavior than if it gives no display. Finally, it is usually combined with some other, rather specific message—the display indicating a conflict between doing some more specific act vs. anything else in the animal's behavioral repertoire. The "anything else" may be obvious from contextual information.

14. Non-agonistic Subset. This message comprises the General Set minus Attack and Escape. Like the General Set message, it is often combined in a display with some other, more specific message.

Every display of birds or mammals studied so far with the approach described above encodes some constant combination of the types of information in this list. The display repertoire of the Carolina Chickadee will be discussed with reference to this list in Chapters 2-4.

### *Carolina Chickadee as a Subject for Study*

Carolina Chickadees are very active, usually easy to see, and highly vocal. Their strong social tendencies lead to a large number of inter-

actions in which display communication is appropriate. In addition, they provide opportunity for a year-round field season instead of the brief period usually available in temperate zone studies of migratory birds.

Social organization in *Parus carolinensis* alternates between pairs holding breeding territories during spring and early summer, and pairs or larger organized groups holding flock ranges during autumn and winter. According to Dixon (1963), who made a five-year study of social organization of a free-ranging Texas woodland population, and Ward (1966), who examined U.S. Fish & Wildlife Service banding and recovery records, the species is highly sedentary. Dixon also found that the pattern of usage of an area by a group of individuals at any one time strongly influences both the future use of the area, and the future opportunities of the individuals. For example, the alpha (first ranking) male of a flock always nests in the flock range, as do beta and succeeding males if there is room, while remaining males have to move out. Conversely, if a male breeds in an area he is very likely to remain on it during the flocking seasons. Females show similar, though slightly less strong, attachments. Dixon found also that the persistence of experienced individuals in an area leads to perpetuation of traditional boundaries. Limits of flock ranges are strongly influenced by their component breeding territories.

The behavior of the individuals in my study area fell within the range of variation seen by Dixon, with minor but interesting exceptions. Thus, even though the study population was in a wooded suburban area where many persons operated feeding stations (sometimes irregularly), it was apparently socially normal.

The persistently maintained social organization that makes the Carolina Chickadee a particularly interesting subject for a study of display communication provides the matrix within which the communication occurs. Because of the complexity and annual cycling of social behavior, the same signals given by the same individuals can be studied in a large variety of social situations. This greatly extends the opportunity to examine the social context of signals over that found in migratory species. Also, where the same individuals can be identified and followed for long periods, the influence of what one might call "temperaments" on communication can be examined. Finally, it is of interest to compare the communication pattern *per se* of this sedentary and winter-flocking species with the communication patterns of species that are migratory and more solitary.

### *Observation, Trapping, and Banding*

The study extended from September 1966 through June 1967, but no observations were made from 16 January to 27 February 1967. Occasional observations were made in July and August 1967, and preliminary observations were made from December 1964 to the beginning

of the study. During the study observations were made for several hours of each week on a group of color-banded, thus individually recognizable, chickadees. Their vocalizations were tape recorded and their behavior noted. Visible signals can be studied only if the birds are close by or under inspection through binoculars. Close attention to visible signalling thus often precludes gathering detailed information on the rest of the interaction. Visible signals are useful only over short distances and when the recipient is already paying attention to, or at least looking toward, the communicator. It was felt that visible communication would be more limited in scope than vocal communication and not worth the sacrifice of other information. For these reasons, considerably less attention was given to visible than to vocal signals.

The study area comprises several residential properties and a swimming and tennis club ("the Club") in Rose Valley, Pennsylvania (12 miles west of Philadelphia). There are open lawns, small woodlots, and many dense evergreen and deciduous hedges. Most of the higher ground slopes towards stream valleys. A few areas along the streams are marshy, most notably in the Club and in a small field to the east of it (Fig. 1.1).

Much of the study was done on the author's property, "Apple Bough," where several feeding stations and nest boxes were erected; most of the trapping was carried out there. Permission was generously granted by many surrounding property owners for work in their yards and, in some cases, for the installation of nest boxes. Where it was not possible to work on a given private property, observations were limited to what could be seen from public roads or from adjoining properties. Although some details were missed owing to this limitation, it is very doubtful that any major categories of behavior were overlooked.

Three feeding stations were installed at Apple Bough and two at the Club. At least four more were maintained by other persons. Most stations provided sunflower seeds which chickadees take readily. Peanut butter and suet were available in at least one location. Of seven nest boxes erected, two were used by chickadees. The boxes were constructed of one-inch pine, dimensions 4×4×12 inches, with a 1⅛ inch diameter hole about 2 inches from the top. The roof was hinged to permit inspection of the contents and banding of nestlings. Following the report by Drury (1958) on nesting in *P. atricapillus*, the boxes were filled to the bottom of the hole with sawdust and small wood shavings which the birds "excavated." The boxes were installed at heights of from one to 3 meters. Figure 1.2 indicates the locations of feeding stations and boxes.

Several chickadees had been banded in the study area during the year and a half preceding the study. A few of these figured in the study population, but most of the birds were banded after the study began. The birds were captured in mist nets in warm weather and in hardware

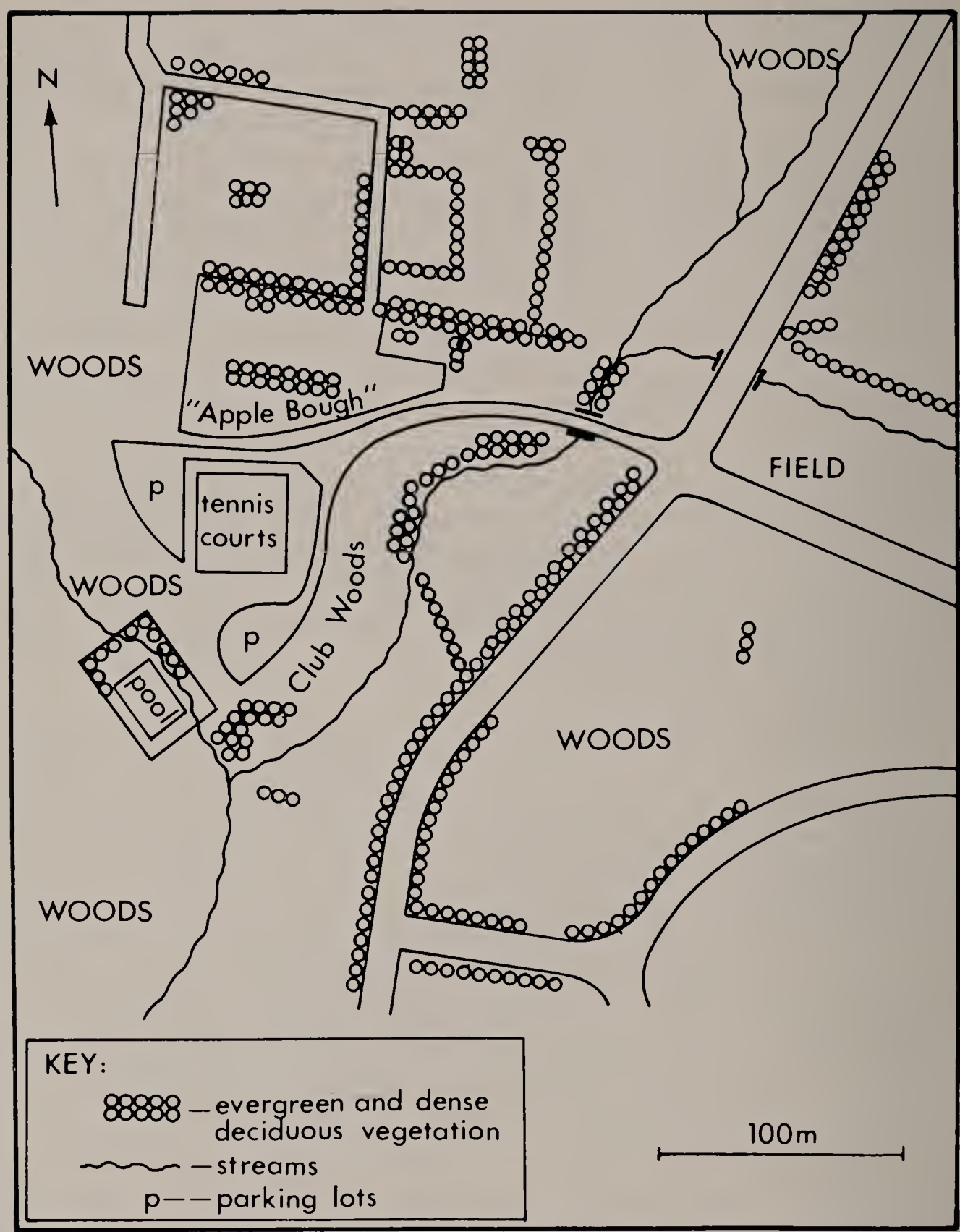



Fig. 1.1. Physical features of western two-thirds of Apple Bough flock range, where most of the observations were made.

cloth box traps placed on feeding stations during cold weather. Each bird was banded with an aluminum Fish & Wildlife Service leg band and one or more colored plastic leg bands in order to form a unique combination. On one male a red Cardinal feather, cut to size, was glued into position to substitute for the right outer rectrix. It did not visibly affect his flight and made his identification in the field rapid and easy.

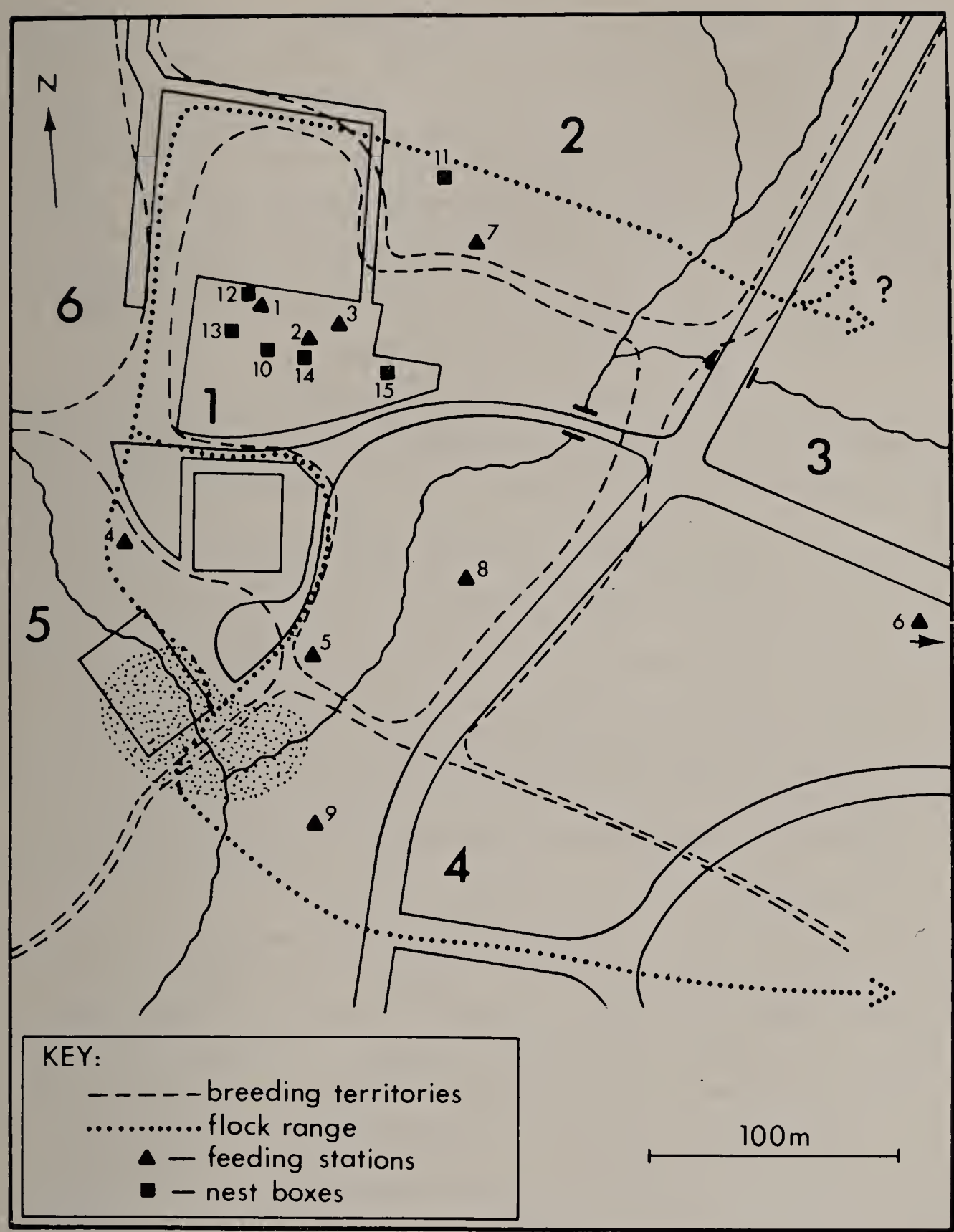



Fig. 1.2. Western two-thirds of Apple Bough flock range and boundaries with other flocks. The Apple Bough Flock range originally included feeding station no. 4, but later this station was relinquished to southern birds. Pair 3–3 nested in box no. 10 and Pair 6–5 in box no. 11. The breeding territories (large numerals) are: no. 1, Pair 3–3; no. 2, Pair 6–5; no. 3, Pair 7–4; no. 4, Pair 8–8; no. 5, Pair 9–6; no. 6, a pair to the west of the study area; stippled area, Pair 2–4.

Each individually recognizable bird was assigned a number, e.g., M1, M2, etc. for males and F1, F2, etc. for females; U1 was a color-marked bird which could not be sexed on the basis of its behavior. Five of nine males were not color-marked but they were recognizable

by persistent association with other individual(s), a particular area, or a combination of these clues. However, M4, an unbanded bird who was active during the autumn and then disappeared, could have been identical with one of four unbanded males identified during the spring. One female was unbanded but was paired and on territory during the spring. Other unbanded individuals were seen, especially during the autumn, but could not be individually identified by their behavior. Pairs were designated by the number of the male, followed by the number of the female. For example, M2 and F2 formed Pair 2–2 and M2 and F4 were Pair 2–4.

### *Methods of Laboratory Analysis*

Vocalizations were recorded in the field with a Nagra IIIB tape recorder and Sennheiser 404 cardioid condenser microphone with windscreen. Whenever possible details of behavior were observed through 8×40 or 10×40 binoculars. An aluminum mount was frequently employed to fasten the microphone to the center post of the binoculars, aligned along the axis of the binoculars. In this way I could manage simultaneous tape recordings and detailed observations. The cardioid microphone is most sensitive to sounds directly in front. It will record less loudly, but with good "flat" response, sounds coming from the sides or from behind. This means that all sounds are recorded faithfully, although sometimes not loudly. In order to obtain and preserve all possible information about the situations in which various vocalizations were used, the field recordings were accompanied by detailed verbal descriptions of the interactions, made in a low voice from behind or below the microphone. These were recorded along with the birds' vocalizations, yet rarely interfered with laboratory analysis. All recorded field notes were transcribed as the tapes were edited.

Because most Carolina Chickadee calls are rapid and complex, sonagraphic analyses are necessary. A sonagram is a printed representation of a sound, with frequencies plotted on the ordinate axis and time on the abscissa. Thus, it shows the frequency composition of a sound moment by moment through its duration. Amplitude (loudness) is represented only very roughly by the degree of blackness of the print. A sonagram permits a more objective description of calls, and is helpful in distinguishing between similar-sounding calls or between minor variations of a call. Also, when different investigators study the vocalizations of the same species, sonagrams provide an unequivocal reference point which usually cannot be matched by verbal descriptions.

Sonagrams were prepared on a Kay Electric 6061A Sona-Graph. Most Carolina Chickadee calls fall within the 85-8000 Hz limit of this Sona-Graph model. For those calls extending above 8 kHz the tape speed on the recorder providing input to the Sona-Graph was reduced by half so that the sonagrams extended to 16 kHz. Probably all

Carolina Chickadee vocalizations are under 11 kHz, and the vast majority are under 9 kHz. Finally, sonagrams can be printed with two different filters on this model of Sona-Graph. One (45 Hz) represents frequency accurately but time is "smeared"; the other (300 Hz) represents frequency less accurately but changes through time are less blurred. Because most chickadee calls change rapidly in time, the latter mode of representation was more useful in this study. All sonagram illustrations are given in the second mode.

## Apple Bough Flock

A brief description of social events and relationships through the year is provided here as background necessary to understanding the analysis of displays. Some of the information is also summarized in Table 1.1.

The study population consisted of the members of one flock and some of their immediate neighbors. The flock ranged over roughly 20 acres, including "Apple Bough," for which the flock was named. When the study began in September the Apple Bough birds were found associated, at least loosely, in three pairs: M1 with F1, M2 with F2, and M4 with F4. M4 was unbanded but is assumed, because of his persistent, amicable association with F4, to have been the same individual throughout. Several "extra" birds, some unbanded, were also seen but most were apparently temporary intruders from neighboring flocks, or were wanderers.

### *Autumn Interactions*

During September and October there was a great deal of patrolling and also many direct encounters between individuals. During October the three pairs foraged separately at times but came together as a flock at other times, especially on cold mornings. From late October through mid-November there was a marked increase in wandering among some individuals. Sometime in October M4 disappeared. F4 was absent during the first week of November but returned on November 7. F2 left the Apple Bough flock approximately October 28 and apparently promptly settled nearby in a flock to the northeast. M1 disappeared approximately October 30 and was not seen again. M2 then associated with F1; this pair established a persistent, amicable relationship. Although the flocks observed by Dixon (1963) did not change composition, the Apple Bough flock was unsettled in composition until late November, after which it remained stable.

Birds not from Apple Bough also wandered during the same period, and three of these birds joined the Apple Bough flock for the winter. These included M3 who had spent the winter of 1964-65 in the Apple Bough flock range and was banded at that time, but had not been seen since then; and F3 who was banded on 6 November 1966, and

TABLE 1.1

SUMMARY OF YEAR'S ACTIVITIES OF STUDY POPULATION

Sept.-Oct.: 3 Apple Bough Pairs: 1–1, 2–2, and 4–4.
Oct. 28: F2 last seen associated with Apple Bough Flock.
Oct. 30: M1 last seen.
Late Oct.: M4 last seen.
Nov. 1: M2 and F1 behave as pair in dispute with birds of another flock.
Oct. 30-Nov. 7: F4 missing; returns Nov. 7; attaches loosely to Pair 2–1.
Nov. 7 (approx.): Pair 3–3 begins associating with Pair 2–1 and F4.
Nov. 9 (approx.): F5 begins associating with Pair 2–1 and F4.
Nov.-Jan.: Apple Bough Flock consists of subgroup M2, F1 (Pair 2–1), and usually F4, and sometimes F5, plus subgroup M3 and F3 (Pair 3–3); subgroups travel independently through flock range part of time, join as single flock at others.
Dec. 22: F1 last seen.
Dec. 30 (approx.): F4 behaves as mate to M2.
Dec. 31 (approx.): M2 no longer alpha male; M3 now dominant; two subgroups operate as before.
Jan. 9 and 15: F2 seen behaving as mate of northern male M5.
[Jan. 16-Feb. 27: Observations suspended.]
Feb. 28: (a) F5 mated to M6 of northern flock; no longer seen with Apple Bough Flock.
(b) M2 and F4 hold very small territory in Club.
(c) M3 and F3 hold western half of flock range.
(d) Unbanded "strangers" (M7 and mate) hold eastern half of flock range.
Mar.: Pairs 3–3 and 2–4 sometimes travel as flock in Pair 3–3's territory; sometimes separate as pairs.
Mar. 22: F4 last seen with M2.
Apr. 1: F3 begins excavating nest box in Apple Bough.
Apr. 5 (approx.): F5 begins excavating.
Apr. 6 (approx.): F4 paired with widowed M7, but attempted nest probably fails.
Apr. 8: M2 last seen.
Apr. 14: F3 begins nest building.
Apr. 15: F5 first seen nest building.
Apr. 25 (approx.): F3 begins incubating.
Apr. 30: Pair 6–5's nest destroyed; pair later renests successfully north of study area.
May 26: Pair 3–3 fledges 6 young, probably 2 survive ensuing period.
June-Aug.: Pairs stay on territory most of the time; young wander more, join different family groups; adults gradually become less tolerant of young, but all birds do some wandering and territoriality is not much in evidence.

appeared at that time to be already paired with M3. In addition, an unmated female, F5, joined the flock.

### *Winter Flock*

The composition of the Apple Bough flock in winter was thus: M2 and F1 (Pair 2–1), M3 and F3 (Pair 3–3), F4, and F5. Dixon found that all flocks observed by him could be ranked in a linear hierarchy, with the exception that high ranking females often dropped in status if their males were momentarily absent. The Apple Bough flock members are listed in their probable initial rank order.

There is some question about the relative status of M2 and M3. No direct encounters were seen between these males until late December, at which time M2's mate died and he slipped noticeably in social status (see below). Dixon observed that often the beta (second ranking) male in a flock avoided using feeding stations with the alpha male; this was also the case in the Apple Bough flock. He also found that flock defense usually fell to the alpha male and sometimes his mate. Both M2 and M3 were seen engaged in disputes with members of other flocks along flock boundaries, but this may have been a consequence of the tendency for M3 and F3 to leave M2 and the rest of the flock occasionally and move through the flock range by themselves. Either male was thus likely to encounter neighboring opponents. With one exception, discussed below, no cases were observed in which both males were present when an interflock dispute started. Hence this criterion for determining the ranking of males cannot be applied. However, M2 did a great deal of patrolling while M3 did none until after M2 had changed in temperament at the end of December. Therefore, it is likely that M2 was alpha male until his mate died.

The linear hierarchy observed in Dixon's flocks and in the Apple Bough birds was apparently based both on dominance, as established by fighting, and on "deference" accorded to some individuals because of their social status. The fact that females sometimes appear to drop in rank, i.e., no longer are deferred to, when their males are absent suggests that if fights were to occur, other males would be "dominant" to the apparently high-ranking females. Such females are presumably deferred to (most noticeably around feeding stations) because of their status as mates of dominant males.

The Apple Bough flock frequently divided into at least two subgroups of constant membership. As mentioned above, Pair 3–3 often traveled separately from the rest of the flock. M2, F1, F4, and F5 traveled as another group. F5, however, was very loosely attached to the flock and was frequently seen alone. F4 often left Pair 2–1 and traveled with F5; she rarely remained alone. Neither F4 nor F5 associated with Pair 3–3 unless Pair 2–1 was also present. Dixon also observed some flocks with a tendency to splinter.

### *Unusual Change in Dominance*

F1 was not seen after the evening of 22 December 1966. It is likely that she died as a result of one (or both) of the heavy snowstorms on 22 and 24 December. On 30 December 1966, F4 was seen associated with M2; although he was aggressive towards her as usual, she was "braver" and retreated less. Thereafter F4 behaved as if mated to M2, although he still occasionally approached her aggressively. F5 followed M2 and F4 more persistently than before. F4 suddenly became very aggressive towards F5, frequently approaching closely, following closely, or even supplanting her.

In spite of the fact that M2 remated very quickly, his behavior changed markedly after the disappearance of F1. There are several indications that his social status changed from probably alpha male to definitely beta male.

First, M3, who had previously avoided direct encounters with M2, began to challenge him. When the two males, with their respective followings, were together as one flock, M3 would occasionally approach M2, forcing him to retreat slightly each time. This occurred throughout the flock range.

On 31 December 1966, M2 tried but failed to fight a male from a southern flock (probably M9) at the tennis courts in the Club. M3 then sang two feet away from M2, and challenged and fought the southern male to a draw. M2 was involved in one interflock dispute on 7 January 1967, from which M3 was absent, but M3 may simply have been elsewhere in the flock range at the time.

Finally, when the flock range was later subdivided into breeding territories, M3 took the western half of the flock range, an unbanded outside male (M7) appropriated the eastern half, and M2 was effectively dispossessed. This suggests that the temperamental change in M2 was a profound one, because Dixon had found that outside males never nested in a flock range if the flock males survived into the breeding season.

When winter observations were terminated on 15 January 1967, M2 and F4 were travelling as a pair, with F5 frequently following them. F4 was aggressive towards F5, frequently making approaches, chases, and supplanting attacks on her. The trio continued to travel alone part of the time and with Pair 3–3 part of the time. However, M3 was now alpha male.

Except for areas in the eastern part of the flock range, where observations could not be made, the limits of the Apple Bough flock range were easily determined. This was accomplished by observing where the flock was active as well as by noting the sites of disputes with other flocks. Most interflock disputes occurred at specific points rather than being evenly distributed along the entire flock range boundaries. Because relatively few individuals apart from the Apple Bough birds were banded, the number of outside flocks involved in these disputes is not known. There were at least two, and possibly three or four. Figure 1.2 shows the probable boundaries of the Apple Bough flock.

## Breeding in the Study Population

By the time observations resumed on 28 February 1967, F5 had withdrawn from the flock and was mated with M6, who took as his breeding territory the area directly north of the western half of the Apple Bough flock range. Pair 2–4 continued to travel alone part of the time and with Pair 3–3, as a flock, part of the time. Breeding

territories were already emerging but were defended only rarely in early March. The territories of M3, M2, and surrounding unbanded males are indicated in Figure 1.2.

*Pair 2–4*

The subdivision of the Apple Bough flock range into two breeding territories differed from that observed by Dixon because an outside male appropriated one territory, in spite of the survival of both males of the flock (see above). The outsider effectively dispossessed M2.

M2 sang and patrolled throughout a tiny territory in the Club during early March, but was challenged—primarily by Pairs 9–6 and 8–8—and relinquished all but the area of the swimming pool enclosure. M3 rarely challenged M2 near the pool, although he did have some mild encounters with him. Pair 3–3 confined their interests in the Club woods to the northern and eastern portions.

M2 neither sang nor patrolled as vigorously as other males. Early in the breeding season he favored six-note songs in which the first couplet was higher pitched than the following two. Later in the season he gave quavering, short Faint Songs instead of the more usual loud Song.

Pair 2–4 was unable to locate a good nest site in their territory—even when it was at its largest. F4 was seen excavating two unsuitable sites within the pair's territory; she also investigated potential nest sites in neighboring territories.

F4 was last seen with M2 on 22 March 1967. M2 remained alone on his tiny territory until 8 April 1967, after which he was not seen again. F4 was next sighted on 15 April (possibly on 6 April), at which time she behaved as if paired with M7. This male had been paired with an unbanded bird and had been observed excavating a potential nest cavity on 3 April 1967. The exact time when this female was replaced by F4 is not known. On 28 April 1967, F4 was observed giving Broken Dee with Wing Quivering (see Chapters 2 and 3), so she apparently had progressed to the stage of egg laying. The subsequent course of her nesting was not followed.

*Pair 3–3*

Pair 3–3 held most of the western half of the Apple Bough flock range as its breeding territory and nested in a box installed in Apple Bough. They laid six eggs and fledged six young, of which probably only two survived more than a few days. Most of the observations on nesting behavior were made on this pair (see below).

*Pair 6–5*

When spring observations began on 28 February 1967, F5 was completely divorced from the Apple Bough flock and paired with an unbanded male, M6, which held the breeding territory just north of

Apple Bough. F5 nested in a box on the northern boundary of the Apple Bough flock range. Pair 6–5 fought Pair 3–3 for a small "buffer zone," and Pair 3–3 relinquished about 1/3 acre to them.

F5's nest was destroyed about 30 April 1967, probably by a House Wren (*Troglodytes aedon*). Pair 6–5 renested in a more northern part of its territory and never returned to its boundary with Pair 3–3. The latter showed no particular interest in reclaiming the area it had relinquished, however.

## General Behavior in the Study Population

### *Feeding*

Winter flocks, typically of from two to seven individuals (Dixon, 1963), work through the flock range, foraging and visiting feeding stations. Winter foraging is done on bark surfaces or by clinging to small twigs and prying into buds. In cold weather the birds forage almost constantly. Foraging flocks frequently are dispersed over as much as an acre. Long movements of the group are usually initiated by one individual flying off with Lisping Tee calls (see Chapter 2). The others soon follow; the first few often also giving Lisping Tee, but the last one(s) silently.

The chickadees were observed caching sunflower seeds obtained at feeding stations. Usually the seeds were hidden unopened but occasionally a bird shelled the seed and hid only the meat. Seeds were usually put in bark crevices but were also poked into rotten logs, the broken ends of dried, hollow stems from the previous year's weeds, and among needles of Norway spruce. In one case it appeared that a seed was deposited in the upright cup of a cluster of fruits on a tulip tree. Caching was at any height from ground level to 60 or more feet.

The chickadees were seen caching seeds only from feeding stations which were *new* to them. This was done by birds familiar with the area when visiting newly erected feeders, as well as by "new" birds visiting long-established feeding stations. The caching behavior was apparently in response to an unexpected concentration of food. In this respect it is similar to the caching of natural foods seen in the Great Tit (*Parus major*) by Hinde (1952).

### *Patrolling, Mobbing, and Disputing*

"Patrolling" was one of the more conspicuous chickadee activities. It is restricted to areas where a bird has, or is making, some claim to ownership. Patrolling birds are highly vocal, and usually moving and foraging. The calls used included T-slink, Click-rasp, Chip, Song, Song Variant, and High Tee-Chick-Dee series. Patrolling birds may be alone or accompanied by a mate or other flock members, but the calls do not seem directed to one of these individuals. Most patrolling is done by males, but females occasionally have been observed patrolling.

Carolina Chickadees will approach and mob anything they apparently consider dangerous that remains near them, including people, cats, and predatory birds. The first reaction upon sighting a predator is usually High See calling. If the predator moves rapidly through the area and leaves it, the chickadees quickly quiet down, which is unlike the behavior of many other species. If the predator remains, however, the chickadees will approach and hop around it excitedly, often Wing Flicking and giving a variety of calls. If the predator remains still the chickadees may fall silent and drift away. If the predator moves it may elicit renewed vigor in the scolding or another burst of High See calling.

Defense of the flock range is accomplished by disputes along boundaries with other flocks. Dixon found that usually only alpha males, and sometimes their females, participated in these skirmishes; with the qualifications discussed above, that was true of this study population. For this reason interflock and interpair disputes are essentially similar. The two males approach one another with much calling, then often "face off," twisting and turning on their perches. They may make supplanting attacks or chase one another in close circles, but rarely engage in direct, grappling combat. Females usually stay back, each on the side of its own male, usually scolding. Occasionally a female makes an aborted approach to the opposing male, but more often she is involved in the fighting only because the opposing male attacks her, or occasionally because of a "mistaken" attack by her mate. From time to time during a fight males fly to perch momentarily by their mates and then return to the opposing male. The fight usually ends with the two pairs drifting apart, scolding. If one pair withdraws before the other it may be considered the "loser." Very rarely an individual is defeated so badly that he crouches and Wing Quivers before his opponent before withdrawing.

Twice on the same day (16 September 1966) two disputing birds, apparently males, were seen to circle one another at a distance of about two feet, while flying in an upright hovering position. This fighting technique was also observed in the Great Tit by Hinde (1952).

Another sort of chasing is seen in pairs at dawn in the breeding season. Females often approach their males as they dawn sing. The male may then abruptly break off singing and chase his mate in a hard, rapid, circling fashion for several seconds. The chase ends when one mate (it was never possible to tell which) calls Variable See-T-slink (see Chapter 2). The male then usually resumes singing. Dixon (1949) observed males of *P. inornatus* chasing their mates early in the breeding season, especially following territorial disputes. Possibly such chases are common throughout the genus.

Many activities of the birds seem to serve to establish or maintain specific inter-individual relationships such as pair bonds. Another such relationship is dominance-subordinance. A dominant individual some-

times supplants subordinates at a feeder and is usually deferred to. That is, it can go to the feeder before others, or join others on a feeder, but other birds rarely join it. When a dominant joins a subordinate on the feeder the subordinate may remain, sometimes retreating somewhat on the feeder, but it does not feed until after the dominant leaves. A subordinate individual may leave the feeder even if the dominant does not supplant it directly.

Sometimes two individuals "face off" against one another, or even approach in little hops. The subordinate individual is considered to be the one which retreats. Sometimes one individual can "push" another by hopping towards it; the threatened bird retreats in advance of the aggressor. Direct supplanting is not seen so frequently, but the supplanter is considered dominant.

The various means of detecting dominance give a consistent picture of the relationships between individuals. Despite occasional reversals, the vast majority of all aggressive encounters between any two flock members demonstrate an unambiguous dominance relationship between them.

Males are dominant to their mates by any of the above criteria. As a rule, males occasionally are briefly aggressive towards their mates, but females retreat little from these attacks. Females can usually stay on a feeder with their mates, or even join their mates on the feeder, but they often defer taking a seed until the male feeds and leaves. In most pairs there is very little fighting.

### *Establishing Pair Bonds and Breeding Territories*

Very little was seen of pair formation, but apparently it consists of a female's associating persistently with a male and enduring his attacks until he accepts her presence. Pairs can form at any time of year. An observer may recognize paired birds, even when they are members of a larger flock, by their amicable and especially persistent association with one another. In the study population two pairs detected in the flock persisted into the breeding season. This is probably generally true of the species. The sexes of the members of the pair can be determined from other sorts of behavior. For example, in the Apple Bough flock two unmated females, F4 and F5, maintained a closer association with each other than with other flock members. They were judged at the time to be females and this was confirmed later when each paired with a known male.

Breeding territories are established by: (1) dawn "singing;" (2) patrolling; (3) two-pair skirmishes along boundaries; (4) increasing aggression towards fellow flock members intruding into incipient territories; and (5) gradual restriction of activities of each pair to its own territory, even though it means giving up visits to feeding stations and foraging areas in other parts of the flock range.

## *Nesting Behavior*

Only two pairs in the study area could be observed in nesting behavior, and most of the detailed observations were made on only one of these (Pair 3–3). Some observations were also made on a pair which nested in the study area in 1965. Behavior differed among the three pairs only in details.

Pairs spend approximately one month nest site prospecting. They move slowly through their territories investigating likely areas. Females may make trial excavations in several sites. One or both members of the pair may call a series of Dee notes (see Chapter 2) as they move along, the males often calling more than their mates. The male may influence the female's final choice of site. M3 visited and made Nest Site Showing displays (see below) at two boxes in Apple Bough, but never at sites in the Club. Although F3 showed considerable early interest in a stump in the Club woods, she subsequently nested in one of the boxes that had attracted her mate.

Each of the three males observed at their nests performed what is probably a Nest Site Showing display at various stages of excavation, and early in the building period. In this display males cling to the entrance of the nest, alternately poking their heads in and out of the hole, and looking back over their shoulders. One male gave Variable See calls during this; the others were silent. The male may partially or fully enter the cavity after a bout of "looking." Females frequently then work on the nest or excavation. Copulation has not been seen to follow a Nest Site Showing display.

At two of the three nests observed, males actively excavated the nest cavity, often taking turns with their females to enter, work, and bring out bits of wood. The third male rarely entered his nest cavity; he brought out one shaving following a Nest Site Showing display but was never seen excavating again. None of the three males was observed nest building; this is also characteristic of the Chestnut-backed Chickadee, *P. rufescens* (Williams, *in litt.*). The male which did not excavate once brought a bit of plant down near to the nest but dropped it after a moment. The nests were made of moss, dried grass, plant down, animal hair, and occasionally tiny bits of wool yarn. In the two boxes which could be opened for inspection the part of the nest immediately surrounding the eggs was constructed almost entirely of animal hair. One nest had a large flap on a side which was sometimes folded over the eggs when the female left; the other nest could not be seen well enough to know if it too had a flap.

During egg laying the females foraged constantly and also begged food from their mates. Begging females called Broken Dee notes nearly continuously (see Chapter 2). They sometimes Wing Quivered, especially when the male approached to pass food, which was accomplished

bill-to-bill while facing one another directly or nearly directly. Males accompanied their begging mates almost constantly, foraging actively and feeding them frequently.

Only two copulations were witnessed; a third probable copulation was not seen, but was identified by calls and circumstances characteristic of the other two. All three copulations occurred near the nest during the day—not at dawn or during the immediate post-dawn period. The females were begging when their males approached with Variable See calling and pronounced Wing Quivering. The females also Wing Quivered and possibly gave Variable See calling during the final stages of the approach. The Variable See calling of the males terminated in a series of T-slink calls at the point of closest approach, or while mounted. In one instance the male then flew away giving the Faint Song; in two other cases the males left the females silently. This is very similar to copulation sequences in *P. atricapillus,* as described by Dixon, Stefanski, and Folks (1970).

The female of the pair on which most of the nesting observations were made continued to beg whenever she was off the nest throughout much of the incubation period and occasionally after the eggs hatched. However, once incubation began the male fed her only when she was inside the nest box. He usually approached the box with Faint Songs, then clung to the entrance and passed the food to the bill of the female, who apparently rose to the entrance to meet him. This continued while the female was brooding the very young nestlings. At this stage the female usually left the nest box only immediately following a feeding. Since the male, who was a very attentive guard throughout nesting, would not go to the nest box if he saw any potential danger in its neighborhood, this was a relatively safe time for her to leave. As the nestlings grew older the female spent more and more time away from the nest, and the male entered the box to feed the young directly. At this stage the female also foraged and brought food to the young, apparently coming and going from the box independently of the male.

For the first several days after this pair's young fledged, the family spent its time in dense evergreens. Later they stayed high in deciduous trees. The young begged vigorously but fell silent if the parent scolded a "predator," such as the observer.

The 1965 nest was watched only casually, but that male also guarded. He was not seen feeding the female on the nest but is known to have entered the nest to feed the nestlings. This family was not seen immediately after fledging but later they also remained very high in deciduous trees.

### *Family Groups*

Three family groups were observed. The young continued to beg from the adults for at least five weeks after fledging, although by the end of this time they were able to forage for themselves and the adults

fed them only rarely. Families wandered throughout the flock range, but possibly this occurs only if other nests in the flock range are unsuccessful. One two-family encounter was witnessed north of the study area in 1967. The fledglings begged as the adults quarreled; then one family withdrew at least 200 feet. Such episodes may account in part for the exchange of young between families. One family in 1967 had at least one unbanded youngster, not its own, five weeks after fledging. In addition an apparent youngster was seen alone in the study area only three days later; perhaps advanced fledglings wander in and out of various "family" groups.

By mid-July adults frequently made aborted attacks on the youngsters accompanying them and sometimes left them for brief periods. Both male and female adults patrolled while away from their "families" or simply foraged quietly. At other times adults associated amicably with young of the year, even if the young gave calls typically used by patrolling or otherwise territorial birds. The youngsters foraged constantly, alternating bouts of amateur quality patrolling calls with periods of silence.

# 2

# VOCAL DISPLAYS

## Introduction

Twenty vocal displays are recognized and described. The exact number is somewhat arbitrary since the vocalizations vary and some intergrade with others to some extent.

The analysis of the vocal displays is based on detailed examination of the situations in which they are used, and the attendant behavior of the communicator. Most displays are used in a variety of situations, but each is more common in some of these circumstances than in others. Conversely, many different displays can be used in the same general kind of situation. For example, many calls are used in a dispute, but different calls are usually uttered by a bird watching the fight, a bird making an attack, or a bird retreating from an attack. The use of displays is also influenced by the past experience of the communicator and of the individuals with whom he is or may be interacting, and by how the communicator feels about his particular physical location (e.g., on a boundary, on secure territory, etc.). This was evident because most of the birds were individually marked and the progress of their interactions with one another could be followed through the year. In addition, each bird's interactions are governed to some extent by his "temperament," or "personality." This feature was not studied systematically—it would be a major undertaking to do so—but some individuals seemed unusually timid, aggressive, calm, etc. Knowledge of these "personality factors" were sometimes helpful in understanding an interaction.

Each display is treated differently in the descriptions below, depending upon its usage, and on the quantity and quality of data available. One set of behavioral categories may be useful for analyzing a given display but be uninformative for another.

For some vocal displays a tabulation was made of the number of individual events, categorized into a variety of types of situations in which the call was uttered one or more times (see Table 2.1). However, various factors limit the usefulness of such tabulations. For example, the recognition of the beginnings and endings of events is sometimes difficult when there is a lengthy period of activity involving repetition of a call. Some of the situational categories defined by behavior, e.g., fights, patrolling, etc., can intergrade; assigning events to a particular category is then occasionally somewhat arbitrary. Sometimes two calls occur in essentially the same range of situational categories, but their usage can be differentiated on the basis of finer behavioral details.

These "fine details" represent yet another set of categories. However, it is usually impractical to make exact tabulations of them because in the field it is often impossible to observe and record as much detail as would be necessary. Finally, not enough information is obtained in the field to classify some events as to the type of situation, and a sizeable number of such "unknowns" accumulates for each display. If certain types of situations are harder to recognize in the field than others, they may be over-represented in the "unknowns" category. That is, a particular display could be proportionately more common in a given category than Table 2.1 indicates. For this reason, comparing the relative frequencies with which one display is used in different situations is less meaningful than comparing the use of different displays in a single situation.

The vocal displays were named with descriptions or phonetic representations of their sounds. Names referring to message, meaning, or function were not used in order to avoid prejudicing both present and future analyses and comparative work.

In the following discussion messages and meanings are sometimes phrased in the first person, as if the mood of the communicator or recipient could be paraphrased in English. For other displays the messages and meanings are not, or not yet, amenable to such simplified expression, and are specified by a summary description of the circumstances in which the displays are used and the subsequent activities of communicator and recipient. In this analysis "meanings" are taken to be the actions of the recipients. However, it is often more enlightening for the reader if the situation is assessed from the point of view of the recipient and his projected action stated as a hypothetical "premeaning," from which the meaning is obvious. The paraphrased messages, meanings, and premeanings are *not* intended to imply that chickadees perform such reasoning—merely that they act as if they had done so, or had done some functional equivalent.

The displays are presented in the following message categories: attack, bond-limited, association, and escape. Although the displays in each category have one message in common, they differ in the probabilities and in the accompanying messages. The groupings are necessarily somewhat arbitrary, since they could have been made for some other set of message categories. This arrangement was chosen because it emphasizes the importance of these messages in the repertoire as a whole. This is discussed further in Chapter 4.

## Displays

### *Displays Encoding Attack and Other Messages*

This section includes one group of vocalizations that are related in form (T-slink, Click-rasp, Slink-rasp and Tee-rasp), plus one other un-

related vocalization (Chip). Each vocalization encodes attack as a likely activity, but each differs in the probabilities and alternative activities specified. Because Chip encodes escape as the alternative to attack, it could have been grouped with the displays encoding escape. But disputes so often follow Chip calling that it seemed more appropriate to discuss Chip in this section.

### 1. T-slink

*Form:* T-slink calls comprise a series of very short notes in rapid succession ("T"), followed by a longer, clear "slink", and sometimes by a second, faint, very high-pitched (frequency over 8 kHz) clear note (Figs. 2.1A, B, C; 2.2A, B). Both clear notes are flattened chevrons. Frequently a second T-slink immediately follows the first; the stuttering introductory portion of the second one is usually abbreviated. Three or four successive T-slinks are not uncommon, and strings up to eight have been recorded rarely. The pitch of the "slink" portion of successive T-slinks may go up, down, or stay the same. The form of both the introductory series and the slink notes is variable. The use of variants by different individuals is discussed in Chapter 4.

*Usage:* The situations in which the T-slink, Click-rasp, Slink-rasp, and Tee-rasp calls were used are summarized in Table 2.1. The categories were selected to facilitate comparisons between different calls.

The following is a list of uses of T-slink, illustrated by examples drawn from Apple Bough chickadees in 1965-67. Some categories in this list differ slightly from those in Table 2.1, since they were designed specifically for the analysis of the T-slink call.

1. Toward potential predators.

Example: On 11 September 1966 an unidentified chickadee directed T-slink calls at a person removing another bird from a mist net. The chickadees were not often observed reacting to predators.

2. Toward non-predatory birds of other species.

Example: On 30 September 1966, M1 was displaced from a feeding station by a House Sparrow (*Passer domesticus*). M1 retreated to a nearby tree and gave T-slink calls while facing the sparrow, but waited until the sparrow had left the feeder before returning to it.

Example: On 22 December 1966, M2 was persistently bothered by an aggressive Tufted Titmouse (*Parus bicolor*). M2 retreated when approached, then gave T-slink calls and approached the titmouse, but retreated again when it in turn approached him. This usage was rare.

3. By individuals not pressing an attack, in agonistic encounters involving two or more birds. Subjects of attacks made with T-slink calls typically retreat only slightly. In eight disputes attacks were associated with T-slink calls; at least three of these attacks were made by males on females that were known to them.

Example: On 10 March 1967, M3 threatened Pair 2–4 in Apple Bough with T-slink calls. At this season M3 was probably experiencing the conflicting tendencies of whether to accept their presence as flock-mates, or whether to drive them out of his breeding territory.

In another five cases T-slink was used by onlookers of a fight; three were known to be females. Although females sometimes show aggressive tendencies they rarely take initiative in a dispute. Typically they remain at a distance, often scolding with High Tee series (see below).

Example: On 19 April 1967, Pair 3–3 squabbled with M7 at a boundary point. F4, newly mated with M7, once closely approached the dispute, but retreated and gave several T-slink calls.

The use of T-slink in territorial disputes was very common.

4. In two-bird encounters between flock- or pair-mates, territorial rivals, and members of different flocks. Of the 19 events in this category listed in Table 2.1, eight were known to involve members of a pair; attack occurred in none of them. At least two others involved members of the same flock; supplanting attacks occurred in both these events. When confrontations occur between pair- or flock-mates the inhibition to attack probably often stems from a tendency to accept the presence of the other individual. The caller must often know, where the relationship is well-established, that the other bird is not a very threatening opponent. In at least one case an attackee used T-slink, apparently as a defensive threat. In some cases where no attack occurred in a confrontation, T-slink may have been used by the potential aggressee.

Example: On 24 October 1966, M2 threatened his subordinate flock-mate F4 with T-slink. She hesitated but did retreat. Again on 11 November 1966, M2 threatened F4 several times, using T-slink. She retreated only slightly.

Example: Members of Pair 2–2 were observed using T-slink toward each other on feeding stations during October, just before F2 left the flock. After her departure M2 mated with F1. On 1 November 1966, early in their paired relationship, M2 directed a T-slink call towards F1 as she approached him; no attack followed.

5. Between pair members during a precopulatory advance and during copulation. In this situation it is preceded by Variable See calling, indicating the simultaneous presence of tendencies to escape and bond-limited behavior (see below).

Example: While F3 was nest building and egg laying, M3 began to use Variable See-T-slink in his dawn calling and during the day as he followed F3's activities. In the copulations that were witnessed, each mate approached the other with Variable See calling and Wing Quivering and the male gave a T-slink at some time during his closest approach to the female, i.e., either just before, during, or just after mounting. No overt aggression followed these copulations, although it is known in many other species.

6. By adults importuned by begging fledglings, perhaps only after the young begin to be independent.

Example: On 6 July 1965, long after the young had fledged, a female fed a persistently approaching fledgling but used broken-sounding Variable See-T-slink (see section on Variable See), probably just before feeding, and then several T-slinks just after feeding.

7. In patrolling. T-slink is a common part of standard patrolling repertoire throughout the year, used by birds patrolling flock or pair territories when alone, with a mate, or in a group. In the last case, usually only one bird (the dominant male) calls, generally while foraging and not performing any other socially relevant actions. Flock- or pair-mates forage quietly near the calling bird and do not seem to avoid it. Patrolling males which were calling T-slink were seen to threaten their companions only three times, twice with supplanting attacks, one of which was on mature fledglings. As is usual for attacks made with T-slink calls, retreat was slight.

*Message:* The message encoded by T-slink is that the calling bird may attack, but the bird also has conflicting tendencies which usually inhibit that behavior.

The call does not state the causes of either the attack tendency or the inhibition. The aggressive tendency of the caller may derive from a mood to patrol some area that he considers his territory, to rebuff a close approach by another chickadee, to defend his position against some other bird at a feeding station, or to mob a predator. However, the bird is at the same time tending toward another sort of behavior, such as retreat, copulation, feeding the young, or accepting the association of another chickadee as a pair- or flock-mate. Since there may be some degree of escape tendency in virtually all close approaches between chickadees, this call is probably agonistic in all its uses, even when the *primary* conflicting tendency is not escape.

Except in the case of chases between members of a pair during the breeding season, T-slink calls are usually not associated with attack, even if the communicator approaches. Attacks which do occur are typically aborted, or very mild, and the aggressee usually retreats only slightly. Apparently the attack tendency rarely fully overrides the conflicting tendency.

*Meanings and Functions:* The meanings and functions that T-slink may have for other chickadees probably relate to the following: (1) T-slink directed at a predator or other species probably alerts recipients; (2) when T-slink is used in fights the recipient can retreat slightly, remain in position, or rebuff the aggressor with a mild threat; these choices are made in different contexts, and depend upon the relationship between the aggressor and aggressee; (3) when T-slink is used in patrolling, the presence of a member of his group (flock or pair) will be accepted while an intruder should anticipate a challenge.

### 2. Click-rasp and Two Related Vocalizations

*Form:* Click-rasp is a variable call, but all variants comprise a stuttering introduction of very brief notes followed by a "rasp" note

TABLE 2.1
SUMMARY OF EVENTS IN WHICH T-SLINK, CLICK-RASP, SLINK-RASP AND TEE-RASP OCCURRED

| | T-Slink | Click-rasp | Slink-rasp | Tee-rasp |
|---|---|---|---|---|
| Patrolling alone | 11[1] | 19 | 3 | 0 |
| Patrolling accompanied by mate or flock-mate(s) | 12 | 14 | 4 | 1 |
| Patrolling; unknown if alone or accompanied | 10 | 5 | 0 | 0 |
| Patrolling, moving toward a dispute | 2 | 0 | 0 | 0 |
| Subtotal: Patrolling-related incidents | 35 | 38 | 7 | 1 |
| During a brief 2-bird face-off | 19[2] | 25[3] | 7 | 5[4] |
| During a longer dispute | 33 | 46 | 16 | 15 |
| Withdrawing in apparent patrolling mood after dispute or 2-bird encounter | 11 | 8 | 1 | 1 |
| Subtotal: Dispute-related incidents | 63 | 79 | 24 | 21 |
| Male defending or guarding nest area | 0 | 7 | 1 | 0 |
| Adults with advanced fledglings | 2 | 4 | 2 | 0 |
| "Patrolling" juveniles, alone or with family | 3 | 3 | 1 | 0[5] |
| Other | 7 | 4 | 1 | 1 |
| Unknown | 59 | 58 | 7 | 19 |
| Fraction of *known* events in disputes or 2-bird face-offs[6] | 52/110 —.47 | 71/135 —.53 | 23/36 —.64 | 20/23 —.87 |
| Fraction of *known* events in patrolling by adults | 35/110 —.32 | 38/135 —.28 | 7/36 —.19 | 1/23 —.04 |

[1] Numbers refer to number of different events in which these calls were used—not the number of times each call was uttered.
[2] At least 8 between mates and at least 2 others between flock-mates.
[3] Eight occurred during course of longer disputes in which Click-rasp was also used at other times.
[4] Three, possibly 4, between mates; 1 occurred during course of a longer dispute in which Click-rasp was also used at other times.
[5] Possibly 1.
[6] Some disputes were very brief face-to-face encounters between two individuals; others were longer, involved two or more individuals, and combinations of hopping about, facing-off, approaching, supplanting, chasing, and direct combat. In some cases in Table 2.1 direct face-to-face encounters occurred during longer disputes; if calls occurred in both, they are counted in both (see footnotes, above). Note that some instances counted under longer disputes might have been classified as direct face-to-face encounters had more detail been observed.

with rapidly oscillating frequency. The brief introductory notes vary in number, form, and frequency. The rasps vary in length, frequency, and rapidity of frequency oscillation. Frequently the latter two characteristics change within one rasp. For example, a very common variation is for a higher-pitched, rapidly oscillating, nasal-sounding rasp to drop to a lower-pitched, less rapidly oscillating, harsh-sounding rasp. Several variants are illustrated (Figs. 2.2C, D; 2.3A, B, C; 2.4A, B, C, D). The significance of the variability of Click-rasp and some other calls is discussed in Chapter 4.

One variant, called Tee-rasp, has relatively long and high-pitched

introductory notes ("tee" rather than "t"). Because of its distinctive sound it was recognized very early in the study and treated separately from other Click-rasps. Tee-rasp is much less variable in form than are other variants of Click-rasp (see Figs. 2.5A and B). Because of the scarcity of data on Tee-rasp, and its rather close similarity in form to Click-rasp, it is not regarded at the present time as being a distinct display.

Slink-rasp (sometimes Rasp-slink) is a composite of T-slink and Click-rasp calls. All components of it also occur in T-slinks and Click-rasps (see Figs. 2.5C and 2.6A, B). It is here regarded as an intermediate to these two displays rather than as a separate display.

*Usage:* Click-rasp is used primarily in patrolling and in two-bird confrontations and other disputes. As shown in Table 2.1, Click-rasp has a range of usage generally similar to that of T-slink. However, they are distinguishable on the basis of other details.

In disputes T-slink is frequently used by females or other onlookers, or by a direct disputant making relatively weak attacks on not very threatening opponents. On the other hand, Click-rasp was used in disputes 20 times by males who were direct disputants and nine times by direct disputants of unknown sex. In five cases it was used by females, sometimes with attacks, but these were all cases when the females were near their nests or near potential nest sites of interest to them. In these circumstances females are sometimes even more aggressive than their mates.

In two-bird confrontations, six cases of Click-rasp are known to have been between pair members and an additional seven between flock members. Only three cases are known to have been between members of different flocks, but these interactions were more typically generalized disputes (in which the use of Click-rasp was common), with close confrontations between opposing males occurring relatively rarely.

Click-rasp was also very common in patrolling. As with the use of T-slink, males calling Click-rasp while patrolling rarely attacked their companions (two cases of attack were observed; one of these was on mature fledglings). Click-rasp was sometimes used with lengthy Variable See prefix in dawn patrolling, but was less common than T-slink in this situation. It was never observed as an accompaniment of copulation.

Slink-rasp and Tee-rasp were used relatively rarely, but in the same spectrum of situations as T-slink and Click-rasp. Slink-rasp was apportioned among situations similarly to T-slink and Click-rasp. Tee-rasp was used relatively rarely by patrolling chickadees; its primary use was in disputes and direct two-bird confrontations, and most of the latter were squabbles between members of a pair. The extent of the difference between Tee-rasp and Click-rasp may have been somewhat obscured since Tee-rasps were probably occasionally misclassified as Click-rasps in the field. Insufficient observations were made on the

details of the behavior surrounding either of these calls to contribute to their interpretation.

*Messages, Meanings, and Functions:* Click-rasp appears to encode an aggressive tendency, but its usage suggests that the probability of attack is higher than is the case for the T-slink call.

Different messages cannot be stated for Slink-rasp and Tee-rasp without more detailed information on their use. Slink-rasp, being intermediate in form between Click-rasp and T-slink, may have an intermediate message, i.e., the encoded attack tendency, or the conflicting tendency, or both, may be intermediate to those of T-slink and Click-rasp. The relatively frequent use of Tee-rasp in squabbles between paired birds and its nearly complete absence when patrolling suggest that it may encode a mood of "defensive aggression." That is, the communicator will fight if attacked, but is unlikely to initiate a dispute. Of the five instances when Tee-rasp was observed in two-bird confrontations, attack occurred only in the one case which was probably not between paired individuals (it was probably between two males).

There was usually no attack on "bonded" individuals by patrolling males, regardless of whether they called T-slink, Click-rasp, Tee-rasp, or Slink-rasp, in spite of the fact that other features in the use of these calls suggest that they encode aggressive tendencies. For all four calls only five cases of attack on companions were observed; three of these were on mature fledglings. A tendency for adults to be aggressive toward fledglings is commonly observed. As the summer progresses adults probably become increasingly ambivalent between accepting the presence of young birds as "family members" and regarding them as importunate intruders. That the aggression encoded by these calls during patrolling is not directed at bonded companions is also shown by the fact that each of the calls is about equally common, whether the males are patrolling alone or are accompanied.

The meaning of these displays used by a patrolling individual must, therefore, vary with the recipient. Actual or potential intruders, e.g., individuals from neighboring territories or flock ranges, or wanderers, can anticipate attack with a high degree of certainty if they enter or remain in the vicinity of the calling male while, on the other hand, "bonded" individuals can at the same time forage near him unmolested. Likewise, the meaning in other situations may be retreat, appeasement, or counterattack, depending upon the identities of the caller and the recipient, and upon the situation at hand.

Click-rasp appears to function in patrolling as an assertion of dominance in a social structure and as a means of claiming ownership of a territory or flock range. As a means of threatening attack or counterattack it assists in the establishment and maintenance of flock structure, in the maintenance of territorial boundaries, and in nest defense. Slink-rasp probably functions in much the same way. If Tee-rasp does

encode defensive aggression, it probably serves to avert attacks between known individuals, thus aiding in maintenance of established relationships.

### 3. Chip

*Form:* Chip notes are chevrons with harmonics. The first harmonic has a slightly heavier emphasis on the descending arm and falls within 2–5 kHz. The next harmonic above it has a strong ascending arm and usually no descending arm; it falls within 3½–6½ kHz. Frequently another harmonic with only an ascending arm is faintly seen above the second. Its lower limit is about 5 kHz and it extends to or above 8 kHz (see Fig. 2.10A, B). This Chip sounds remarkably like the "chip" call of the American Robin (*Turdus migratorius*) and was formerly named Robin-like Tee (S. T. Smith, 1968).

Chips were nearly always given in series of 3–6 notes, and they were always loud. High See calls were often used before or after Chip notes, sometimes even as a direct prefix to them. Loud Tee was sometimes used during bouts of Chip calling but was rarely a direct prefix to a Chip series.

*Usage:* Most Chip series were given on alighting from a flight or hop. Of the remainder, about half were given from perch and half in flight. When High See notes prefixed a Chip series they were usually uttered in flight, just before the bird touched down. However, the High See notes sometimes began on touchdown.

Thirty-seven events in which Chip was used were observed between 16 September 1966 and 8 April 1967, but often more than one call or series was given in each instance. The events fall into the following categories:

1. Interflock disputes occurring at conventional dispute sites or areas (seven observations).
2. Birds patrolling their own flock range, but approaching or entering one of the interflock dispute sites (four observations; one was a female, F4).
3. Males patrolling within their flock range. These were all males that were dominant, or perhaps were trying to establish dominance, as follow: three cases, M1 up to 30 September 1966; three cases, M2, 14 October-15 November 1966; two cases, M3, 31 December 1966-2 January 1967 (eight observations in all).
4. Disputes by two males or two pairs of which four or possibly five involved birds from two flocks (seven observations; the large proportion of interflock disputes is probably due in part to the fact that only one male in the Apple Bough Flock was a successful breeder).
5. Predator mobbing (three observations; two of these were directed at the observer).
6. Miscellaneous situations, as follow: one by M3 rapidly

approaching his nest box which F3 was beginning to excavate, but probably this was a mistaken attack-approach and no encounter materialized; one by F1, patrolling the north end of the Club woods, apparently alone, provocation unknown; two in disputes not known to involve two males (four observations in all).

7. Circumstances unknown (four observations).

*Message, Meanings, and Functions:* In all of the circumstances listed it is very likely that the caller had some attack tendency, but the fact that Chip was often given on landing during an approach to a dispute or potential dispute suggests the presence of at least a momentary hesitation. The hesitation was probably due to a simultaneous escape tendency. The frequent use of High See with Chip is consistent with this interpretation.

The message of Chip is somewhat similar to that of T-slink. For the latter, however, the primary tendency conflicting with attack is not always escape. Another difference between the two may be in the "strength," or "level," of the conflicting tendencies. Probably they are both much higher for the Chip call, because it is used so often in circumstances where the outcome may be a serious dispute with important social consequences. For example, many instances of Chip calling were related to actual or potential disputes between males from different flocks. It is unlikely that these males avoid or appease one another, as is often the case with males within flocks. Males probably also anticipate difficult encounters at times when they are establishing their alpha position in the flock. All cases of Chip given by known males patrolling within their flock range (M1, M2, M3) were by individuals establishing or trying to establish such dominance.

Females probably use Chip only at times when for some reason they feel unusually strongly motivated to undertake territorial defense, as it was used solely when they were alone. The circumstances leading to Chip calling are not known, but it is possible that the females had encountered intruders during the absence of flock-mates.

Chip is probably directed to a select group of recipients—those whose position and status dictate that they must respond to a challenge. To these recipients, at least, it must be a strong threat even though Chip is rarely given during attack.

Chip probably alerts mates or flock members to important fights. Mates, and possibly other birds, would doubtless join or follow such a fight. Since Chip is restricted to use in situations that are very important to the caller in terms of his status and territorial holdings, it is likely that its use helps to establish certain social conventions, such as identifying the alpha male both to flock members and to the alpha males of surrounding flocks. (In the absence of the alpha males other individuals apparently can temporarily assume his role, as in the case of Chip calling by females.)

### *Displays Encoding Bond-limited Behavior and Other Messages*

Displays in this section fall into two groups. Song and three Song-like vocalizations comprise one group; they are related to one another in form and usage. Two of these vocalizations encode agonistic (primarily attack) tendencies, as well as bond-limited tendencies. The second group comprises Variable See and Broken Dee. In form and usage they are related to each other, but not to the Song group. Variable See encodes agonistic (primarily escape) tendencies as well as bond-limited behavior. Both groups of these vocalizations are used primarily in the breeding season when the bond-limited behavior is related to nesting and raising young.

4. Song; 5. Song Variant; 6. Faint Song; 7. Faint Song Variant

*Form:* The vocalization commonly recognized as Song in the Carolina Chickadee is a clear, high-pitched call in which higher and lower notes are always alternated. The higher notes usually fall between 6 and 7½ kHz, the lower notes between 3 and 4 kHz; occasionally very high-pitched Songs extend to 8 kHz, or higher.

The notes themselves are usually flat, although a very brief slide in pitch sometimes occurs at the beginning or end of a note (see Fig. 2.7A). Songs nearly always start with a higher note; they usually have four or six notes, but from two to eight notes have been recorded in the study population. Very rarely one clear Song-like note is heard—these may be one-note Songs. Sometimes the first lower note is higher pitched than succeeding low ones, or whole bouts of lower pitched Songs may be followed by bouts of higher pitched Songs.

All males used several variations of Song but showed preferences, in some cases very marked, for one variation. For example, M2 gave many six-note Songs in which the first lower note was higher pitched than the succeeding ones. A male in the study area in 1965 frequently sang low- and high-pitched four-note Songs, sometimes stringing them together without interruption.

The display called Song Variant is not simply a variation of Song. It has a different usage and, therefore, encodes a different message than does Song. Song Variant can be distinguished in form from Song in that, first, the higher notes tend to slide upward in frequency from beginning to end and, second, the alternation of higher and lower notes is imperfect or lacking. Many variations in the pattern of alternation have been recorded from the study population. Using "H" for high and "L" for low notes, the following is a list of common Song Variant patterns: HHLL, HHLLL, HLLH, and LLL. Many other patterns have been heard and recorded. Even in the rare cases where most of the Song Variant alternates high and low notes (e.g., HLHLL) there is still the sliding frequency of the notes. Song Variant has the same frequency range as Song, except that very high-pitched Song

Variants have not been heard. As with Song, each male used several patterns but definitely had favorites (see Figs. 2.6C, 2.7B, and 2.9B).

In certain circumstances chickadees give both Song and Song Variant very faintly. Because of their distinctive usage these have been separately named Faint Song and Faint Song Variant. In form the faint calls are nearly identical to loud Song and loud Song Variant, except that (1) they are usually shorter (have fewer notes), (2) they often quaver slightly, (3) they are often prefixed by Lisping Tee notes, and (4) they have never been heard to be as high-pitched as the highest loud Songs (see Figs. 2.8A, B; 2.9A).

*Usage:* Song is used primarily by patrolling males in the spring. Its most conspicuous use in patrolling was in "dawn singing" by breeding, territorial males. Such males moved about their territories giving Song and Song Variant, as well as T-slink, Slink-rasp, and Click-rasp. They were alone at first light, although toward the end of the dawn singing period they were sometimes joined by their mates. Later in the day they gave additional Song as they travelled about with the females. Frequently two, or even three, males countersang; boundary disputes often followed.

Although Song often was a prelude to a fight, it was rarely used during a fight, and then never directly during an attack. It was used only before or after a chase or combat, during a lull in the fighting, or as males hopped around one another. It was also relatively rare for Song to be used as a fight was being resolved and the disputants were withdrawing. Well-developed countersinging was almost never heard at the conclusion of a fight.

Males often sang near the nest site as their mates excavated or built. M6, however, never sang in the vicinity of his nest, which was very near a boundary. Males did not use Song close by the nest except sometimes during dawn singing, but Faint Song was commonly used at the nest (see below).

The use of Song during the autumn and winter was relatively infrequent but essentially similar to that of the spring, viz., sometimes in patrolling, rarely in direct confrontations. Songs in the autumn and winter often were rather quavering and faint; probably many approached true Faint Song.

Females used faint two-note Songs on at least four occasions. F1 and F4 were each observed patrolling alone using some two-note Song. F1 and F2 also used two-note Songs as they faced intruders without their mates. Neither female really challenged the intruders, although both seemed very disturbed by them.

M1 also gave a rather faint two-note Song, with Bill-up and Wing Droop, in a direct, close, standoff encounter with an unbanded bird (possibly M2).

It is possible that many of the "rather faint" songs used by many birds which sing in the autumn and winter, and by females and

intimidated males at any season, are, in fact, Faint Songs. Another possibility is that the loud and faint song versions intergrade with one another. No attempt was made to measure the loudness of song utterances; the vast majority were conspicuously either loud or soft.

Song Variant was used much less frequently than Song and was very rare in the autumn and winter. It was used primarily in patrolling and countersinging, and was sometimes followed by a bout of T-slink calling. Song Variant sometimes preceded disputes but was never used during or following one. In one interesting case, M3 sang and approached a site of frequent boundary disputes. However, the neighbor, M9, did not answer and probably had recently disappeared. M3 changed to Song Variant as he approached the boundary and then intruded into the other territory a short distance. After a minute or two he withdrew and changed to Song again. In a unique use, M1 gave two very loud Song Variants after spending perhaps a minute or more trying unsuccessfully to find the entrance to a trap in which he could see sunflower seed bait.

Faint Song was used primarily in the breeding season and mostly by males. They gave it as they foraged and moved to and from their begging mates, and while approaching the nest entrance to feed the female as she incubated or brooded young. Faint Song Variant also was occasionally used in the latter occasion. Once M3 was observed giving Faint Song Variant as he approached his nest box with a tuft of down. F3 was inside the box and had just taken in some plant down; M3 dropped his and left. M3 never excavated or built in earnest; his approach with building material may have been a kind of Nest Site Showing display. The male observed in 1965 also gave Faint Song Variant while clinging to his nest entrance; he was almost certainly disturbed by the observer's presence. Males also gave Faint Song while moving around young fledglings; there is some possibility that females also gave it in these circumstances.

A single unbanded bird, probably M6, used Faint Song while approaching a dispute between two families that occurred just outside his territory. He stopped short of the fight and continued to give Faint Song. One pair eventually withdrew from the dispute and briefly challenged the Faint Singing onlooker with T-slink calls, but this situation did not develop into a real fight. M7 occasionally used Faint Songs when moving with his mate near his boundary with M3. This may have been another case of "pseudo-patrolling," or the pair may have been near their nest site, which I never definitely located. Finally, M2 frequently used Faint Song at dawn, especially near the end of his tenure on his tiny territory. He was not known to give Faint Song Variant under these circumstances, however.

*Messages, Meanings, and Functions:* Song identifies the caller as a breeding or pre-breeding individual, prepared to undertake territorial defense and to interact suitably with mate and family, i.e., it indicates

a readiness to perform agonistic and bond-limited behavior. The specific behavior that the caller next engages in is probably governed to large extent by how the situation develops, but it is selected from behaviors characteristic of breeding (or pre-breeding), territorial individuals. Song is used occasionally outside of the breeding season, but it is possible that territorial defense (of the flock range) and the presence of a mate are sufficient to put a chickadee into the appropriate mood even in autumn and winter. This may be especially true of Carolina Chickadees since flock range and breeding territory are so often the same.

It is possible that short and odd-numbered Songs indicate the presence of a hesitation or conflicting tendency or that the caller is close to the threshold for singing, but insufficient evidence is at hand to decide this question. If it is the case, however, such Songs should be followed by the start or cessation of full singing (i.e., be more prevalent near the beginning or end of the dawn singing period) or by some other activity—perhaps just flying to another area, or moving more frequently between Songs, or perhaps joining a dispute.

Song Variant carries a message very similar to Song, but probably indicates that the bird is also thwarted and perhaps tending towards an aggressive mood. Its nearly exclusive use in patrolling, and absence from disputes, suggest that the caller is anticipating a territorial interaction that is not materializing. The communicator is thwarted if the other male does not answer or if he continues to sing from a distance but does not approach and fight (at the same time the Song Variant singer cannot cross the boundary to engage the other male). There are no data to determine whether Song Variant is also used when the male is thwarted from interacting with the female, such as might occur if she were absent temporarily or permanently. Mate chases during dawn singing followed both Song and Song Variant.

Song Variant is similar in many regards to the Tumble Flight Display of many flycatchers of the genus *Tyrannus* (see W. J. Smith, 1966). Tumble Flights express the mood of a frustrated fighter, and in many species the vocalizations used during them are derived from their most Song-like call ("Rapidly Repeated Vocalization"), or a call which is given by birds losing a fight, or from both.

Faint Song and Faint Song Variant probably express messages differing from their louder counterparts in that apparently they are directed specifically to females, or to females and young. The accompanying behavior is chosen from the repertoire of breeding, territorial males which are concerned primarily at that moment with mate and family.

This may explain their use by "intimidated" males. For example, M2 often used Faint Song and Faint Song Variant near the end of his stay on territory—he was so intimidated by that time that he was only willing to behave as a breeding male toward females and apparently was

avoiding encounters with other males. M7's occasional use of Faint Song when he was near his boundary with M3 apparently indicated to his mate that he was in the mood of a breeding male, but by its use he avoided advertising that same information to M3. Similarly, M6's use of Faint Song while watching a dispute beyond his boundary may have reflected his reluctance to engage in the fighting unless it drifted into his territory. Birds which use Faint Song in direct confrontations may be potential losers attempting to escape their opponent's aggression by emphasizing bond-oriented behavior.

The data on Faint Song Variant are few. By comparison with the other song versions it might be expected that it encodes a thwarted tendency to engage in mate- and family-oriented behavior. Its use by males approaching their nest cavities may have been because of the observer's presence, which had the potentiality of thwarting their trip to the nest.

It should be noted that Carolina Chickadee Song differs from the Song of many other passerines in that it apparently contributes little or nothing to attracting a mate. Pairing occurs at all seasons of the year, including those in which Song is rarely used. It probably does aid in maintaining a pair bond, or in some way indicates to the female that the situation is right for proceeding with nesting activity.

Dixon and Stefanski (1965, 1970) studied the use of Song by Black-capped Chickadees; it is very similar to Song usage by Carolina Chickadees. Aspects of Song held in common by the two species include: (1) frequent use in patrolling but infrequent use in disputes; (2) use in countersinging preceding disputes; (3) use to indicate readiness to defend an area; and (4) its use is not a prerequisite to pair-formation, which often occurs before the season when song becomes common.

Data were not presented by Dixon and Stefanski on the use of "phoe-be" as opposed to "phoe-be-be", so it is not clear whether Black-caps use these as equivalents of the Song and Song Variant displays of the Carolina Chickadee. They did remark (1970, p. 60), however, that at times "we gained the impression that males were 'seeking' song exchange." This is a situation which could be thwarting if the neighboring males proved to be absent or indisposed to sing. The absence of bonded individuals, especially mates, also stimulated males, and sometimes females, to sing—another situation where the communicator is thwarted, this time from engaging in bond-limited behavior.

There is a possibility that the Song display of the Carolina Chickadee also encodes a low level of frustration, but my observations do not make this point clear. It is possible, for example, that even a male singing in the presence of his female can be thwarted because she is not proceeding to some bond-limited behavior other than simple association (e.g., nest site prospecting). Or, perhaps, the male is not only "ready" to perform agonistic behavior, but also frustrated because no territorial encounters materialize, or because his mate seems unwilling

to accompany him to a boundary. (I often gained the impression that males were more timid in disputes when their females were not present as onlookers.) The available data are not adequate to settle this question.

### 8. Variable See

*Form:* Variable See is made up of a series of rapidly repeated chevron-shaped notes, most of which peak well over 8 kHz. Usually the chevrons are simple, but occasionally they have two or more peaks. In rare instances the peaks separate completely into narrow chevrons which are uttered in couplets or, occasionally, singly or in triplets. There is also a tendency for the usual simple chevron to terminate in another narrow chevron, which often has a lower harmonic, giving the note a "squeaky-sounding" ending (see Fig. 2.13A, B). Variable See has a continuous, liquid sound, except where it has the more peaked form—then it sounds like dry chatter. Variable See sounds markedly different from High See, even though the two are superficially similar in form. Variable See differs from High See in having a higher frequency and in having the terminal narrow chevron with its harmonic.

Long series of Variable See, whether the notes are unbroken, broken, or mixed, show a rise and fall in frequency and a concomitant rise and fall in amplitude. The waxing and waning are somewhat irregular, but each wave of the higher pitched, louder calling is usually sustained longer than the lower pitched, lower amplitude calling.

Variable See series almost always terminate in one or more T-slink calls. Very occasionally Variable See series terminate in Click-rasp, or end with no other call following. Usually, if no call follows directly, the bird gives another burst of Variable See calling after a pause. After a few to several such bursts a terminal T-slink is then given.

*Usage:* Variable See-T-slink is used in (1) breeding-related situations, (2) aggressive encounters between chickadees, and (3) patrolling.

The vast majority of Variable See-T-slink utterances are given in breeding-related situations. Males begin using it in their dawn calling about the time when females begin to excavate one nest site in earnest, i.e., give definite evidence of nesting intention. Males also use Variable See-T-slink during the day, usually as they follow and watch the females excavating and building. M3 occasionally used it when his mate apparently was not present; however, possibly she was nearby but not seen by me. Males often Wing Quiver during the loudest, most "intense" portions of Variable See calling.

As F3 approached her nest box with the first load of building material, she apparently gave several brief bursts of faint Variable See. The calls possibly were uttered by her nearby mate; they are high-pitched and hard to locate, especially when faint.

Variable See calling, with Wing Quiver, is used by males and very probably also females in the final approach for copulation. The male

usually gives T-slink at some point during his closest approach to the female. F3 once briefly gave Variable See and briefly followed her mate immediately after a copulation attempt which may have been unsuccessful.

Once during the period when Pair 6–5 was excavating its nest box, the male entered the box while the female was inside. He remained there several seconds, during which Variable See calling was heard, but not T-slink. The male then left and the female remained inside the box several more seconds.

When used by a breeding pair Variable See calling was either given with no ending or was terminated by T-slink, but never by Click-rasp.

The next most common use of Variable See-T-slink was in disputes and direct aggressive encounters between chickadees. Relatively few cases were observed; it was used only by birds that were badly defeated and facing another possible attack, yet remained in the fight area rather than fleeing. Such birds also Wing Quivered when the aggressor was very near. For example, on 7 January 1967 Variable See-T-slink was used by a chickadee that was losing badly in a fight, but apparently was reluctant simply to flee. It gave several Variable See-T-slinks, retreated a short distance giving Variable See calls while in flight, gave several T-slinks after landing, then more Variable See calling (with Wing Quiver), and, finally, some prolonged High See notes. It then was attacked again.

Variable See-T-slink was also used in early morning chases between mates during the breeding season. One such encounter was witnessed on 12 March 1967 when F4 approached M2 as he sang on the south side of the Club. He chased her vigorously for several seconds and then the pair circled away from the pool and into the nearby stream valley where I could not observe them. The chase apparently ended when one of the pair gave Variable See-T-slink calls. M2 then moved to the side of the valley and resumed song; F4 was not seen. It is not known whether the pursuing males or retreating females give the calls in chases between mates.

Variable See calling, both with and without terminal T-slink or Click-rasp, was heard occasionally in disputes in September and October. The details of its use were never ascertained, partly because of the difficulties in following several active chickadees in foliage and partly because the bursts of calling were generally brief and hard to locate quickly. In one case, however, it was determined that the bird calling Variable See was subsequently attacked, but retreated only slightly.

In addition, Variable See was occasionally used by birds that seemed to be patrolling. It was heard twice from M1 during September and once from an unidentified bird (which may have been M1) on 8 October. It was not heard from a patrolling male again until early January, when M2 used it on two occasions. It is particularly interesting that

these were the periods during which each male was trying, unsuccessfully, to achieve or maintain an alpha position. M3 was not heard to use Variable See during the day until late March and early April. In none of these cases was he clearly patrolling his territory; he was probably directing these toward his mate. In one instance immediately after he gave a burst of Variable See-T-slink calling, she was seen to leave the nest box and join him.

The use of Variable See in dawn patrolling was discussed above.

*Message, Meanings, and Functions:* In all uses of Variable See the caller probably had a strong escape tendency and possibly a weak attack tendency. Close approaches between chickadees are rare, so the birds probably never become accustomed to them; agonistic tendencies are probably present even during copulation approaches. Sometimes Variable See callers openly retreated a short distance, but no cases were observed in which they attacked during or following the use of Variable See. The possible presence of an attack tendency is only inferred by the frequent use of T-slink and Click-rasp with Variable See and from the supposition that a weak attack tendency would be likely in the situations in which this vocal display is used.

It is also to be noted that most uses of Variable See are obviously "bond-limited." Specifically, most are related to nest building activities, copulation, and to associating with females during the breeding season. The use of Variable See by chickadees badly defeated in a dispute, and by males that are very uncertain of maintaining their status, also suggests a bond-limited aspect to the message of this call. Such individuals may be attempting to insinuate a bonded relationship with the chickadee to which the call is directed, thus forestalling a possible aggressive response. This may also be true with some uses of Faint Song (see above).

The overall message of Variable See is probably that the caller is experiencing a conflict between agonistic tendencies (certainly at least escape) and some bond-limited activities. In most cases the birds proceed with some kind of bond-limited activity. If the caller retreats it does so only slightly, never making an outright departure from the arena of activity, even from a fight.

A recipient may respond as if the caller poses virtually no threat to him, so that the two may proceed with bond-limited activities. Variable See probably functions primarily to forestall aggressive responses, thus facilitating copulation attempts and helping defeated chickadees to avoid further fighting.

*Broken Notes:* Variable See notes sometimes were irregular in form and occasionally broke completely into discrete subunit chevrons (see under *Form,* above). Often these occurred during long bouts of Variable See calling in which many of the notes were of the unbroken variety.

Broken notes followed by T-slink were used, for example, by the 1965 female as she was being importuned by a large fledgling. She fed the youngster, however, and did not attack him. They were also used, together with unbroken notes, by F3 as she approached her nest box with the first load of nesting material, although there is some possibility these were given by her mate, M3, who was nearby. On the following day M3 gave a prolonged bout of Variable See calling while watching F3 work about the nest. He used a full range of variation, from completely unbroken, to completely subdivided notes.

The significance of the variations in form of Variable See is not known. There may be a shift in the message concomitant with the increase in "brokenness," possibly a reduction of emphasis on the escape portion of the message. This notion is supported by the possibility that broken Varible See notes are related to Broken Dee notes through an intermediate called a "trill" (see under Broken Dee, below).

W. J. Smith has pointed out (1969 and pers. comm.) that in a number of birds a bond-limited message is encoded in a display characterized by series of short notes that rise and fall in frequency and amplitude. He cites galliforms (Stokes, 1961, 1967) and tyrannids (W. J. Smith, 1966, 1970b) as examples. To this can now be added the parids, since the Variable See of the Carolina Chickadee fits both physical and usage descriptions, and the homologous call in the Black-capped and Mountain Chickadees (*Parus gambeli*) is closely similar (see Dixon, Stefanski, and Folks, 1970). It is not known with certainty that the Variable See homologue of the latter two species undulates in pitch and amplitude, but the form and spacing of the notes is similar. In addition, the Broken Dee notes are made up of rapidly repeated subunits, at least in Carolina Chickadees and probably in other parids. Further, a number of infant mammals, including raccoons, polar bears, and humans, use pulsating calls in situations where they are soliciting such aid as food, warmth, etc. (Ristau, 1970). The fact that this pulsating pattern is so widespread in situations calling for bond-limited activity suggests that there may be some psycho-physical feature held in common by a large number of higher vertebrates.

### 9. Broken Dee

*Form:* In frequency, frequency spread, harmonic structure, and overall pattern Broken Dee series are very much like Dee series. However, the individual Broken Dee notes have irregular frequency fluctuations and often subdivide into shorter chevrons. The notes of a Broken Dee series sometimes become longer, louder, and slightly higher in frequency as the calling bird is approached closely for feeding (see under Usage). Sometimes Broken Dee notes are continued after the caller receives food, but they are fainter then (see Figs. 2.18B; 2.19A, B).

Broken Dee is used by large nestlings, by fledglings, and by adult females. Presumably both adults and juveniles can produce the same range of variation in form. Females probably use more of the chevron subunits than the irregularly fluctuating form. Juveniles, especially when very young, probably do not have the vocal control required to produce the regular subunits and may use mostly the irregular notes. Insufficient recordings and sonagrams were made to prove this, however.

*Usage:* Broken Dee notes are used in narrowly specific situations. Females beg from their mates, and are fed by them, throughout the period of egg laying and into early stages of incubation. They use Broken Dee extensively during this, and also Wing Quiver occasionally. The calls are given as the females forage. The females are almost always accompanied by their mates during this period. It is not known whether females that are fed on the nest beg from inside the nest cavity, but no indications of such calling have been heard; probably it is unnecessary, because the situation is quite specific. In the few copulations that I witnessed, the females were begging when the males initiated the copulation approach. The Broken Dee notes were stopped once it became clear that the male was approaching for copulation, although M3 appeared to feed his mate just before one mounting.

Nestlings and fledglings used Broken Dee also; it is the only vocalization, aside from Screams and Hisses, that was recorded from them until at least a month after fledging. Pair 3–3's nestlings begged only after a parent had entered the nest box to feed them, and the calls subsided within 30–60 seconds after the adult left. Very young nestlings used a "peeping" call but no recordings were obtained of it.

*Message and Meanings:* The message of Broken Dee is apparently "I am prepared to engage in appropriate bond-limited activities." What is "appropriate" is determined from context, e.g., caller is a female, a juvenile, etc. The meanings Broken Dee has to a male hearing this call from his mate include (1) feeding her, (2) guarding her, and (3) copulating with her. Parents respond to Broken Dee from their young offspring by feeding and guarding them. The meaning to parents with older fledglings is primarily to accept the presence of the calling chickadee.

*Trill:* One variation was heard from a female (F3) but not from any young birds. In this form the Broken Dee series ended in a rising "trill" at the moment of the male's closest approach with food. Only two good tape recordings were obtained of this. The sonagram of one series (Fig. 2.19A) shows that the last few Broken Dee notes are composed of discrete subunit chevrons which are more irregular than usual both in form and frequency. The notes in the trill are short and irregular, and made up of very short connected chevrons. In another instance this same female broke off her Broken Dee calling

as her male approached to feed her and gave two longer bursts of "trill" notes which, as in the previous example, looked like a low-pitched version of broken Variable See notes. Possibly trills are intermediates between Broken Dee notes and broken Variable See.

Some parids are known to beg with what is probably a Variable See homologue. For example, Dixon (1949) reports that Plain Titmouse females give an "invitational or begging display" using a twittering call, consisting of soft, rapidly uttered *sit-sit-sit* notes, and wing quivering. He further notes (p. 122) that ". . . as the twittering becomes more vigorous and is continued for longer periods, he may respond by feeding her. As the sporadic twitter becomes more pronounced and continuous, it resembles the chattery call notes of fledglings a day or two out of the nest. At this stage her posturing and begging notes act as releasers of the feeding behavior of the male." This is especially interesting because males of this species are said by Dixon to be rather aggressive toward their mates early in the breeding season. Early feedings are accomplished by the male's leaving food on the branch beside the female. Only later, as the aggression is toned down, are the feedings accomplished bill-to-bill.

In Carolina Chickadees Variable See also indicates that the bird is prepared to engage in bond-limited behavior, as well as that a simultaneous escape tendency is present; it is used in situations where it functions to appease the recipient. Use of the Variable See homologue by Plain Titmouse females when begging early in the season may help to forestall some of the aggression of the males. Later the females can beg with the equivalent of Broken Dee. In Carolina Chickadees begging females were not known to use Variable See; aggression by males does not normally occur at this season. The trill was used by F3 when her mate was at his closest point while feeding her; this would be the most "dangerous" time with respect to a possible attack from him. Very close approaches are not otherwise common, and even in Carolina Chickadees there may be some nervousness on the part of pair members engaged in a feeding. Use of the trill, if it is intermediate to Variable See, would be appropriate at such a time.

Broken Dee and Variable See both encode readiness to engage in bond-limited behavior; Variable See also encodes simultaneous escape tendency. Considering their similarity, it is not surprising that an intermediate between these two calls should exist.

### *Displays Encoding Association and Other Messages*

This section considers two vocalizations which frequently are used together, but which are dissimilar in form. The first, Lisping Tee, encodes a conflict between association and locomotory activities. The second, Soft Dee, is less well understood but probably encodes a conflict between association and the general set. Although association is a form of bond-limited behavior, these two vocalizations are treated

separately because their usage is less specialized and less seasonal than the vocalizations presented in the bond-limited category.

### 10. Lisping Tee

*Form:* Lisping Tee notes are chevrons with strongly emphasized descending arms which are usually longer and louder, and often more gently sloped, than are the ascending arms. It is this skewing which distinguishes Lisping Tee from High Tee. Lisping Tee notes are rarely given singly. Usually at least two are uttered and often longer series, in which it is common for the notes to be clustered into pairs or triplets, preceded and sometimes terminated by a single note. The pattern is quite variable, however.

Lisping Tee notes usually fall between 4 and 8 kHz; occasionally some peak as high as 9 kHz (see Figs. 2.8A; 2.9A; 2.17C; 2.19C; 2.20A-C).

The emphasis on the long, slow descending arm gives this note a distinctive lisping sound which is easily recognizable to a practiced ear.

*Usage:* Lisping Tee notes are given only by a bird associating, at least loosely, with one or more individuals; most Lisping Tees are given in flight.

In the autumn and winter Lisping Tee is used both between mates and in flocks. It is most frequently used as one member of a foraging pair or group flies away from the other(s) to a new area some distance away. If the group is large, the next one or two individuals to follow may also give Lisping Tee notes. However, the last bird (or few birds) follow(s) silently.

In at least four cases Lisping Tees were recorded from an individual flying to *join* other birds. In three of these cases the caller was probably rejoining his mate after an absence of a few to several minutes. In the fourth case the birds involved were not identified. Lisping Tees were recorded twice from birds flying to and from feeding stations. In both cases other chickadees, including the mates, were present; their presence may have been relevant to the use of the call.

Very occasionally, in the fall and winter, a Dee note follows Lisping Tee or is inserted in a series of Lisping Tees.

Lisping Tees were used a great deal in the spring and summer by M3 and M6 during pre-nesting and nesting periods. M3 was observed using Lisping Tees as he moved around his begging mate, at some distance from their nest box (they rarely foraged near their box). He used the calls both in flight to and away from her and while perched. M6 used it once when flying northward from the vicinity of his nest box into his territory. His mate was also near the box, but she was not seen to follow immediately. M6 also used Lisping Tees while foraging near his begging mate. Often he followed Lisping Tees with soft Dees (see below). M6 used Lisping Tees most frequently when flying away from F5 after feeding her; these series were often terminated by Faint

Songs. Similarly, after a probable copulation attempt, M6 flew away calling Lisping Tee, Soft Dee, and Faint Song. Occasionally regular Dee notes followed Lisping Tees in this sort of situation.

Both males continued to use Lisping Tee while their mates were incubating. M3 used it when approaching to feed F3, or even while just guarding. For example, on 1 May 1967 he approached the box to feed F3, paused on a perch near the nest, and called several Faint Songs, one of which was prefixed by three Lisping Tee notes. On 5 May he was observed guarding in the vicinity of the nest, using several couplets of Lisping Tees. Some of these were given from perch, others as he moved about. On 8 May he landed while approaching the box to feed F3 and gave Lisping Tees followed by Faint Song. Later that day he perched near the box, called two Lisping Tees and then flew away.

Similarly, on 25 May 1965 another male in the study area was seen using Lisping Tee followed by Faint Song Variant during an approach to feed young in his nest. He was disturbed by the observer, however, and flew away without feeding. Both this male and his mate used Lisping Tees and Faint Song while moving around their fledglings. Because their family tended to stay high and in dense foliage, details of usage were obscured, but juveniles could be heard begging throughout.

Although Pair 3–3 usually scolded (Tee-Dee series) when approaching their box while it contained nestlings, they often used Lisping Tee and Faint Song near their fledglings. Again, the exact circumstances of the calling are unknown, even as to which (most likely both) parent used these calls. As in the 1965 family, however, the fledglings begged loudly in the vicinity as the Lisping Tees were given. Lisping Tees were heard from Pair 3–3 with their family as late as 4 July 1967.

*Message, Meanings, and Functions:* A feature common to situations in which Lisping Tee is used is that the communicator is concerned with maintaining physical proximity to one or more chickadees (i.e., associating). This is apparently in conflict with some other locomotory activity, usually for the purpose of foraging. Many Lisping Tees are uttered while the caller is flying *away* from his associate(s), i.e., the conflicting tendency overrides the association. Lisping Tees given while the caller is approaching his associates, or when perched near them, reflect the predominance of the association tendency.

Some of the possible meanings and functions of Lisping Tees in various situations are as follow: (1) to a bird in a foraging flock it means "follow the caller" and it functions to coordinate long flock movements; (2) to a begging, incubating, or brooding female it means "pursue nesting activities" and it functions to facilitate nesting activities (probably by reassuring the female that the male is attentive to her, poses no threat to her, and perceives no danger) and also acts to coordinate pair movements; (3) to a parent, fledgling, or both, it indi-

cates that the calling parent is moving in a certain direction, is still concerned with the family, and perceives no danger. It functions to keep the family members, especially the parents, in contact and aware of each other's positions and interest in the family at the moment, and apprised of the apparent absence of danger.

### 11. Soft Dee

*Form:* Soft Dee notes are narrow chevrons, usually with rounded peaks, and always consist of two resonance harmonics. The "arms" of the chevrons are nearly vertical. Most Soft Dees fall in the frequency range of 3-7 kHz. The peaks of both harmonics usually fall in the 5–7 kHz range. Soft Dees are nearly always given in well-spaced series. They are often directly prefixed with Lisping Tee notes or are given soon after Lisping Tees. The relatively rapidly uttered Lisping Tees followed by the well-spaced Soft Dees give an overall impression of a High Tee-Dee series. Soft Dees are never given very loudly, hence their name (see Figs. 2.20A-C).

Soft Dee notes may intergrade with Dee notes through broadening of the chevron. Intermediates have been recorded which are as broad as Dee notes, but have only two harmonics, like Soft Dee (Fig. 2.20C). Such intermediates sometimes follow Soft Dee notes in a series; these in turn are occasionally followed by regular Dee notes. Very rarely are Soft Dee notes followed directly by regular Dee notes.

Soft Dee notes also bear some similarity in form to Loud Tee (see above). Loud Tee also has two harmonics, but sometimes also a third faint one, and each Loud Tee note is much longer and usually higher pitched, as well as very loud.

*Usage:* Soft Dee is used infrequently; in only a very few cases were the circumstances known in detail.

In autumn and winter there were no instances of use by a bird known to be alone; the caller was usually known to be in the vicinity of one or more other chickadees, and usually near a feeding station. In one case a perched bird listened to the beginning of a fight along the northern border of the flock range. It gave several of these calls, including many intermediates to Dee notes, and then moved toward the fight. In another case the call was given by one of two birds which were very close together; the caller then joined some other chickadees and apparently moved with them as a flock-mate. Finally, the Dee-intermediate form was recorded during a fight between Apple Bough birds and a southern flock, but the details of the event are unknown. However, the Soft Dee is not known to have been used by a patrolling or challenging individual.

All examples from the spring are from males near their nests, females, or both, with one possible exception where the call may have been given by F3, also near her nest box. They are given by both

perched and flying birds, and both when approaching the female as well as when flying from her. They are very frequently associated with Lisping Tees in these cases.

*Message:* Many of the situations in which Soft Dee is used are similar to those in which Lisping Tees are used. In fact, Lisping Tees are often prefixes to Soft Dees or are used in the period immediately before or after Soft Dees, especially in the spring. It is my impression that Soft Dees are most commonly heard in early autumn and early spring—the two seasons when concern over forming bonded relationships is highest. Because observations were not made in a quantitative manner, and Soft Dee was used relatively infrequently, this cannot be stated with certainty.

Lack of detailed information on the use of this call makes it difficult to formulate hypotheses on its message content. However, it may encode some association tendency, as suggested by its use in Lisping Tee situations. Possibly Lisping Tee-Soft Dee series parallel High Tee-Dee series but specify that one of the conflicting tendencies is association, rather than escape.

### *Displays Encoding Escape and Other Messages*

This section comprises three disparate groups of vocalizations, all of which encode escape in combination with other messages.

The calls in the first group, High See, High Tee, Chick, Dee, and Loud Tee, are frequently used in combination with one another. High Tee, Chick, and Dee, in series, comprise the well-known "Chick-a-dee" call.

The second division consists of but one call, Tseet. It is unrelated to the first group in form and never occurs in combination with them or with any other calls. The escape tendency encoded by this call is relatively weak; its other message is general set.

The last group comprises three "distress" calls, Squeal, Scream, and Hiss. Since they are used only by trapped birds they apparently encode frustrated escape tendencies, plus varying degrees of attack tendencies.

### 12. High See

*Form:* High See notes are broad, sometimes flattened chevrons which fall between 7 and 9 kHz (sometimes the arms extend down as far as 5 kHz). They sound high, clear, and longer than High Tee notes, with which they intergrade through progressive shortening of each note. At the other extreme, High See notes intergrade (see below) with the longer Squeals (see Figs. 2.11A, C).

High See notes are sometimes given singly, but they usually occur in series of from two to six or more notes. Sometimes one or more High See notes are used as a prefix to Chip, or to Tee, Chick, Dee, and combinations of this set of calls.

*Usage:* One of the most conspicuous features of the usage of High

See is that the communicator is nearly always perched and momentarily inactive. It sometimes Wing Flicks (see below) or pivots on its perch, but usually no visible display coincides with calling. Most High See notes are given from a perch, although occasionally they are given in flight or on alighting. High See is more likely to be uttered just before alighting when it prefaces Tee, Chick, Dee, or some other combination of these notes (with the Tee-Chick-Dee combination being uttered upon alighting) than when it is used alone. High See is most likely to be uttered in flight when used in series with Chip notes.

In addition to Wing Flicking and pivoting on its perch, the bird usually gives other signs of an escape tendency, which are manifest either before or after the call. Examples of these signs are: a hesitant approach to a feeding station; abortive trips to, or passes at, a feeding station; flitting around an intruder but not actually attacking it; intention movements of flight; intently watching the observer; and sometimes outright retreat. Frequently the call comes as the bird pauses from some activity, which may or may not be resumed after the call.

Certain features that may elicit the escape tendency can usually be identified. These include the presence of one or more human observers, a recent squabble in the area, or the presence of other chickadees that are cause for concern, including intruders, rivals along a boundary, or birds with which association is tenuous and uncertain, as a new mate or flock-mate. Other avian species are sometimes relevant too, for example, a Tufted Titmouse on the feeding station or a Blue Jay (*Cyanocitta cristata*) in the area. High See was also at times given in response to Sparrow (*Falco sparverius*) or Red-tailed (*Buteo jamaicensis*) Hawks overhead. Unusual aspects of a feeding station, such as the presence of a trap, also sometimes elicited the call.

In addition, it is usually possible to identify some activity that the caller is doing or seems about to do that is interrupted by the High See calling, or is performed after the High See calling. These activities are very diverse and include guarding, patrolling, pressing a challenge, or attacking, as well as going to the feeder, remaining on the feeder to take seed, opening and eating seed, and foraging.

In most cases the caller does proceed with his activity, although the escape tendency sometimes has the upper hand. Occasionally the bird does something ambivalent, e.g., moves toward a feeding station in stages, then veers off at the last instant, or continues foraging for a few seconds before flying away. Some cases when the bird remains on his perch doing nothing are also probably indicative of ambivalence; the bird remains indecisive. However, in other of these cases, remaining quietly on a perch is probably the alternate activity to escape.

Some examples of the use of High See are as follow.

1. On 14 October 1966, F2 was frightened by a Tufted Titmouse on a feeding platform. She called High See, then dashed forward, grabbed a seed, and flew out, passing the titmouse on the way.

2. On 3 October 1966 an unidentified chickadee working on a seed near a feeding station gave High See series when a Blue Jay flew into the same tree, and another High See series when it flew out again.

3. On 27 October 1966 another unidentified chickadee sat very still after finishing a seed, looked around and called several High See series, then foraged briefly, apparently satisfied that it was not in danger.

4. Similarly, on 14 October 1966, F2 paused from her eating on a feeding platform, looked alert, looked over her shoulder and called High See. Then she grabbed another seed and darted from the feeding station.

5. On 5 November 1966, M2 and an unidentified bird, probably his mate F1, used several High See series in response to an overflight by a Sparrow Hawk.

*Message:* All birds calling High See seem to exhibit an escape tendency. They also show signs of undertaking some other activity; nearly any other activity with the possible exception of bond-limited ones. No use of High See occurred during copulation approaches and no instances were observed where the High See caller was clearly attempting to associate with another chickadee as an alternative to escaping. In a few instances such an association tendency may have been present, but other interpretations of the situations are possible. Bond-limited activities conflicting with escape tendency seems to be the message of Variable See, but some of these activities may also be included in the message of High See. If so, High See indicates that the caller is experiencing a conflict between escape and the "general set."

Since the High See caller is so frequently perched and inactive during the call, even if momentarily, the escape tendency must momentarily balance with the alternative. Subsequent to the call the bird takes some action, usually the alternate activity, sometimes escape, and occasionally ambivalent activities or waiting.

*Meanings and Functions:* The meanings for a recipient might include: (1) there is something in the area he should be afraid of or at least alert to; (2) his mate is experiencing difficulties around the nest and he should investigate; and (3) the caller is intimidated and probably will retreat without further attack.

High See calls probably function to alert pair- or flock-mates to danger or potential danger. They may also avert, or reduce the intensity of, a possible attack from another chickadee by indicating a relatively non-aggressive state in the caller.

### 13. High Tee; 14. Chick; 15. Dee

*Form:* High Tee is a clear-sounding short note. It is a simple chevron with a rounded peak usually between 6 and 8 kHz, but sometimes reaching as high as 9 kHz. Sometimes it has a lower and fainter harmonic. The tails extend down to 5, 4, or even 3 kHz, and have a

nearly vertical slope. High Tee notes are usually very short, about 0.05 sec., or less. However, they intergrade completely with High See notes by lengthening and flattening. High Tee is also similar in form and in sound to Loud Tee, but these two can be distinguished, both by sonagram and by ear. Intermediates between High Tee and Loud Tee do occur, but rarely.

High Tee occurs as a single note rather infrequently; usually two or more are given. High Tee notes occur most often, however, in series with other notes. High Tee combined with Chick and Dee notes comprises the commonly heard "chick-a-dee" call. It also occurs in combination with Chick or Dee alone, as well as with High See and Loud Tee (Figs. 2.15A, C; 2.16B, C; 2.17A).

The Chick note is based on a narrow chevron with sharply pointed peak, usually with three or four resonance harmonics. However, the ascending arm(s) of the upper chevrons are greatly extended, with the peak of the chevron often not even appearing. The "mushy," unclear quality of the Chick note is probably due partly to the harmonics and partly to the rapid repetition of sound in the same frequency range (Figs. 2.15C; 2.16B; 2.17A, B). The overall duration of most Chick notes is about 0.05 sec.

The Chick note is often preceded by High Tee, or rarely Loud Tee, and very rarely by High See, and is usually followed by Dee notes. Intermediates occur between Chick and High Tee, but not Loud Tee, and possibly between Chick and Dee. In these latter cases the beginning of the first Dee note following Chick has a short chevron, followed by an otherwise normally flat note (Fig. 2.16B).

Dee notes are broad, usually very flat chevrons, with several closely stacked harmonics. The frequency range covers as much as from 1½ to (rarely) 9 kHz, but usually falls between 3 and 6 or 7 kHz.

Dee notes are rarely given singly; they are usually in series of three to 10 notes. Most Dee series are prefixed with High See, High Tee, Chick, or any combination of these notes in the order they are listed here. Very rarely Dee series are prefixed with Soft Dee, or Lisping Tee (Figs. 2.15C; 2.16A-C; 2.17A, C; 2.18A).

Dee notes may be long, giving the Dee series a slow, deliberate sound, or short and repeated rapidly. Occasionally the Dee notes are rather "formless," similar to white noise; this creates a harsh quality. Finally, Broken Dee notes used by nestlings, fledglings, and adult breeding females, and which are probably closely related to Dee notes, are discussed above.

*Usage of each call alone* (i.e., *when not in combination with other notes*)*:* About half the time when High Tee is used as a single note, or in series not containing other calls, the bird is *in* flight. Of the remainder, about half are given as the bird alights and the rest when a bird is already on its perch.

High Tee is used by a bird going to or from a feeding station, mov-

ing to take seed on a feeding tray, or moving to a perch. It is sometimes used by a bird following another in association. Long series of High Tees are often used by onlookers (probably mostly females) to disputes; these individuals usually remain at a distance from the active disputants, sometimes moving away from them, or occasionally moving partway toward them but then withdrawing again. Occasionally it is used by a chickadee challenging another; if attack follows it is usually mild and brief.

High Tee-calling birds typically show signs of escape tendency. They may Wing Flick, pivot on their perch, make abortive trips to or past the feeder, or use a bobbing flight (see below). Features of the situation which may cause or contribute to the escape tendency include a current or recent dispute in the area, the fact that the caller is an intruder, the presence of the observer, and the presence of other bird species. The presence of another chickadee may also provoke an escape tendency if the relationship of the caller to it is, for example, that of a rival male, a new mate, or flock-mates with whom a firm bond has not been established.

The use of High Tee in combination with other notes and the message of the call are discussed below.

Most Chick notes or series are given *in* flight, sometimes *ending* just as the bird alights, and sometimes coinciding with a sudden swerving or change of course. Occasionally Chick is given on touchdown, or from the perch; in the latter case it may be accompanied by pivoting or be given as the bird turns around on the perch.

When given in flight the call sometimes comes at "choice points." For example, it may be given as the bird veers from a perch at the last instant, suddenly shies away from the observer as he passes by him in flight, suddenly darts for cover, or dives into the leafy portion of a branch.

Chick series are sometimes used in disputes. When used by combatants it is during long, confusing, chasing melees involving several birds, or in a tumbling combat. In one instance a single Chick note was used at the moment of an abortive flying attack by one chickadee on another that was perched. Chick series are also used by onlookers to a fight; in some of these instances one can see that the bird is concerned about something in addition to the dispute, such as the observer, or a nearby bird of another species.

Chick notes also are frequently heard around feeding stations. They are given in flight to, or more often, from, a feeding station, as, for example, when the caller leaves the feeder after another bird has suddenly landed on it with him. Sometimes the caller immediately returns, or turns and looks back at the feeder. It is used by birds pausing before going to the feeder, on an approach to a perch, landing on a perch near the feeder, or moving from one perch to another (some-

times with hesitant landings), or on turning on a perch to face the feeder. It is also given as a bird changes perches after leaving the feeder. It was given once by an individual disturbed by a trapping arrangement on the feeder; he hopped to the edge of the feeding platform, called Chick as he turned around, then remained on the feeder several more seconds.

Chick was heard in a variety of other situations. Once a juvenile interrupted a bout of patrolling and made an awkward flight, during which he called two Chick notes. It was used by a chickadee just passing over the observer's head, by a chickadee in flight retreating from a larger species of bird, and by a female retreating from mild attacks by her mate. It was used by a perched chickadee as another bird flew close over her on a feeding platform. Another female used Chick notes as she flew from the entrance of a nest box she was inspecting; she then looked at the observer. It was also used in an erratic, circling flight by a chickadee that apparently saw a Blue Jay flying directly at him just as he took off from his perch; the Blue Jay landed exactly where the chickadee had been, while the chickadee landed nearby.

Dee notes or series with no other notes prefixed are usually given *on* or *just after* alighting. Sometimes they are given when the caller is already on its perch and, rarely, they are given entirely in flight.

Dee notes were used by birds forage-feeding or using a feeding station, either alone or with one or more companions, both while moving about, and while perched and eating. They were used by a male hearing a rival in the distance, in countercalling with a rival, or in facing-off against a rival, as well as by individuals (probably females) watching a dispute or following a chase. They were also used by individuals in what appeared to be a tense association with another, for example with a new mate, or with a mate or flock-mate immediately following a lengthy interflock dispute.

The caller usually gave signs of an escape tendency, immediately before or after, and often during the call. These included Wing Flick, bill wiping, pivoting on the perch, looking around frequently, moving a great deal, bobbing flight, and hesitant or abortive approaches to a feeding station. Occasionally the caller actually did leave the area. Features of the situation which caused or contributed to the escape tendency include: (1) the caller was alone and possibly was new in the area; (2) the presence of a human observer(s) or predators; (3) the caller was startled or alarmed by another species; (4) the presence of a rival; (5) the presence of a trapped bird; (6) the caller was visiting a newly established, unfamiliar feeding station; and (7) the presence of other chickadees with whom association was uncertain, e.g., after a dispute or during the period when flock composition was being established.

Series of harsh-sounding, rapidly uttered Dee notes, without prefix,

were heard occasionally. Only a few observations were made of this variation. It was most often used by males that appeared disturbed by the presence of a rival, the observer, or both (i.e., "scolding").

*Usage of combinations of High Tee, Chick, and Dee:* The combination High Tee-Chick-Dee comprises the commonly recognized "chick-a-dee" call. High Tee-Chick, High Tee-Dee, and Chick-Dee are also heard; of these, the combination High Tee-Dee is most common. The order of these notes in combination with one another is *never* reversed. Such series may comprise from one to many of any of the different notes.

High Tee-Chick-Dee: Most Tee-Chick-Dee series are given with the High Tee occurring during flight and the Chick portion, or the beginning of the Dee portion, occurring while alighting. Since the Chick portion is typically short (one or two notes is common), it is often difficult to determine with certainty whether the bird touched down during the Chick notes or at the beginning of the Dee notes. Entire Tee-Chick-Dee series are sometimes given on the perch or, rarely, during flight.

The situations in which Tee-Chick-Dee is used are more or less the same as those in which the individual components are used. It was given by chickadees foraging or visiting a feeding station either alone or with companions; by birds disturbed in the area of their nest; by males approaching a distant rival, nearing a boundary when the rival is absent, and during low-key encounters with rivals; by spectators to fights; by a female disturbed by intruders while her male was absent; by a bird in a trap; and by mobbing individuals. It was also occasionally used by males during bouts of dawn or daytime singing; usually these males appeared to be disturbed by my presence.

As with individual components of Tee-Chick-Dee series, the birds showed signs of escape tendency during or at about the time of the call. These tendencies included hesitant approaches to a feeding station, abortive passes or visits at a feeder, hesitant behavior on the feeding platform, much moving or pivoting on a perch, watching the observer, Wing Flicking, and occasionally outright retreat. Features of the situations which were relevant to the escape tendency included: the presence of observer(s); the presence of other species; the presence of other chickadees such as intruders or new pair- or flock-mates; the caller was taking part in a dispute; the caller was watching a dispute involving its mate; and, finally, the caller was caught in a trap.

Other behaviors which the bird seemed to be tending toward at the same time include: visiting a feeder; taking seed; foraging; foraging in association with a companion; approaching, chasing, or attacking a rival or intruder, observer, or predator; defending the nest; going to the nest; and patrolling.

While most Tee-Chick-Dee series had only one or two Chick notes, a few had at least five or six. These were always in situations where

the bird probably had a strong attack tendency conflicting with his escape tendency. For example, long Chick portions were used when the caller was a spectator to a fight that probably involved its mate, when the caller was in a countercalling dispute with a rival male, and when the caller was patrolling or singing and patrolling his territory, sometimes near a border dispute point.

Usually a Tee-Chick-Dee caller proceeded with the alternative behavior, although ambivalent behavior was frequent, and escape occurred sometimes.

Tee-Dee: Tee-Dee series are very similar in usage to Tee-Chick-Dee series. Most are given on landing or just after landing; the remainder generally are given from a perch, sometimes as the bird sidles or turns around; occasionally a series is given entirely in flight. The bird shows much the same signs of escape tendency, for the same reasons, and simultaneous tendencies toward the same sorts of alternative behaviors, as when Tee-Chick-Dee calls are used. An exception is that there are no known instances of its use by a spectator to a fight.

Usually a Tee-Dee calling bird proceeded with an alternative behavior; escape occurring in about 1/4 to 1/5 of the cases.

Tee-Chick: Unlike Tee-Dee and Tee-Chick-Dee series, most Tee-Chick series are given *in* flight. Often the call is followed by a different series, usually Tee-Chick-Dee, when the bird subsequently touches down on its perch. Of the Tee-Chick series not given entirely in flight, about half are given as the bird lands from a flight and half are given from a perch.

As with other calls and combinations of calls in this group, the bird shows signs of an escape tendency, and for the same reasons. The other behaviors in which the bird is engaged, or is tending toward, are also the same as for Tee-Dee and Tee-Chick-Dee series, except that its use in disputes is restricted to spectators; it was not heard from direct disputants. Tee-Chick is also used in mobbing.

The number of instances in which the escape tendency gained the upper hand is about equal to the number of times the bird engaged in some alternative behavior. Occasionally Tee-Chick callers were ambivalent, e.g., they approached a dispute but stopped short or they foraged briefly before flying away.

Chick-Dee: Chick-Dee series usually begin just before the caller lands. In most of the cases where the precise relationship of the notes to landing can be determined, the Chick portion is given in flight and the Dee portion is given just at the moment of alighting. A few Chick-Dee series are given entirely from a perch, and occasionally one is given entirely in flight.

Chick-Dee series were given by chickadees foraging or visiting feeding stations, both alone and in the presence of pair- and flock-mates, intruders, and rivals. They are also utilized while investigating nest boxes, during disputes by both spectators and disputants, and in re-

sponse to an overflight by a hawk. The usual signs of escape tendency are typically present, including those which can be given in flight, such as diving for cover, veering from landing at the last minute, dashing to and from a feeding station, and bobbing flight. The alternative behaviors which the escape tendency was in conflict with include foraging, visiting a feeding station, landing on a perch, taking seed, changing a perch, working on a seed, approaching a newly bonded individual, and investigating a nest box.

In some cases the Chick portion of the Chick-Dee call was long, with five or more Chick notes. As in the Tee-Chick-Dee series, these were all cases where the bird was probably experiencing strong agonistic conflict, i.e., attack as the alternative to escape. They included: the caller was in a dispute or watching a dispute; another chickadee, another species, or the observer was interfering with use of a feeding platform; or caller was in a tense association with another chickadee, e.g., as with a new mate.

In most cases the Chick-Dee caller did proceed with the alternative behavior. Sometimes the bird chose escape and sometimes he apparently was ambivalent.

*Messages of High Tee, Chick, and Dee:* In most cases when High Tee is used, an observer can identify escape behavior or tendencies toward escape behavior, as well as tendencies toward some alternative behavior which involves locomotion. High Tee is usually given *in* flight. Some of these flights are escape flights, while others represent the alternative, conflicting behavior. High Tees are given from the perch when the caller is being ambivalent, but remaining on the perch is *not* one of the alternative behaviors specified in the High Tee call. For example, birds do not interrupt seed opening with High Tee as they do with Tseet (see below).

Dee calling apparently encodes escape tendencies and simultaneous conflicting alternative behavior of nearly any type (general set), excluding possibly only some bond-limited activities such as copulation.

A High Tee caller is about equally likely to choose escape, the alternative locomotory activity, or to remain ambivalent. A Dee calling bird is more likely to proceed with some alternative activity, rarely escapes, and is occasionally ambivalent.

Chick is apparently intermediate in message between High Tee and Dee. It always comes after Tee and before Dee in any series of these calls. Usually the Chick stage is passed over rapidly, but when a bird uses many Chick calls he shows a high degree of ambivalence, as if suspended in an intermediate state. Chick is uttered during erratic flights and at "choice points" in other flights. When the call is given from a perch the bird may pivot or turn while calling. If a Chick caller elects to "escape," e.g., leave a feeding station, he may then return and complete the alternative choice, which is to take a seed. Chick is uttered by combatants when the action is rapid and confusing.

In Tee-Chick-Dee series, or partial series, the Chick portion is longer when the bird is apparently experiencing agonistic tendencies; these presumably cause strong ambivalence. A Chick caller which does not perform some ambivalent behavior is more likely to proceed with the alternative behavior than to escape.

Outright escape is more probable with Tee than with Dee calling; choice of the alternative behavior is more likely with Dee than with Tee calling. Ambivalent behavior occurs with all three calls but is highest for Chick.

### 16. Loud Tee

*Form:* Sonagrams of Loud Tee show that it is a chevron which is skewed slightly so that the ascending arm is longer, less steeply sloped, and has greater amplitude (loudness) than the descending arm. It has at least two loud resonance harmonics and sometimes a third faint harmonic occurs above them. Unlike Chip notes, all the harmonics emphasize the ascending arm. Loud Tee is almost always given very loudly, and the notes are well-spaced; these two features probably account for the emphatic quality of this display. Loud Tee notes are usually repeated in series of two to five notes; occasionally the series are longer. It commonly precedes or follows High See or High Tee notes and is also heard with various combinations of High Tee, Chick, and Dee. It was rarely used as a prefix to Chip (see Fig. 2.15A, B).

*Usage:* Loud Tees are uttered with about equal frequency from a perch, in flight, and while landing. They are used in a very wide variety of situations, including foraging, visiting feeding stations, forage-patrolling, guarding a nest, sighting a hawk, and during disputes. They are not employed in face-to-face, standoff encounters. The activities of the caller may be either locomotory or non-locomotory; for example, it was used by a bird pausing while eating a seed.

Usually the caller exhibits some sign(s) of escape behavior. These include veering in flight, bobbing in flight, making an abortive visit to a feeding station, hesitating while landing, or retreating partially, e.g., from other chickadees or from a feeding station. Loud Tee callers sometimes escape, at times proceed with some alternate behavior, and occasionally behave ambivalently.

In many cases it appears that the bird is experiencing a sudden rise in escape tendency. For example, it makes an abortive trip to the feeding platform, lands nearby, calls Loud Tee, and leaves the area without taking a seed. In other cases the bird could be experiencing either a rise *or* a decline in escape tendency. In this instance, for example, it may call while clinging to the side of the feeder and then take seed. Its use in disputes is especially relevant to this question, but is not known in detail. In at least some cases the call was given by an active participant rather than by a watcher. Some of these were episodes when a female was briefly involved, although it is not known that

she gave the call. While there were several instances in which the bird apparently experienced a rise in escape tendency, and several equivocal cases in which the caller might have been experiencing a rise *or* a fall in escape tendency, there were none in which it is certain that the escape tendency was declining. The suddenness of the change in escape tendency may explain the absence of Loud Tee from standoff encounters, where the situation is briefly static with no sudden surprises for either participant. There is no evidence to suggest that Loud Tee callers have an aggressive tendency.

*Message:* Loud Tee apparently encodes escape tendency, conflicting with virtually any other non-agonistic behavior, excepting some kinds of bond-limited behavior. It probably also encodes a changing level of escape tendency—most likely a sudden rise. If so, it obviously functions as a warning. Its loud, emphatic quality is well-suited to this function.

W. J. Smith (1969) did not recognize *changing* probability as a parameter of the probability message. He has since gathered convincing evidence that a decreasing probability of escape is encoded in a display of the Black-Tailed Prairie Dog (W. J. Smith and coworkers, in prep.). The evidence for changing probability in Loud Tee is still unclear, but may yet contribute to understanding the nature and limits of the probability message.

### 17. Tseet

*Form:* Tseet notes are variously shaped, very brief, and high-pitched. The shape is basically a chevron, but the ascending and descending arms vary in shape and slope. Occasionally there is a waver or irregularity in the smoothness of the chevron. One variant appears to be a prolongation of the descending arm. The frequencies spanned by Tseet notes, including those with the longest arms, range from 5-9 kHz. The peak of the chevron, which is usually the loudest part of the call, usually occurs between 7 and 9 kHz (Figs. 2.11B, D, E; 2.12A, B).

Tseet notes usually are given singly, well-spaced from each other and from any other calls. They are not used as prefixes to other calls.

*Usage:* Most Tseet notes are uttered by birds either on a perch or in flight, with about an equal number falling in each category. Relatively few Tseet notes are given by birds as they alight or take flight. Some are given by birds when they are turning around, sidling, or hopping on a perch. When Tseet notes are given during a bobbing flight they often come at the low points of the "bobs." Tseet notes are sometimes uttered at places where it is difficult to maneuver, as when the bird is flying through branches, coming in to land in a dense thicket, or, occasionally, when veering suddenly in flight.

Tseet notes are used abundantly in a wide variety of situations. They are heard frequently around feeding stations, from birds visiting alone,

in pairs, or in flocks. They are used at all points, including on an approach perch, in flight to the feeder, landing on the feeder, while pausing or choosing seed, in retreat from the feeder, on retreat perches, and on changing retreat perches. Tseet notes are also used by foraging individuals. It was not uncommon for a chickadee with a seed or other food to call Tseet while working on it, or to pause, look about, and give a Tseet note.

Sometimes patrolling individuals interrupt their loud patrol-foraging with bouts of quiet foraging in which they use Tseet notes. Males use Tseet while guarding their nests and females and while going to, or returning from, visits to feed the female. In the latter use the form intergrades with the form of Lisping Tee, which is also used at such times.

Tseet is frequently used in close approaches, both by rivals and by tense associates, e.g., new mates or flock members. Typically, several Tseet notes are uttered at the moment of closest approach. Attacks following such close approaches are usually mild. Probably both the bird approached, as well as the bird approaching, utter Tseet, but this is uncertain. Tseets are also occasionally used during or after mild flying or supplanting attacks. Again the identity of the caller(s) is uncertain.

Tseet is also used by birds moving warily about a trap and by birds inspecting and pecking at new bands.

In most instances certain features of the Tseet-caller's behavior indicate the presence of at least a mild escape tendency. These include hesitant approaches to a feeding station, pivoting and sidling on the perch before taking flight, looking at the observer or other chickadees, or acting "nervous" on a feeding platform by clinging to the edge, hurriedly grabbing seed, or leaving without seed. Sometimes Tseet-callers pick up their seed and move to a new perch to continue eating. Features of the situations in which Tseet is used which would contribute to the escape tendency include the presence of other, at least potentially threatening chickadees; the presence of other species such as Titmice and Blue Jays, or of the observer; the fact that the caller is an intruder (sometimes intruders call even in the absence of the residents); or, last, perhaps the guarding and patrolling birds are in an especially wary mood and anticipate potential trouble, even if none is immediately apparent.

The activities in which Tseet callers engage, or show signs of tending to engage in, are numerous and diverse. They include guarding; patrolling; foraging; associating with companions (usually while foraging); visiting a feeding station; taking seed; remaining in the area or on a given perch to eat; and probably also attacking, making decisions about the direction, or the continuation of a flight, or whether or not to take flight.

*Message:* It seems likely that Tseet encodes a conflict between an escape tendency, usually a weak one, and the remainder of the general set, i.e., any other category of behavior. While Tseet was not heard in precopulation and copulation situations, it did occur in other bond-limited activities, notably that of association in various situations and of males feeding females at the nest. Tseet was not restricted to activities which involved locomotion. In fact, it was frequently used by birds perched and working on food.

The message of Tseet is, therefore, very similar to that of High See. Unlike the latter, however, the bird is not at a balance point between the two conflicting tendencies. Usually the Tseet caller is engaged in some activity, even though perhaps hesitantly, or soon engages in some activity after a period of hesitation or ambivalent behavior. For example, it may go to a feeding station after calling Tseet but make an extra stop enroute, or it may pause to look about or change perches before opening a seed. Outright retreat by Tseet callers is rare. Escape is thus weaker, relative to the alternative behavior, in Tseet than in High See. In addition, the encoding of some bond-limited behaviors is more certain for Tseet than for High See.

There is some possibility that Tseet-calling encodes Social Interaction Hesitance, rather than escape. This could be the case even though it is used by associating individuals—they may seek to continue the association without engaging in a more active interaction. The use of Tseet in potentially aversive situations might be because the bird is seeking to avoid a social encounter so that he can give more attention to the problem at hand. It will take more detailed observations to demonstrate the encoding of Social Interaction Hesitance in Tseet. This message has been recognized with certainty in only one bird, the tyrannid *Myiozetetes similis,* and it is, therefore, best to be cautious about assuming that it is present here.

*Meanings and Functions:* Recipients react to Tseet calling in various ways. A foraging companion might look about for a potential problem in the area. A bird on whom a close approach is being made, as at a feeding station, can remain in position without fleeing or attacking, although he does not usually take food either. A begging female continues her begging. A territorial individual may react to an intruder calling Tseet by making a milder threat or attack than he might have done otherwise. Tseet calling thus functions to alert other chickadees to potentially aversive situations, to appease or reassure a bird to whom a close friendly approach is being made, perhaps aiding in the formation and maintenance of bonded relationships, and to adjust the level of aggression or retreat to the minimum necessary for the situation at hand. It is so commonly uttered that it probably also functions to keep pair or flock members apprised of each other's position. The homologous call in the Black-capped Chickadee is frequently referred to as a "contact note" (Odum, 1941).

### 18. Squeals; 19. Screams; 20. Hisses

*Form:* Squeals are chevrons, longer than High See notes, and skewed so that the descending arm is long and sloping gently. Squeal notes are very loud, and have a distinctive sound. A series of squeals usually drops in frequency from beginning to end. In many series the notes gradually become longer, more irregular, and with more harmonics, thus developing into harsh-sounding "Scream" notes. "Hiss" notes are nearly formless and similar to "white noise." Screams and Hisses intergrade completely (see Fig. 2.14A-D).

*Usage and Messages:* Squeal, Scream, and Hiss were heard only from chickadees in mist nets, traps, or in the hand. Squeal is probably an expression of escape tendency. In at least some instances birds using Scream and Hiss notes were known to struggle, peck, and bite, or at least attempt to do this. At other times I was preoccupied with removing the bird from the trap so I do not know if this behavior is generally the case. It is not unlikely, however, that Scream and Hiss encode attack tendencies probably in addition to escape. The difference in usage between Scream and Hiss is not clear.

Since these calls were used only by trapped birds which were thwarted from escaping, frustration is probably also encoded. Thus a tentative message for Squeal is frustrated escape tendency; for Scream and Hiss both a frustrated escape tendency and an attack tendency.

*Meanings and Functions:* When a chickadee is trapped for banding it usually is mobbed extensively by nearby chickadees and other species, especially titmice and nuthatches. Predators may occasionally be distracted sufficiently by the mobbing and by the distress calls of their victims to release their prey.

In one interesting case, Pair 3–3 scolded two people removing its young from the nest box for banding. Whenever one of the youngsters Hissed or Screamed (the only calls they used), both parents instantly stopped calling until the nestling fell silent again, then they resumed mobbing. The significance of this behavior is not understood.

### *A Dubious Display: Abrupt Tee*

*Form:* Abrupt Tee notes are chevrons with much less steeply sloped ascending than descending arms. The ascending arm is usually the louder and is often slightly broken or jagged. Most of these notes are brief (0.05 sec) but some longer ones (up to 0.15 sec) have been heard. Short Abrupt Tee notes are very similar in form to High Tee, but very strongly skewed. In a few instances one or more long notes preceded a string of short ones. Usually, however, the short units are given without such a prefix. Series of short Abrupt Tee notes often break into couplets.

Abrupt Tee notes have a distinctive sound and are easily recognized by ear, even when included in a series of other notes. The high pitch

and nearly vertical descending arms probably contribute to the markedly abrupt sound of the notes. The loudest portion of the ascending arm is usually between 6 and 8 kHz, occasionally up to 9 kHz. The bottom of both ascending and descending arms may drop to as low as 4 kHz (see Fig. 2.10C, D).

*Usage:* Abrupt Tee calls were rare; only three tape recordings of them were obtained.

1. On 13 March 1966 three bursts of Abrupt Tee were given by an unidentified chickadee as a Sparrow Hawk flew overhead. A Sparrow Hawk probably poses a genuine threat to a chickadee.

2. On 11 December 1965 a chickadee and a Tufted Titmouse were trapped together in a box trap on a feeding station. The titmouse appeared no more disturbed than is usual for a bird that discovers it is trapped. The chickadee, however, appeared terrified of the titmouse and gave a range of calls encoding escape tendency, including Chick, High See, Squeals, Screams, and harsh Screams (intermediate to Hiss), as well as several Abrupt Tee notes. During the long bout of calling, Abrupt Tee series both preceded and followed other sorts of notes and were also given by themselves. The only long Abrupt Tee notes known are from this incident. They usually preceded short Abrupt Tee notes but also preceded series of Squeal notes.

Although details of most of the movements of the two birds in the trap were not described and correlated with the use of the different calls, it is known that one burst of Abrupt Tee was given when the titmouse moved so as to block the chickadee into a corner.

3. On 20 November 1965 an unidentified chickadee gave three short Abrupt Tee notes as a Red-tailed Hawk passed some distance away. The chickadee in this case was probably also responding to the close presence of the observer. It then flew to a feeding station.

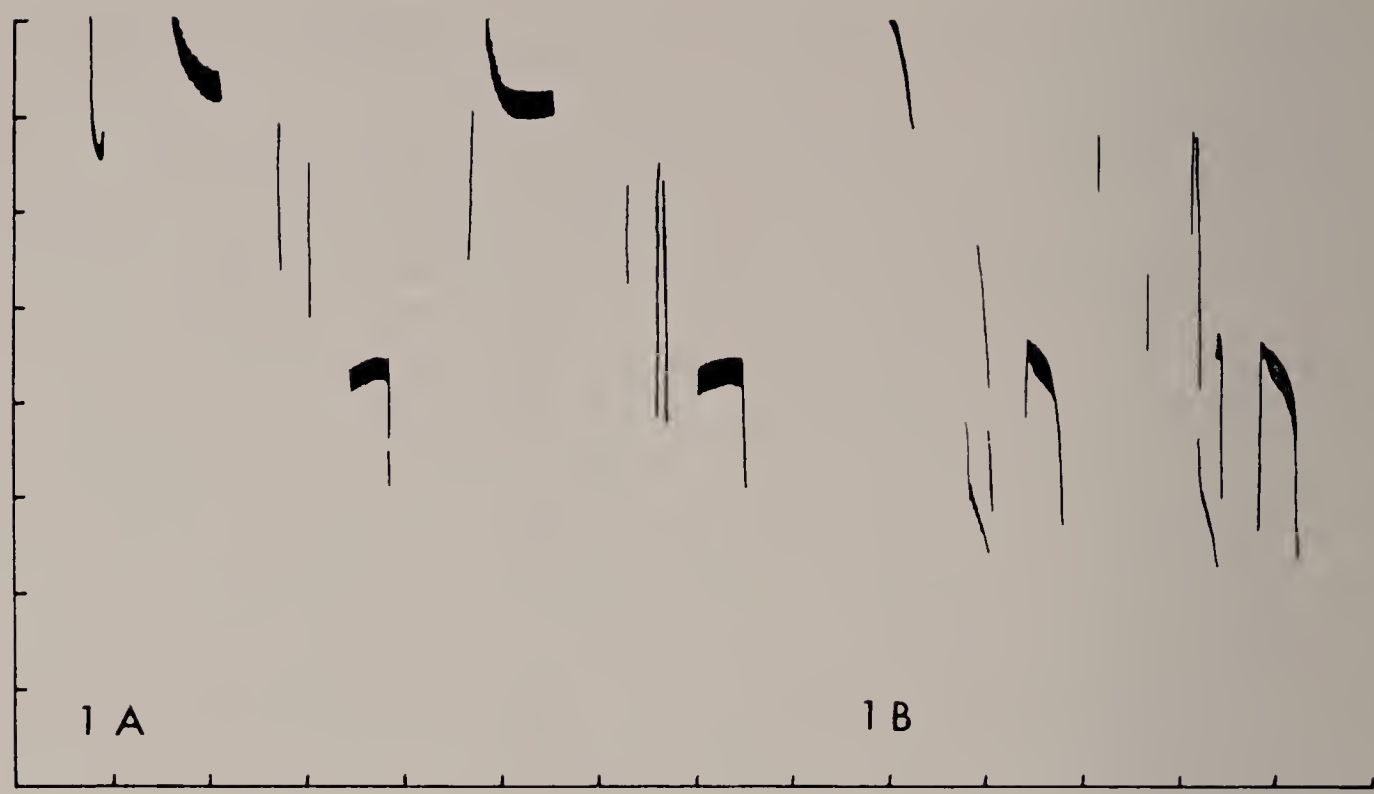
*Message:* In the first two cases the birds calling Abrupt Tee clearly had reason to feel endangered. In the third case the Red-tailed Hawk at some distance posed very little threat to the calling bird. However, the bird may have been distracted by my proximity. The series was composed of only three notes, and the bird went to the feeding station within a few seconds after calling. Probably this bird over-reacted, but became calm after reassessing the situation.

*Wrong Species?:* There is a strong possibility that all "Abrupt Tee" notes were recorded from Black-capped Chickadees. Black-caps occur in the study area during the winter; in some years they are common and in others relatively rare. All three recorded examples were from the 1965-66 winter, when Black-caps were numerous in the area. They were rare during the study year 1966-67.

Tape recordings of Black-capped Chickadees from South Lincoln, Massachusetts made in November 1965 and from Lake Ariel, Pennsylvania made in September 1967 were analyzed. Sonagrams were prepared of several examples of what were obviously High Tee notes

(e.g., from "chick-a-dee" calls). The form of these Black-cap High Tee notes was identical to that of Abrupt Tee notes originally thought to be from Carolinas.

The most likely interpretation of Abrupt Tee is that the notes were, in fact, High Tee notes given by wintering Black-capped Chickadees. The situations in which they were used would all have been appropriate to High Tee usage. Lacking better evidence, it would be preferable not to regard Abrupt Tee as a vocal display of the Carolina Chickadee.



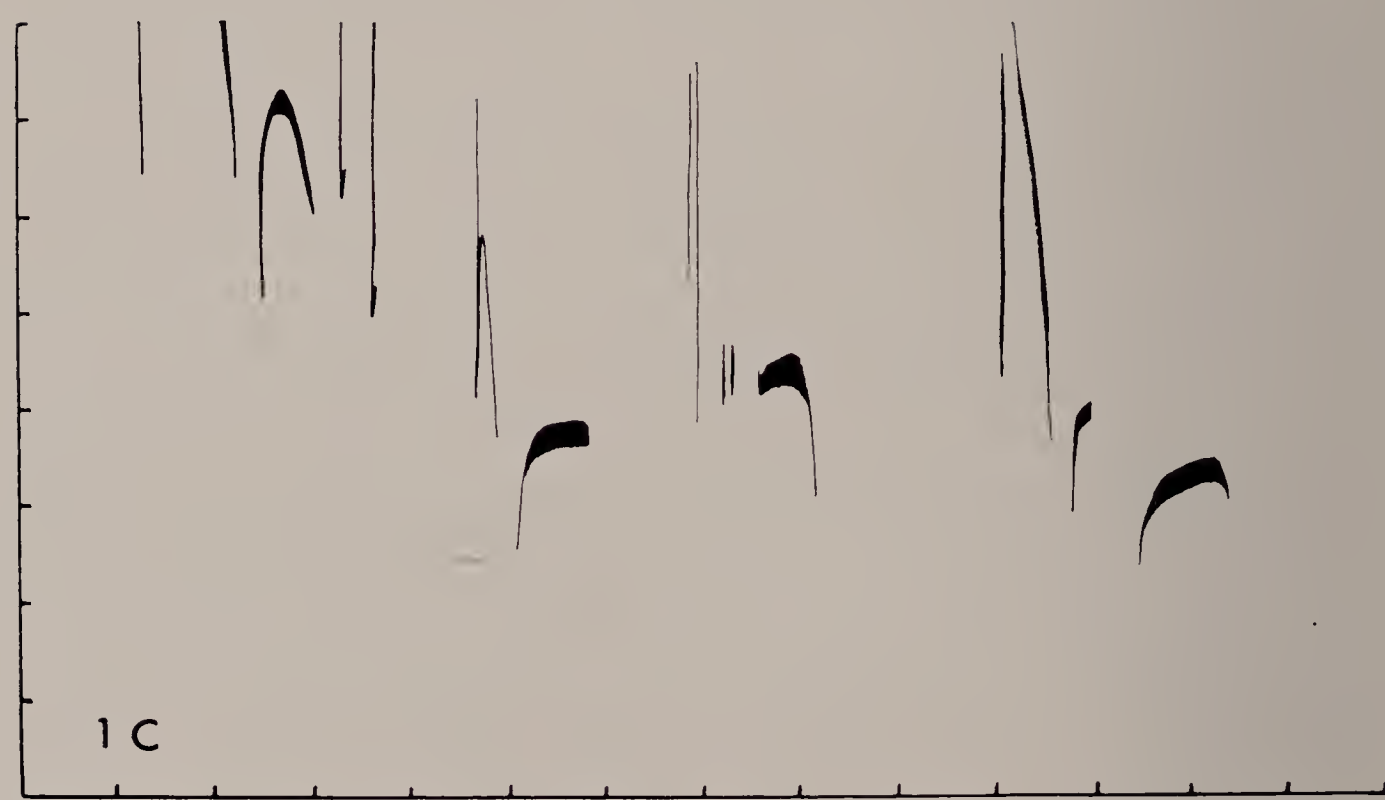
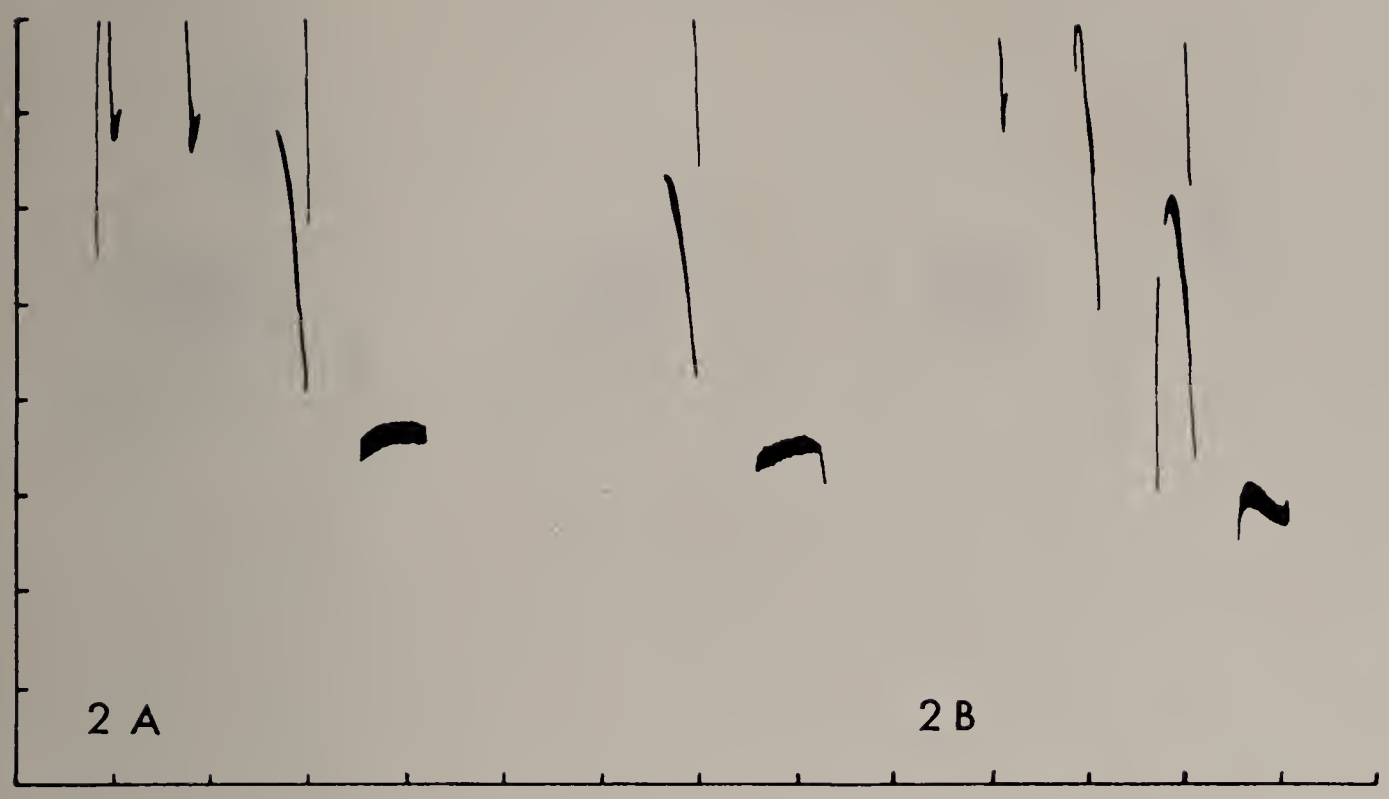




Fig. 2.1A. T-slink-T-slink, given by M2 just after supplanting F4. She retreated 20 ft. and was not approached again. 11 Nov. 1966. This, and all subsequent illustrations of vocalizations, are ink tracings of sonagrams. The vertical scale is 1 kHz (0-8 kHz, unless noted otherwise); the horizontal scale is 0.1 second.

Fig. 2.1B. T-slink-T-slink, by F5, approaching a dispute between her mate and M3, along their territorial boundary. 14 Apr. 1967.

Fig. 2.1C. T-slink-T-slink, T-slink. Second "slink" note has higher frequency and sounds higher pitched than the other two. Given by M3 during dawn calling. 12 Mar. 1967.



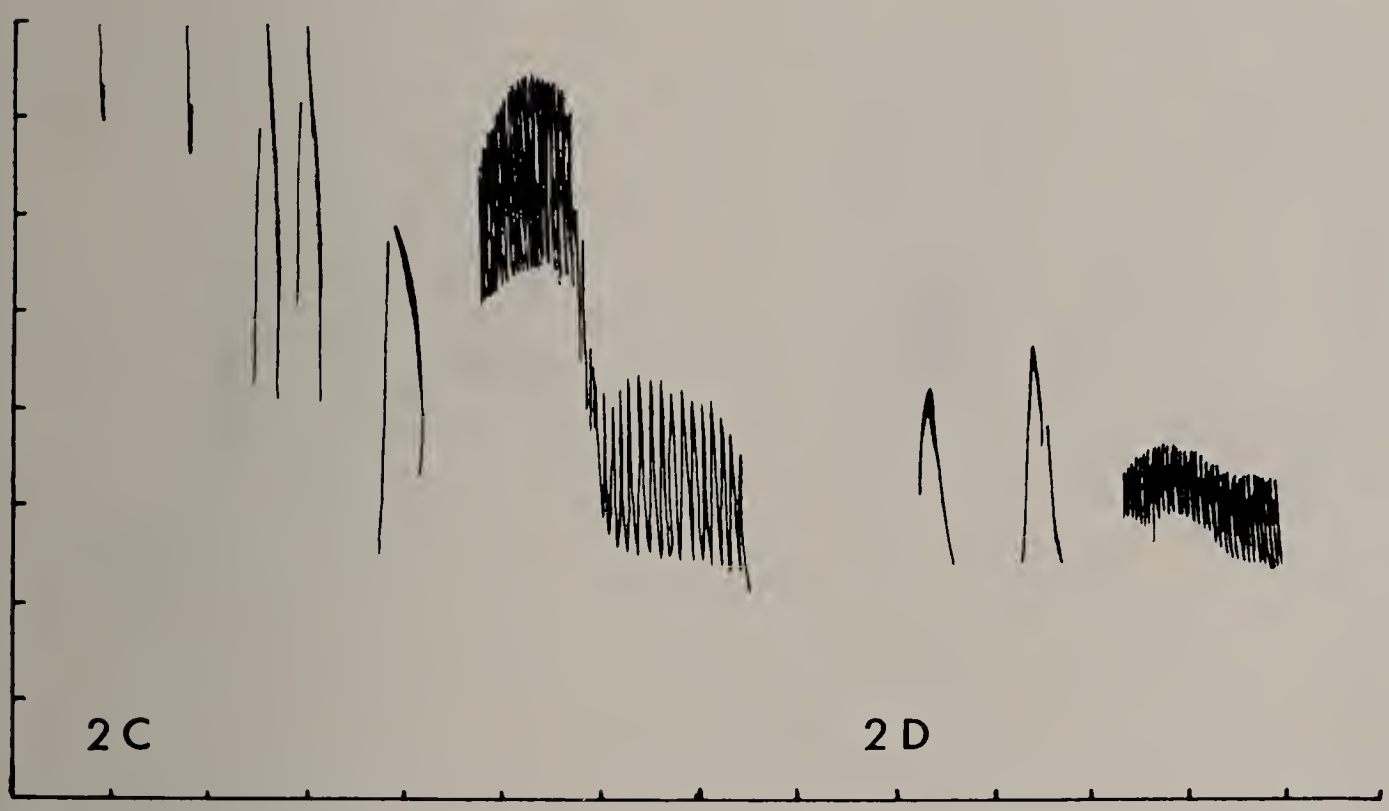
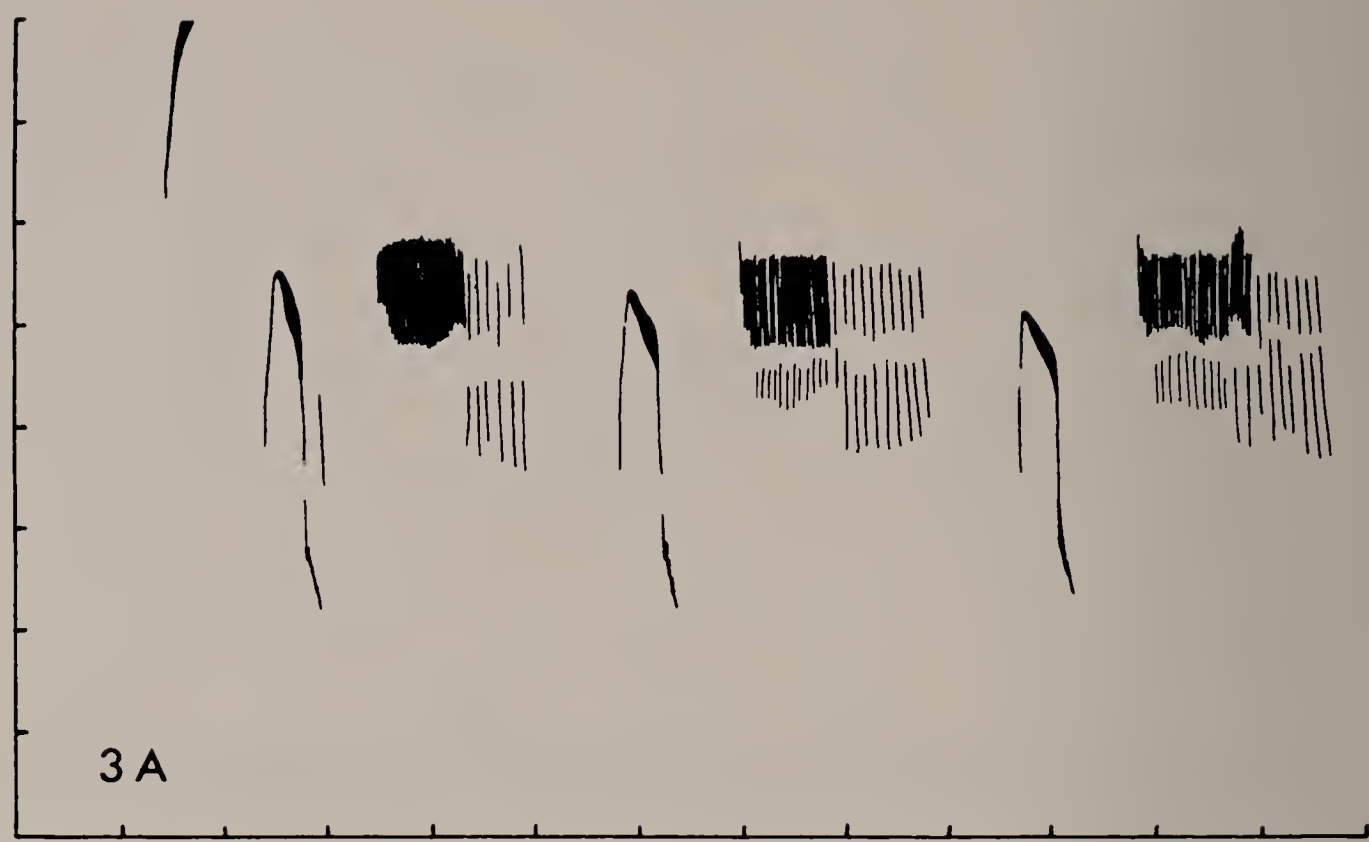




Fig. 2.2A. T-slink-T-slink, given by one of two birds in a close confrontation on a feeder. 3 Oct. 1966.

Fig. 2.2B. T-slink, given by an unidentified bird in a 4-bird chase. 22 Dec. 1966.

Fig. 2.2C. Click-rasp, given by M3 near border with Pair 6–5. He had been skirmishing intermittently with M6 during the preceding several hours. 26 Mar. 1967.

Fig. 2.2D. Click-rasp, by M5 in a boundary dispute with M2. He is the only individual known to give this particular variant. 27 Oct. 1966.



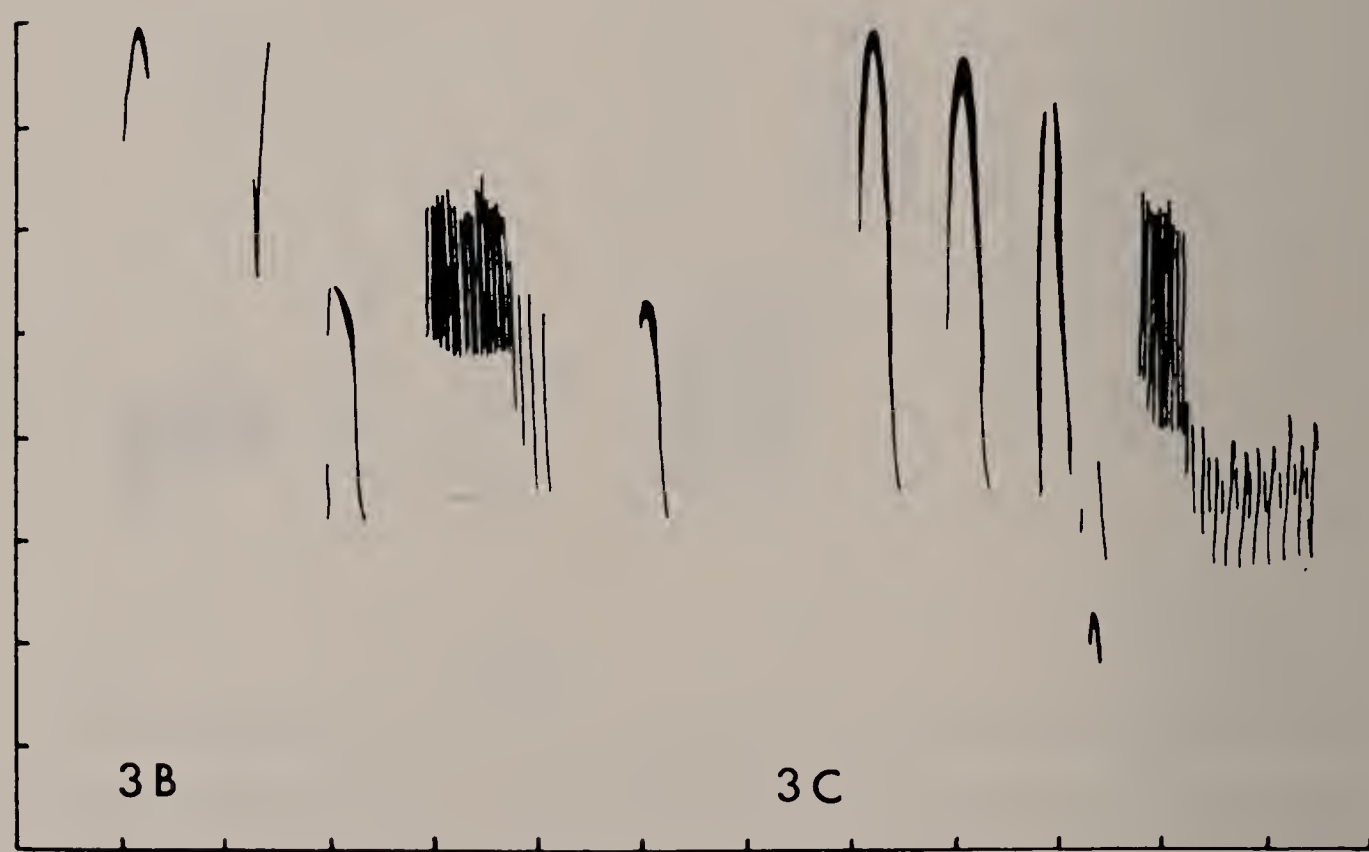
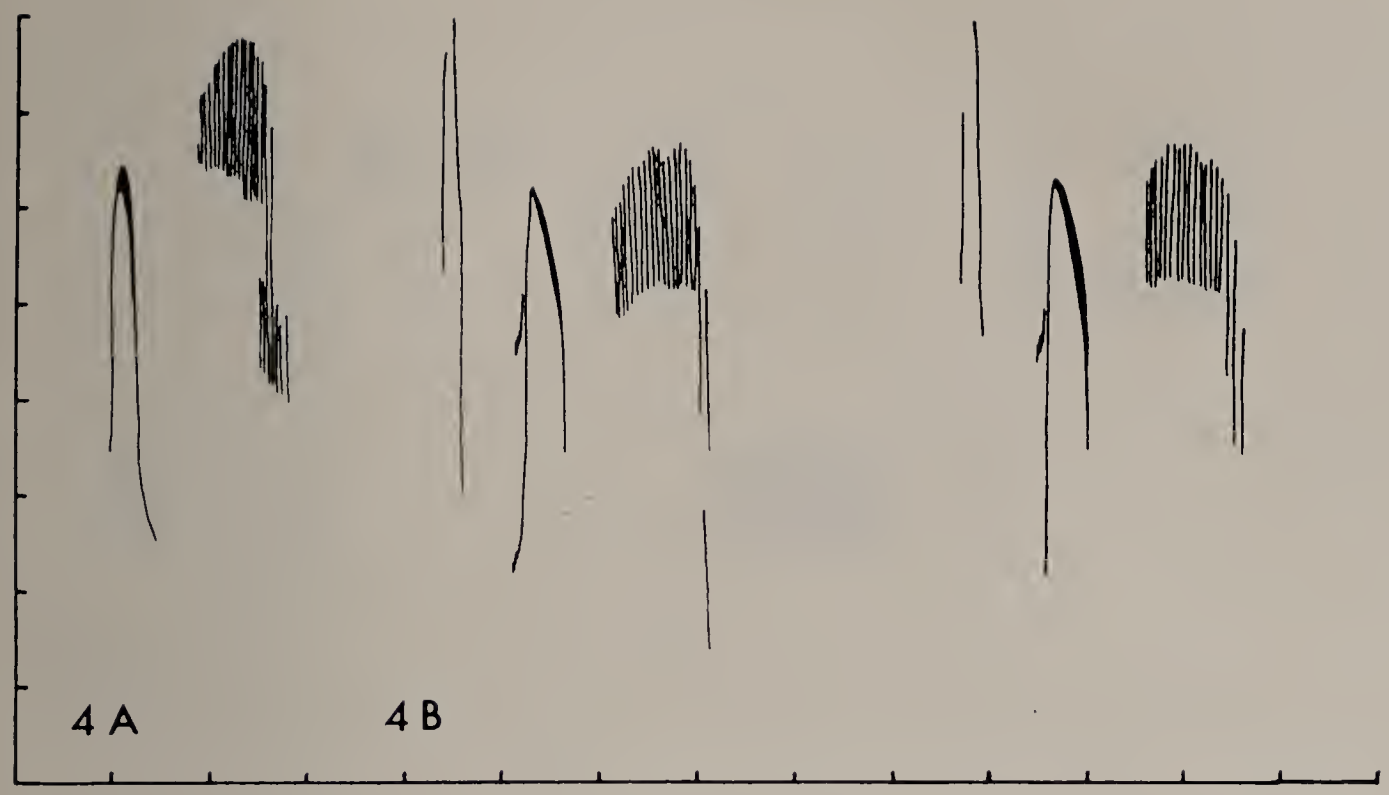




Fig. 2.3A. Click-rasp, by F5, just after excavating in a nest cavity located right on the border with Pair 3–3. Pair 6–5 had recently skirmished with Pair 3–3, and Pair 3–3 was still in the vicinity. M6 was guarding nearby; he approached Pair 3–3 and initiated another dispute soon after F5 began calling. 24 Mar. 1967.

Fig. 2.3B. Click-rasp, by F1, alone, foraging, and apparently patrolling. 12 Dec. 1966.

Fig. 2.3C. Click-rasp, by M2, approaching F4. 15 Nov. 1966.



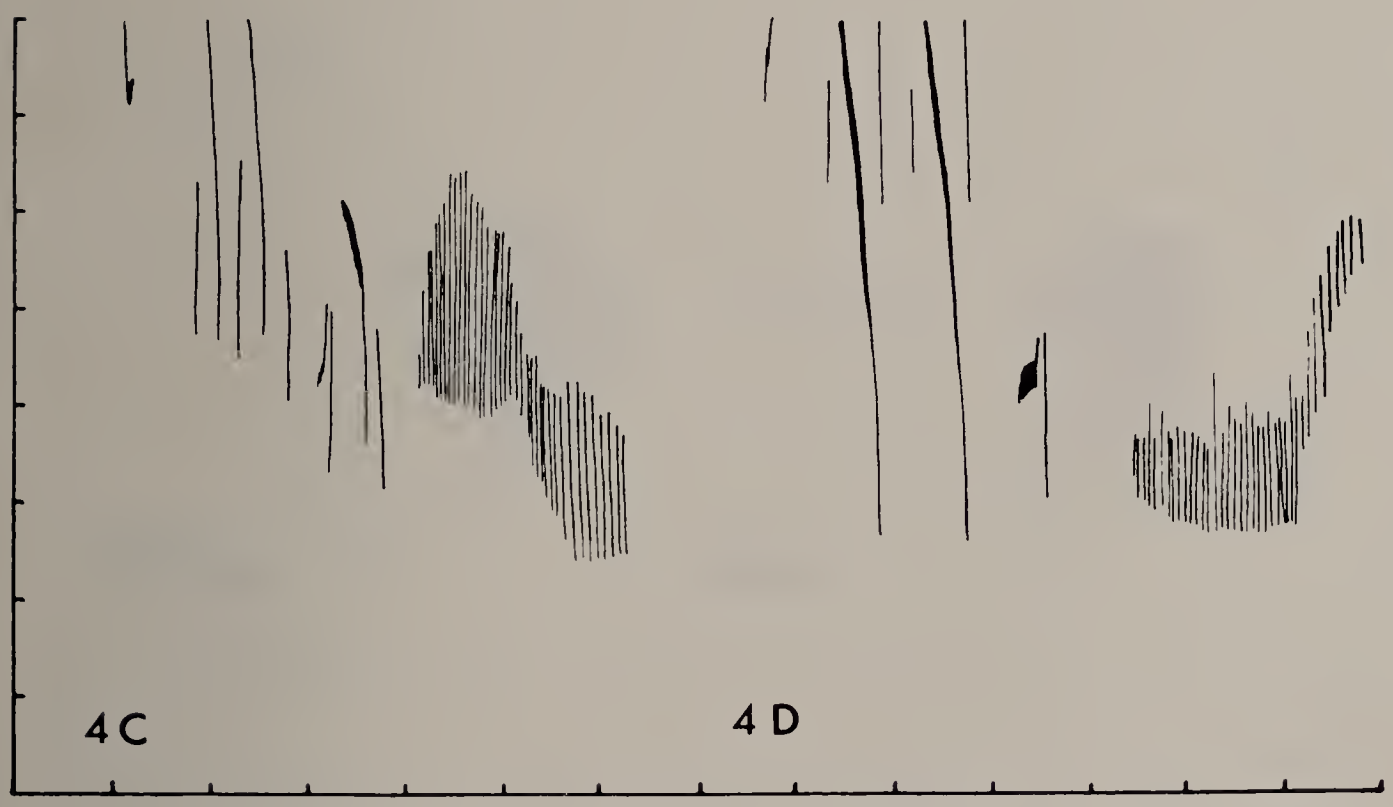
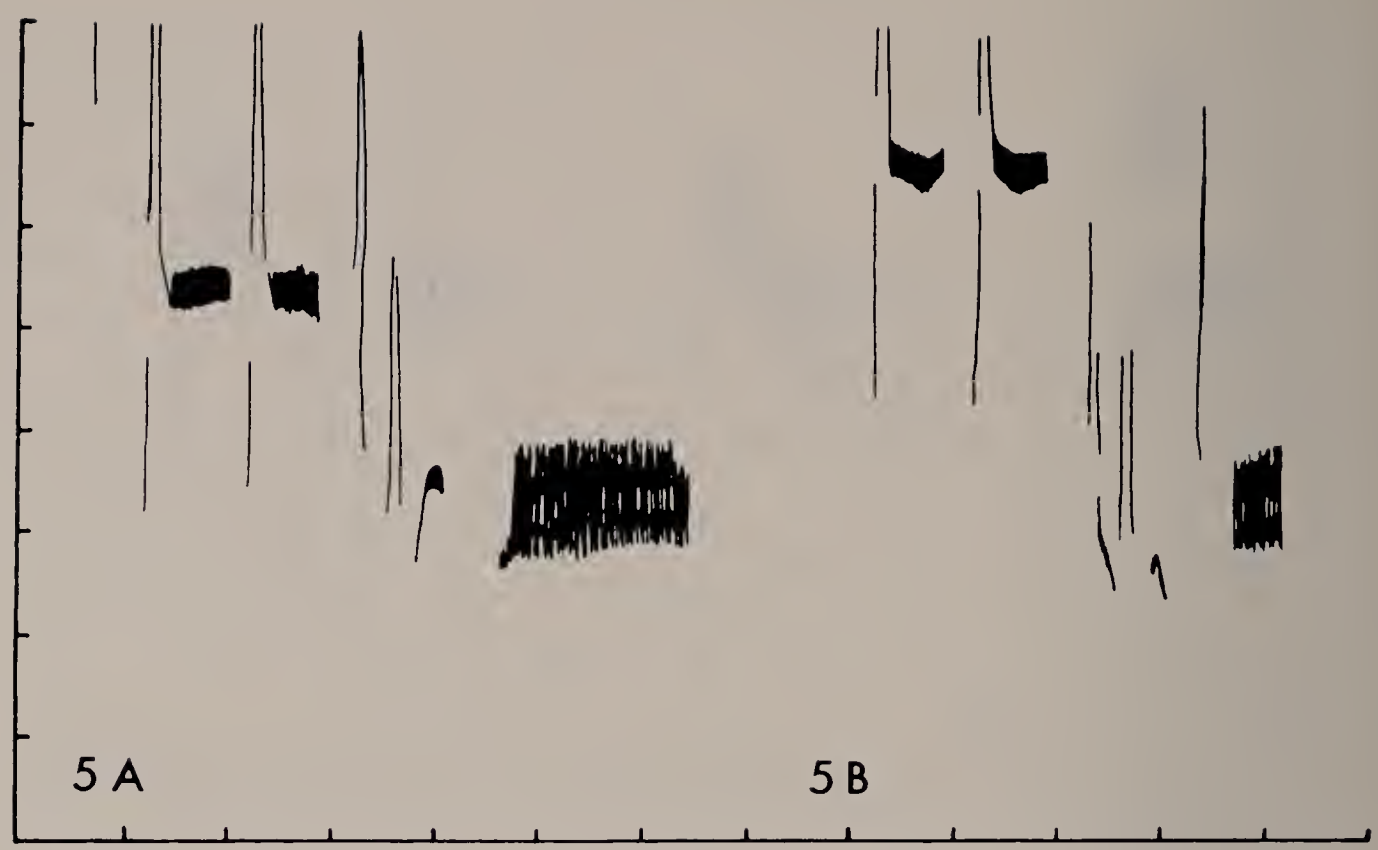




FIG. 2.4A. Click-rasp, by F3, alone, foraging, and apparently patrolling. 20 June 1967.

FIG. 2.4B. Click-rasp, by M6, in a dawn dispute with M3 at their mutual boundary. 11 Mar. 1967.

FIG. 2.4C. Click-rasp, by M3, patrolling alone after a dispute involving 3 pairs. 31 Dec. 1966.

FIG. 2.4D. Click-rasp. M3 pushes M2 away from a feeding station in M3's territory by repeatedly approaching him with these calls. 2 Apr. 1967.



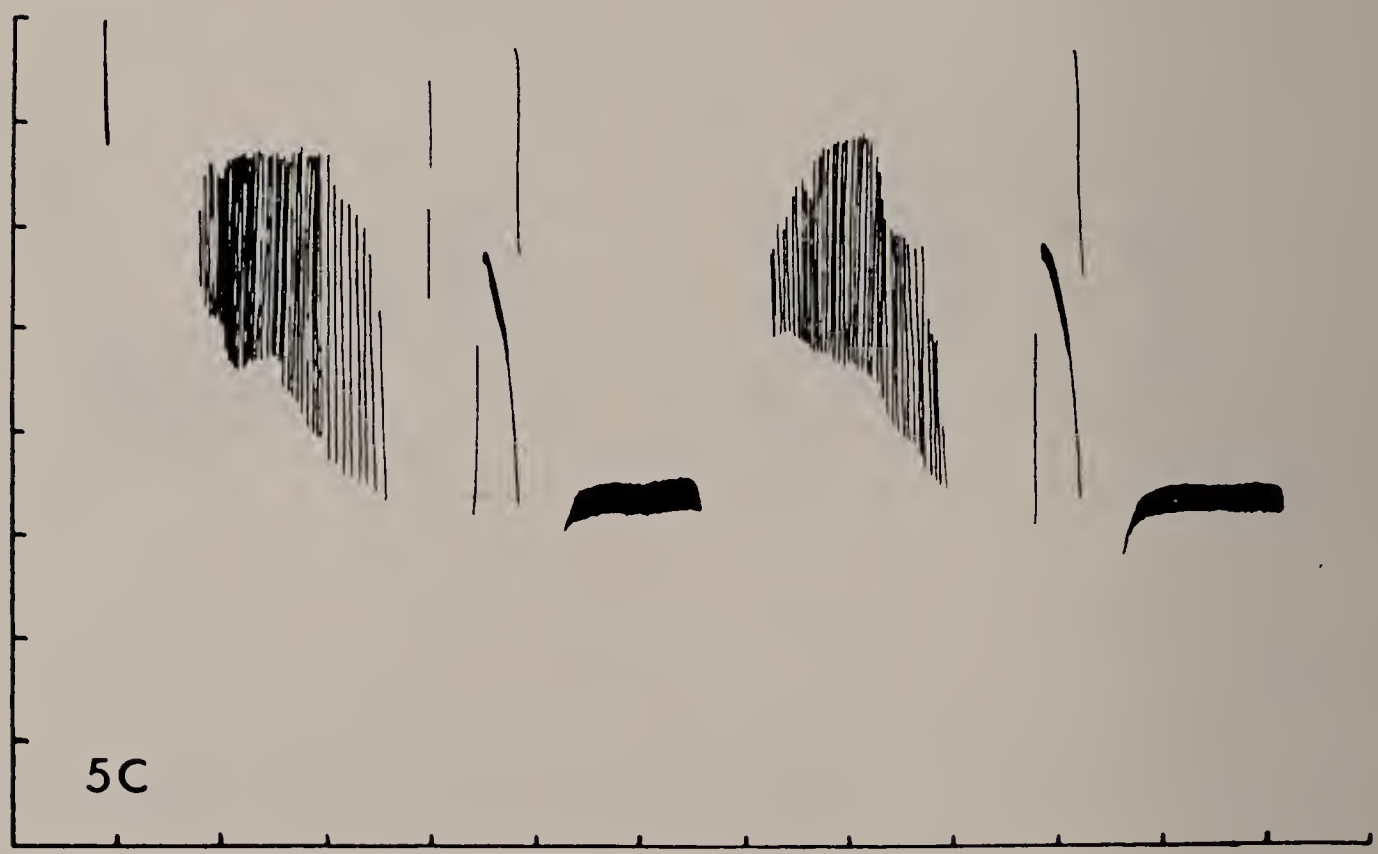
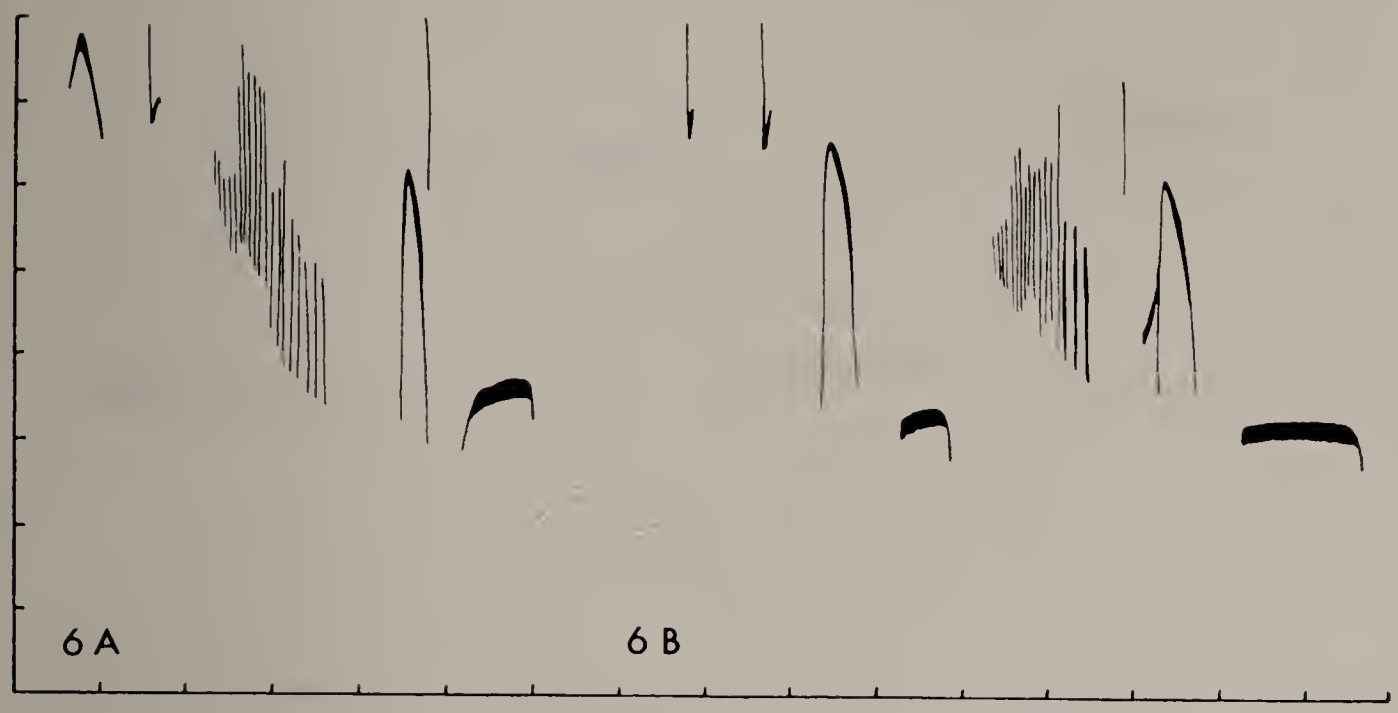




FIG. 2.5A. Tee-rasp, probably by M3, during a 2-pair skirmish between Pair 3–3 and Pair 6–5 at their mutual boundary. 18 Apr. 1967.

FIG. 2.5B. Tee-rasp, by an unidentified bird in a 2-pair encounter. 9 Oct. 1966.

FIG. 2.5C. Rasp-slink-rasp-slink, by M3, during skirmish with M6, along their mutual boundary. 11 Mar. 1967.



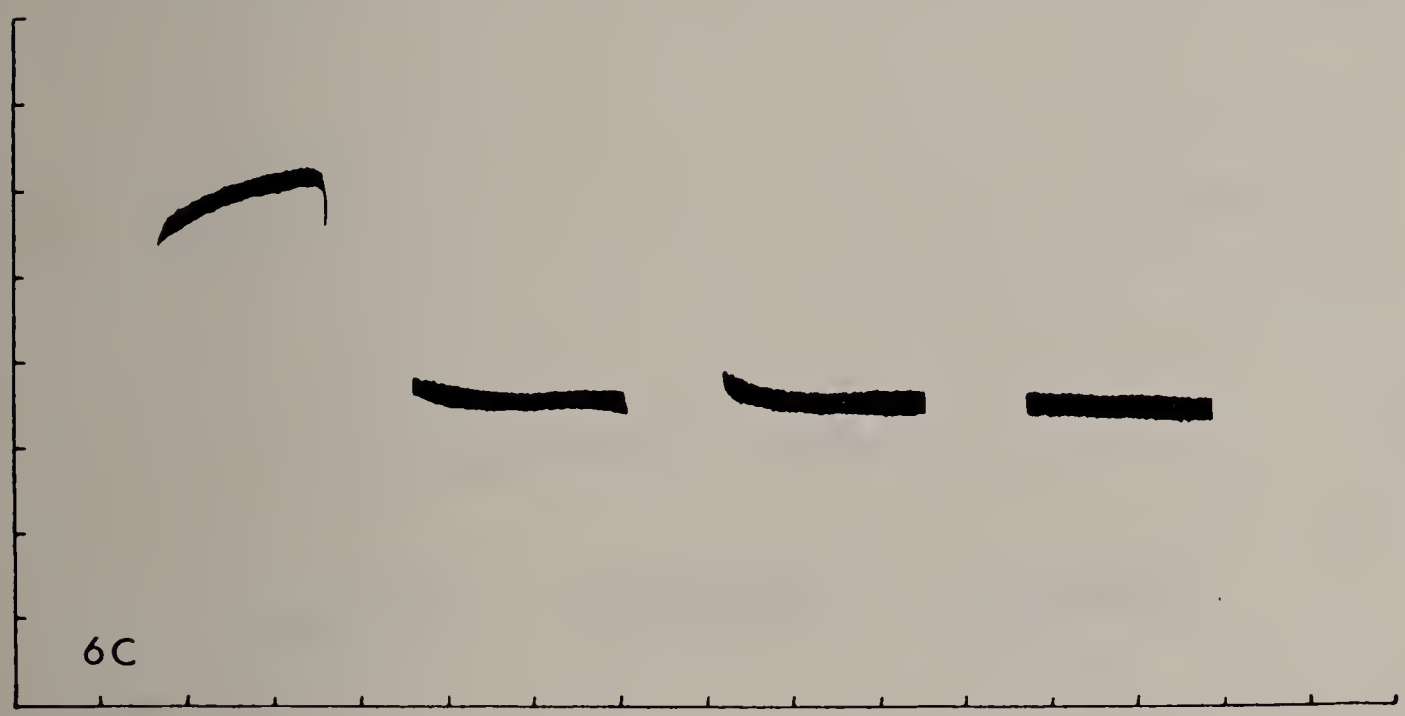
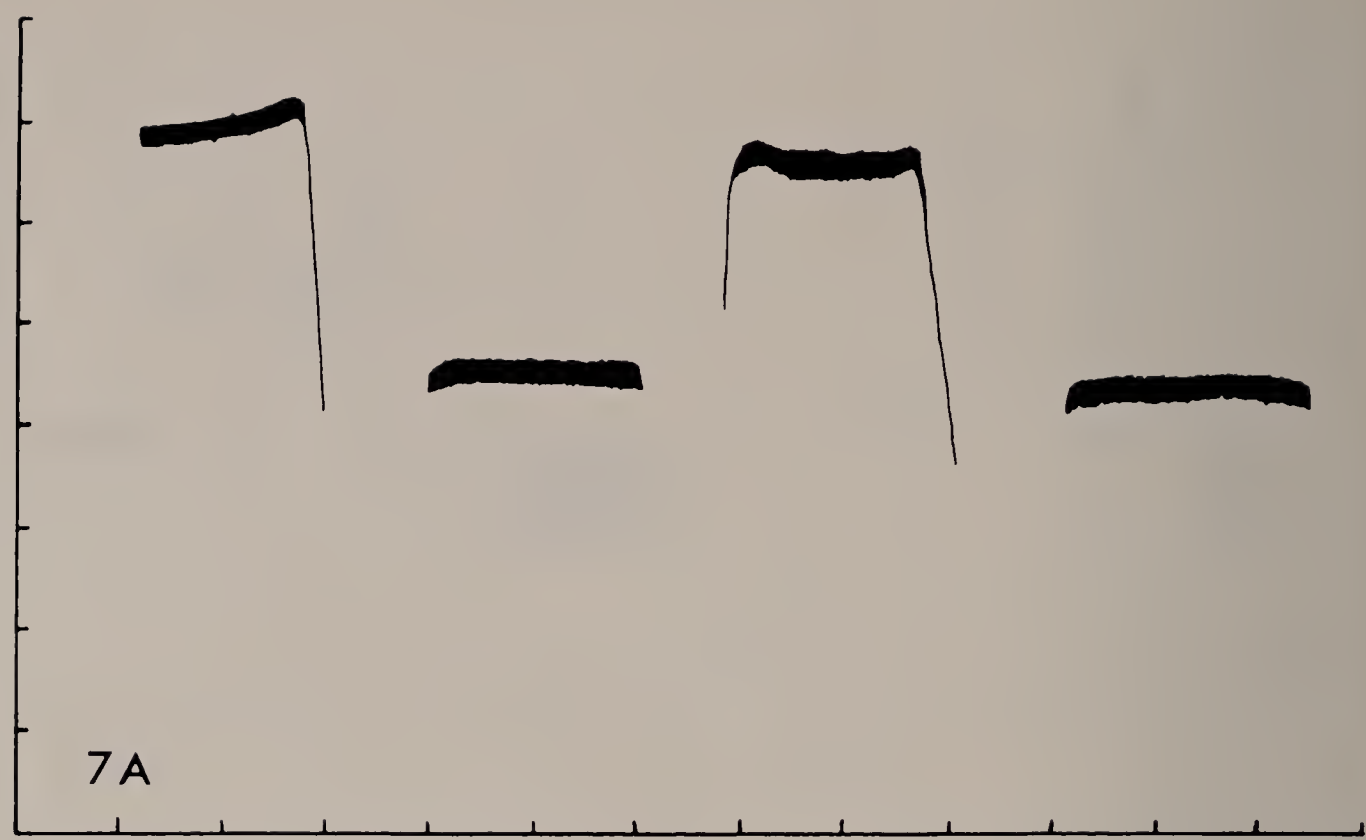




Fig. 2.6A. Rasp-slink, by F5, during a 2-pair skirmish with Pair 3–3. 18 Apr. 1967.
Fig. 2.6B. Slink-rasp-slink, by M7, during a dispute with Pair 6–5, 11 Mar. 1967.
Fig. 2.6C. Song Variant, by M3, during dawn calling. 1 May 1967.



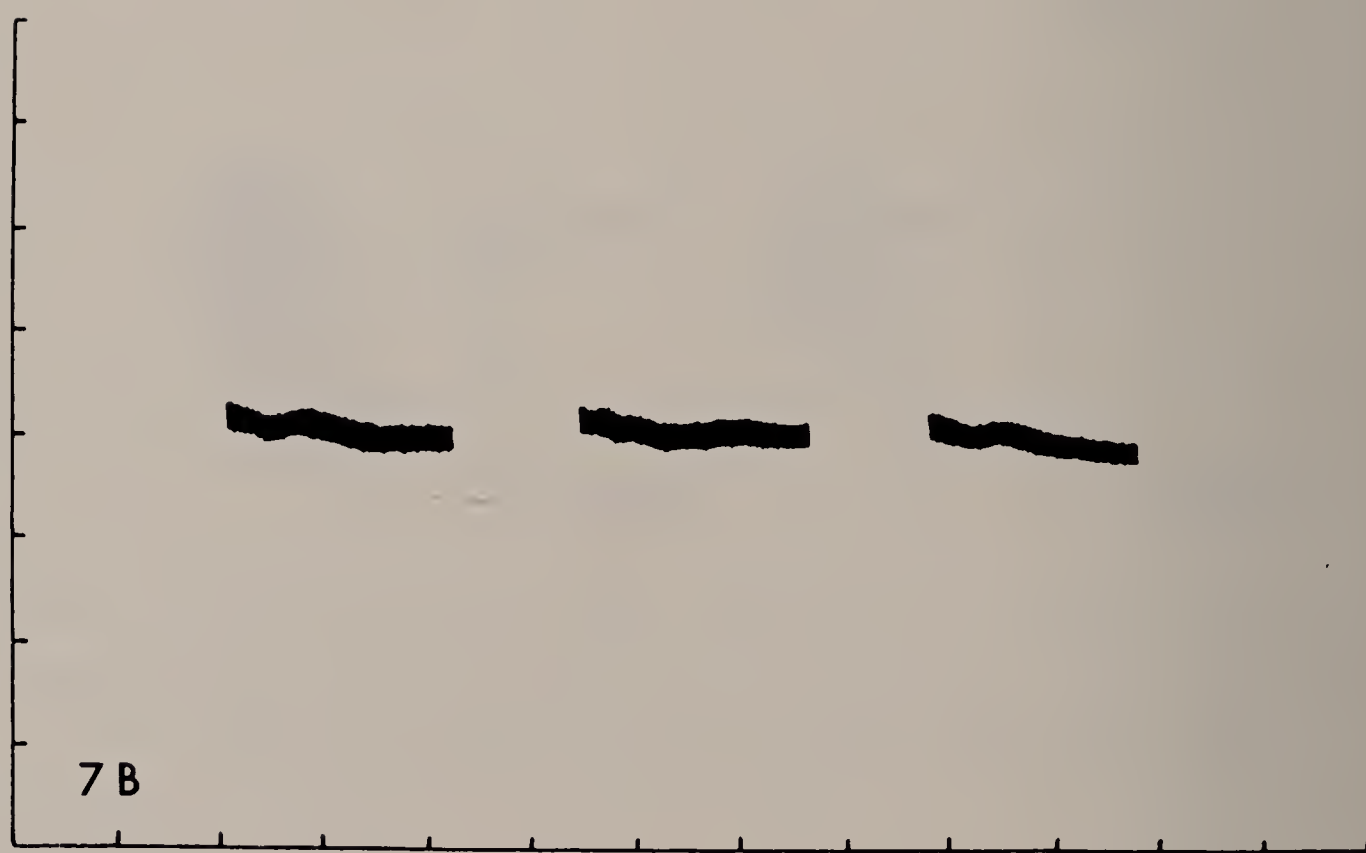
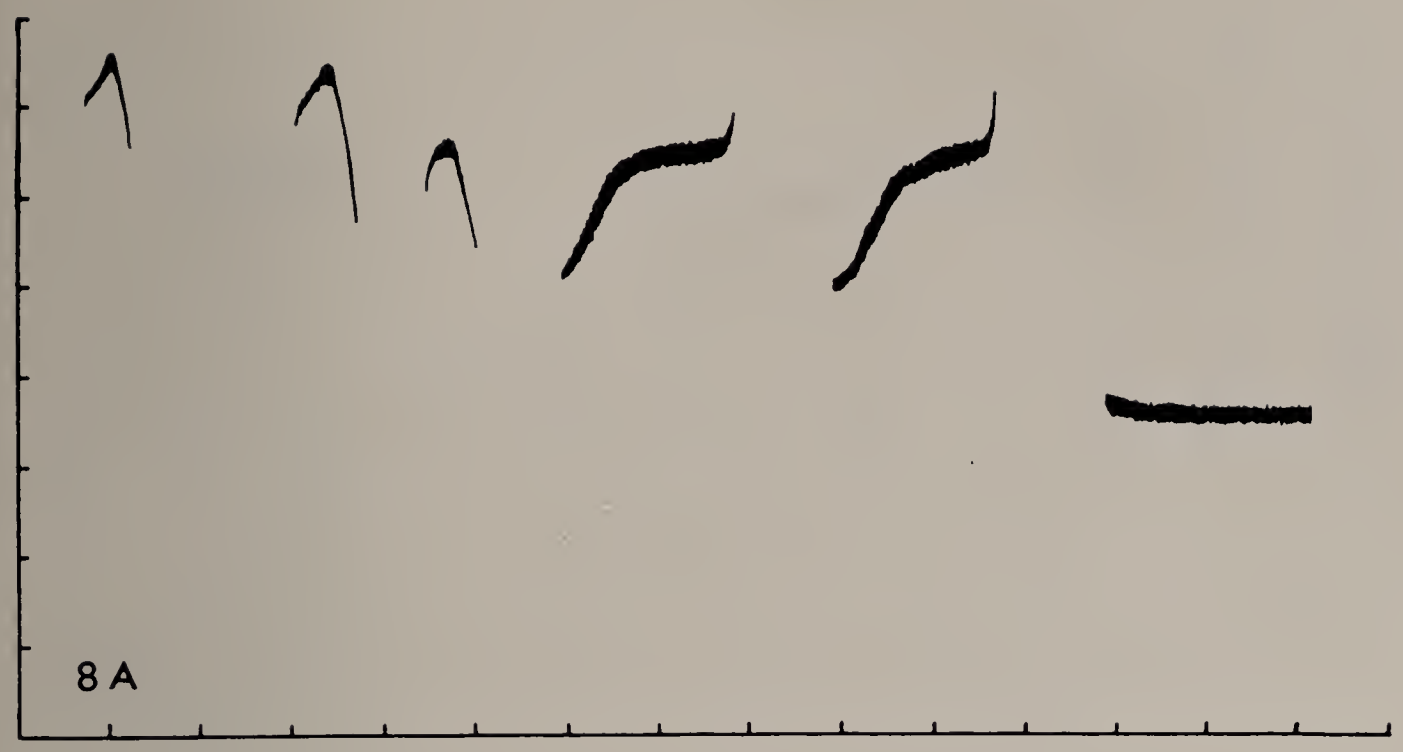




FIG. 2.7A. Four-note Song, by a male in the study area in 1965. 27 June 1965.
FIG. 2.7B. Song Variant made up of low notes. Given by M1 after trying unsuccessfully to enter a trap in which he could see sunflower seed bait. 12 Sept. 1966.



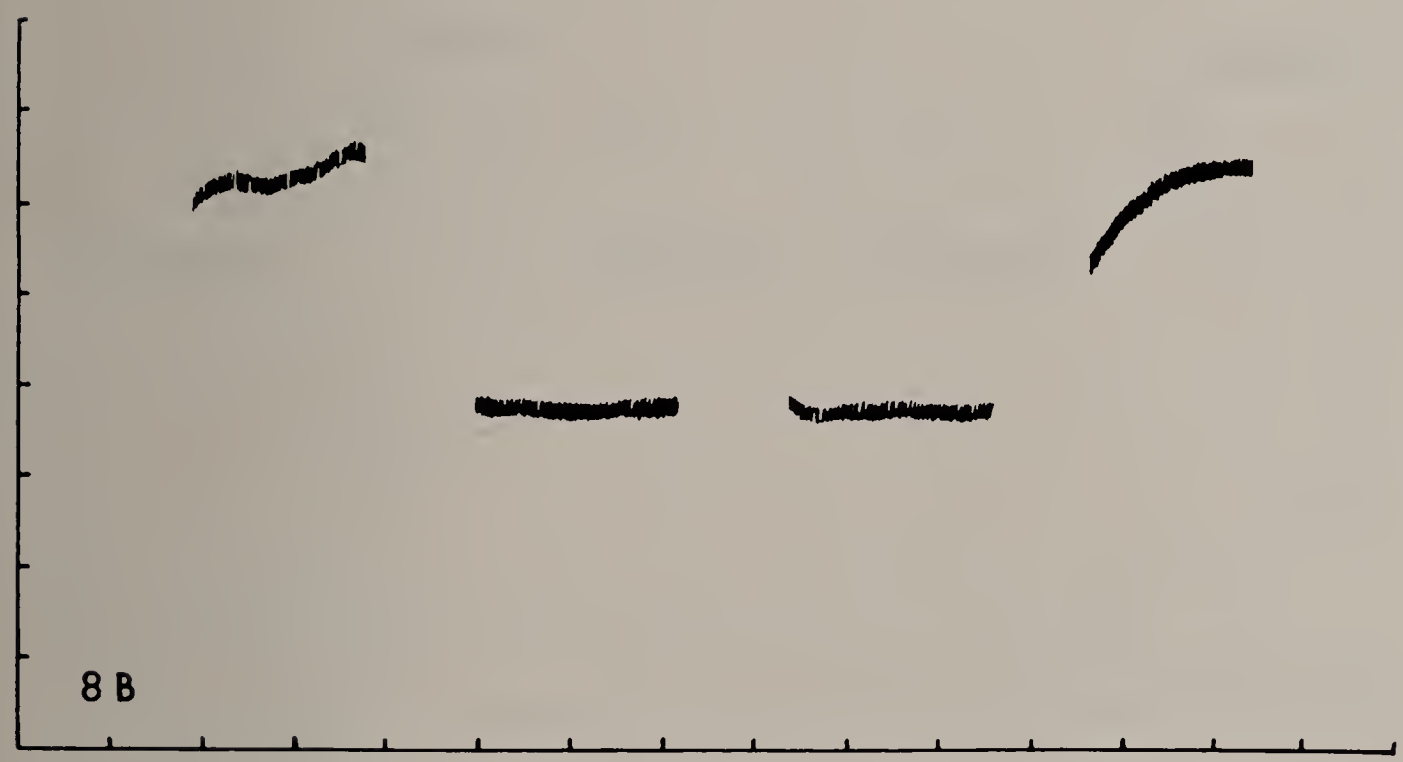
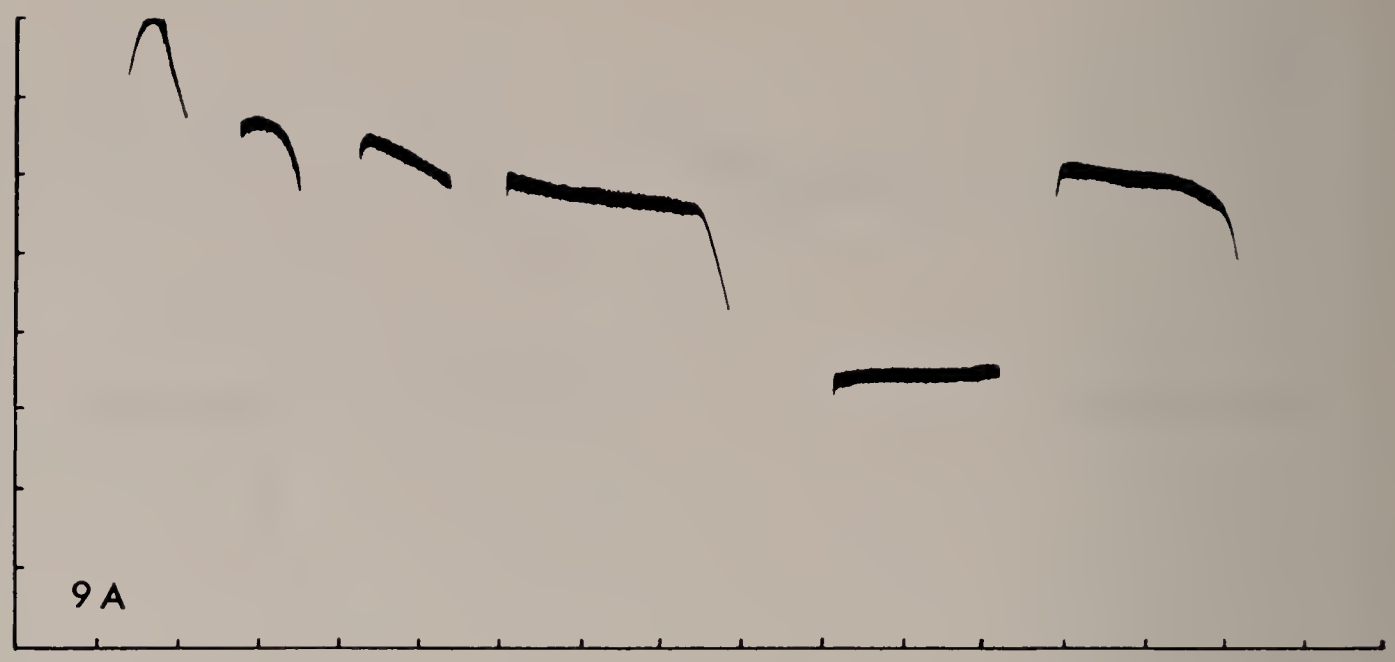




Fig. 2.8A. Three Lisping Tee notes followed by Faint Song Variant. Given by the 1965 male as he clung to nest entrance with his mate nearby, possibly giving a Nest Site Showing display. 1 May 1965.

Fig. 2.8B. Faint Song Variant, by M3, just before going to nest entrance to feed F3. 9 May 1967.



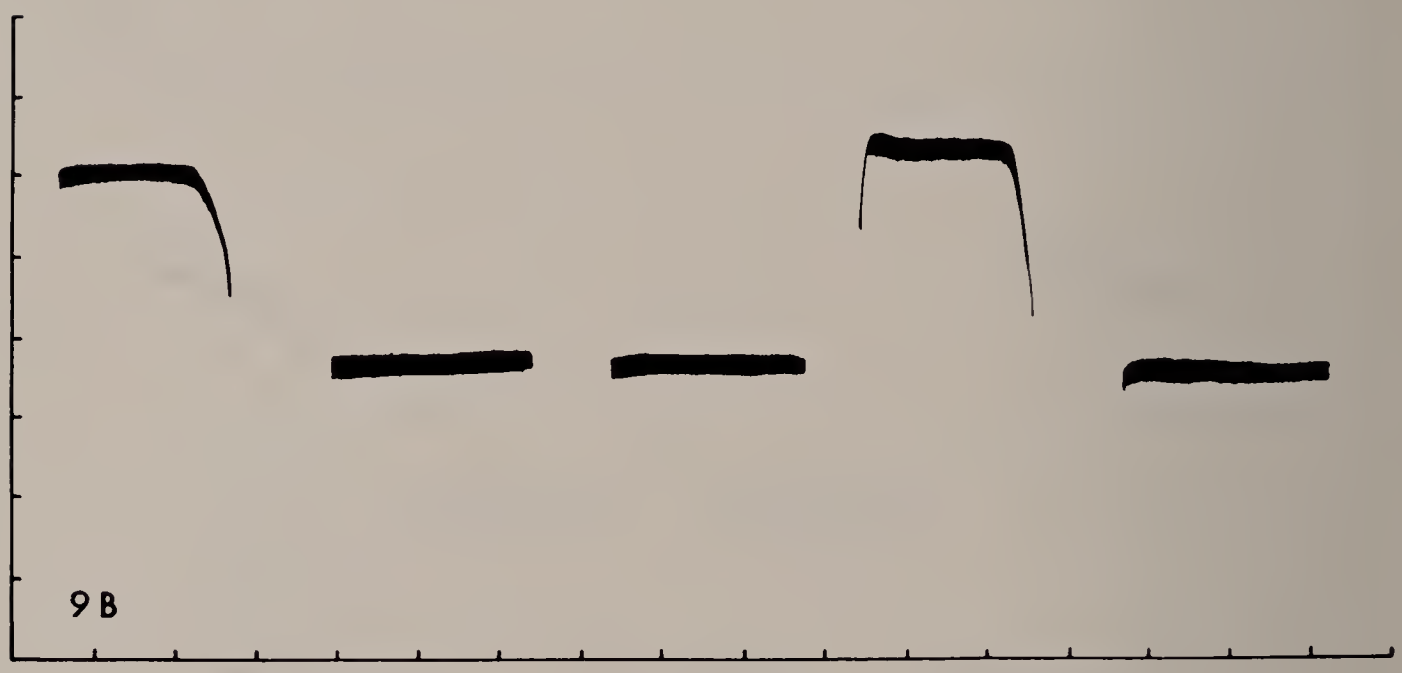
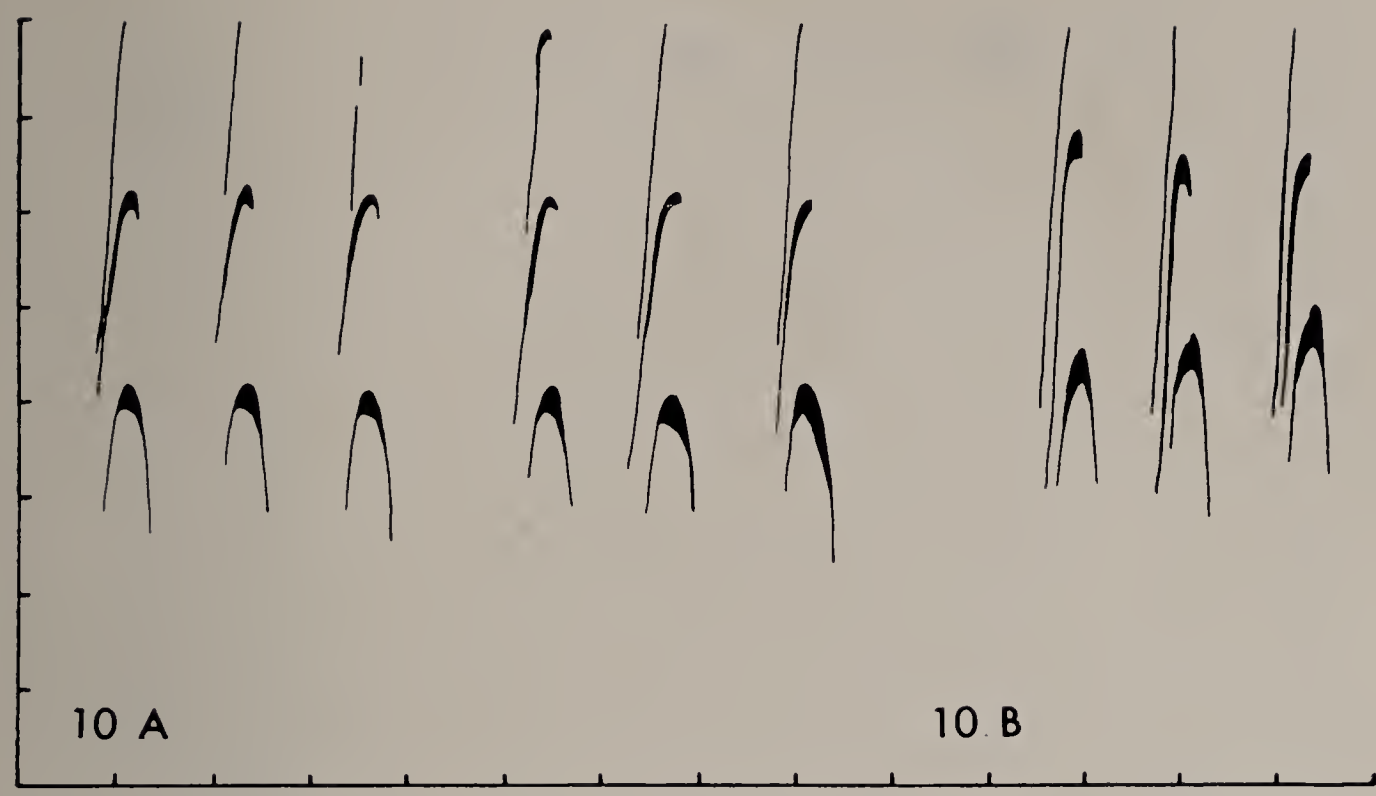




FIG. 2.9A. Three Lisping Tee notes followed by Faint Song. Given by M3 approaching box to feed F3. 1 May 1967.

FIG. 2.9B. Song Variant, By M3 during dawn calling. 16 Mar. 1967.



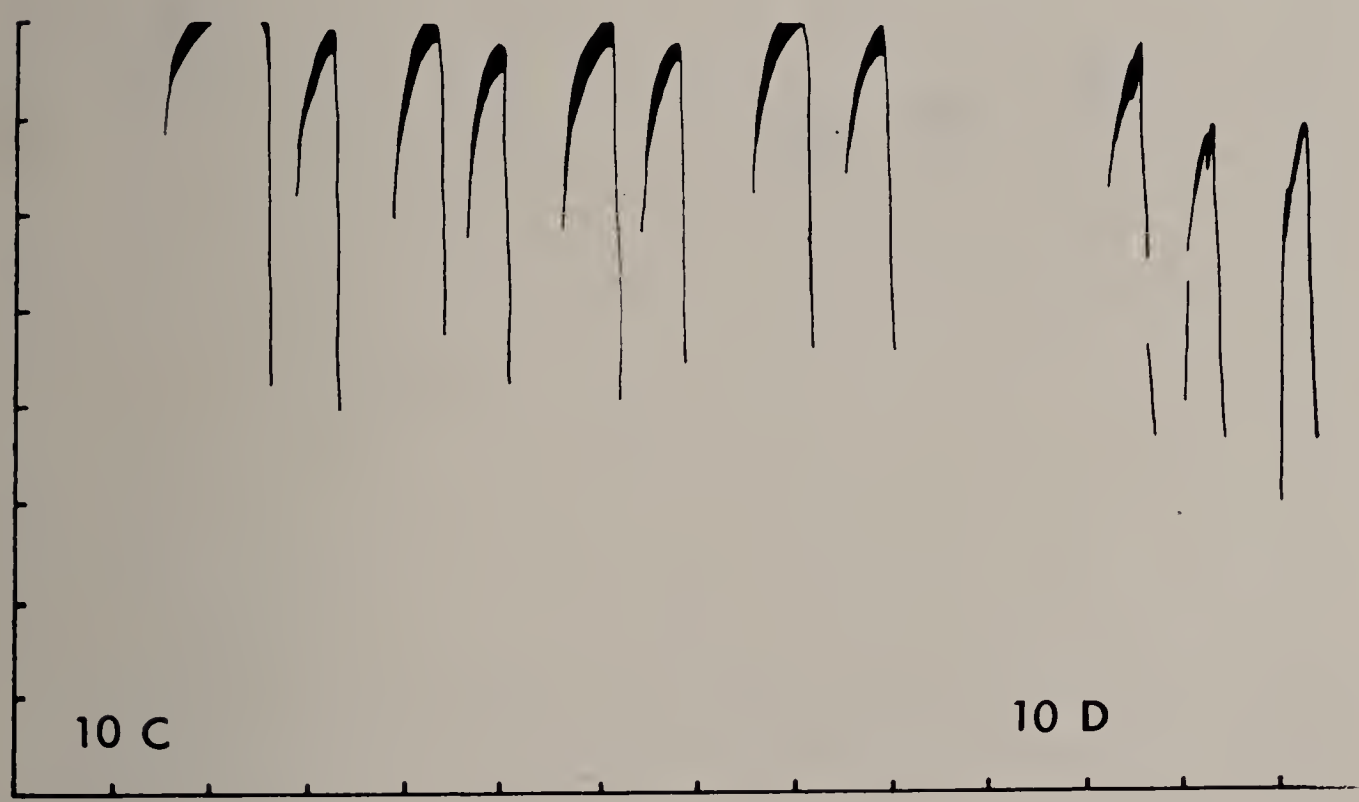
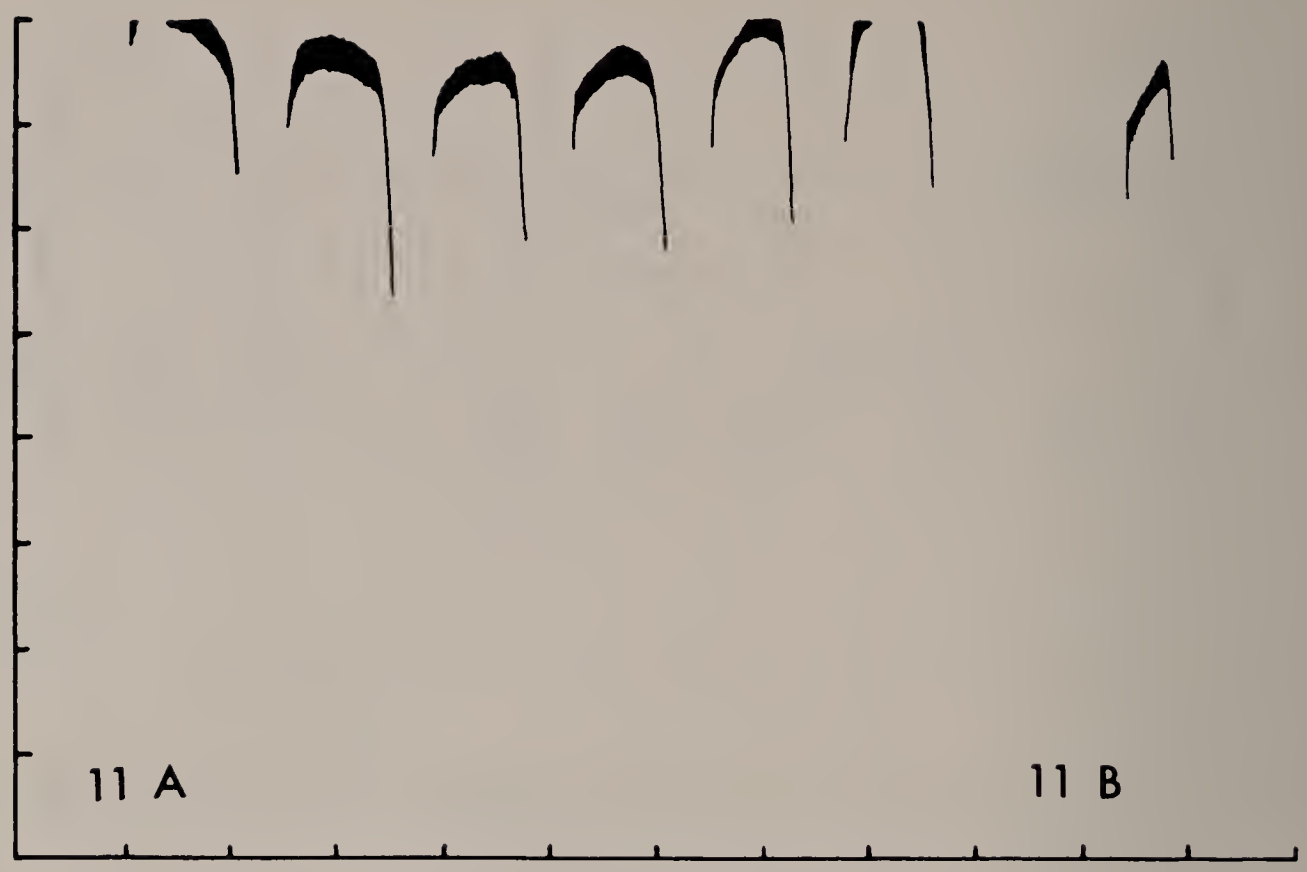




Fig. 2.10A. Chip series, given by an unidentified bird during a 2-pair dispute. 9 Oct. 1966.

Fig. 2.10B. Chip series, by Fl, alone, foraging, apparently patrolling. 12 Dec. 1966.

Fig. 2.10C. Abrupt Tee series, by a chickadee in a box trap with a Tufted Titmouse. Note slight tendency for the series to break into couplets. 11 Dec. 1965.

Fig. 2.10D. Abrupt Tee, another example by the same chickadee as in 10C. There is a slight tendency for the ascending arm to break.



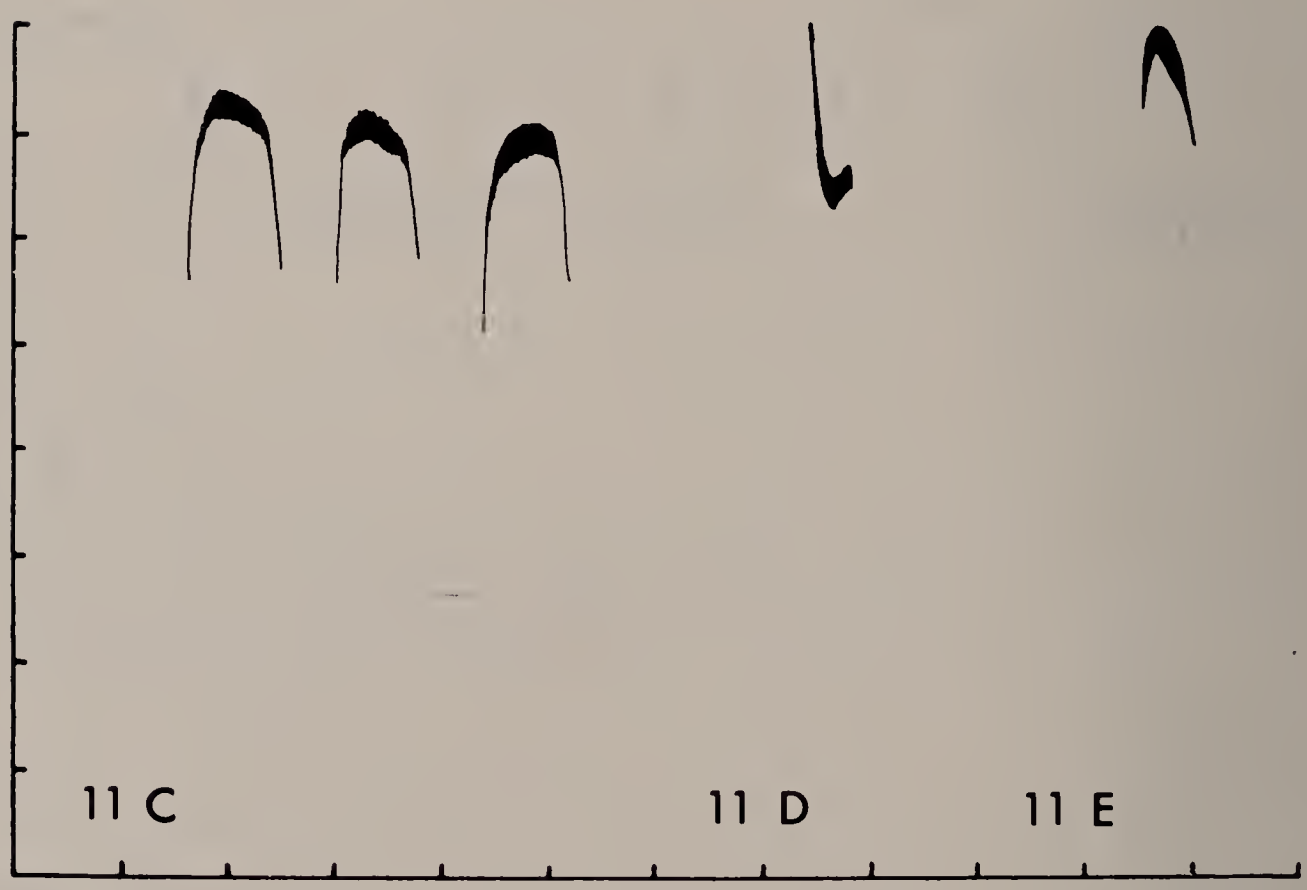



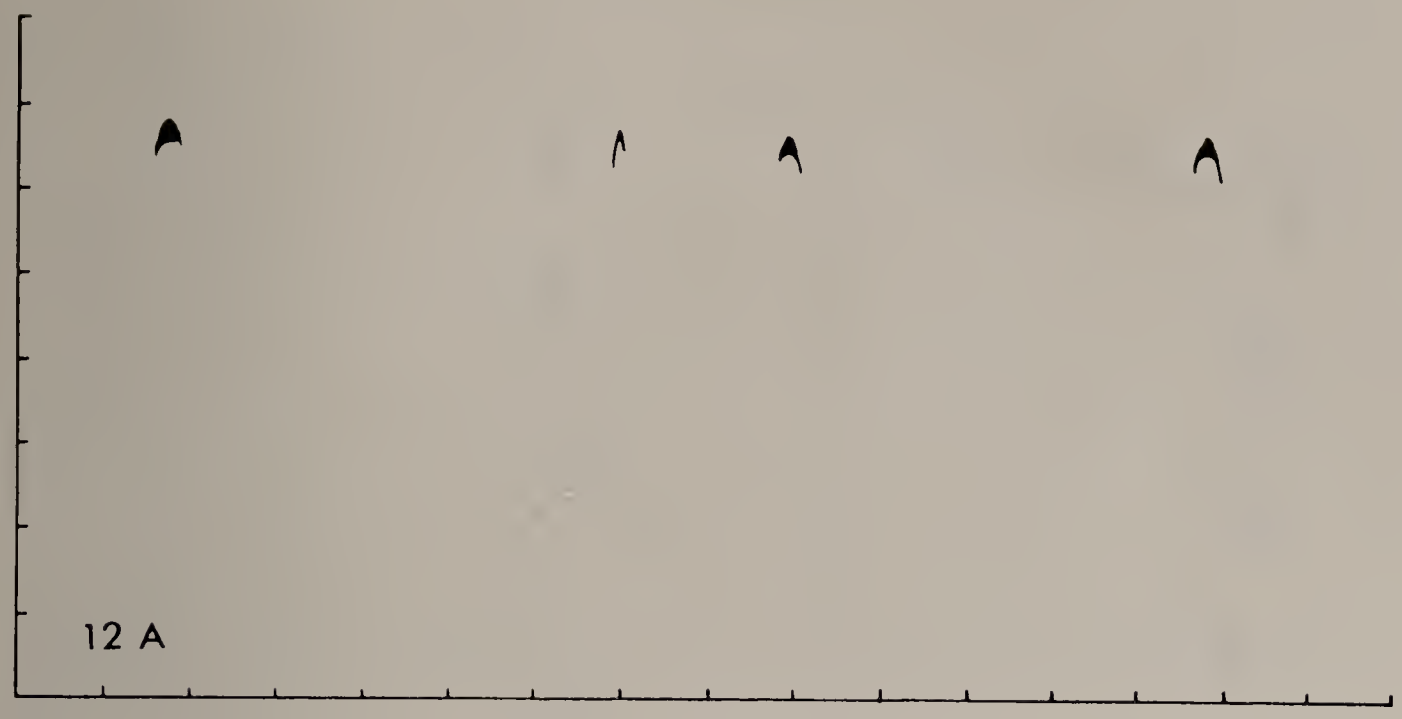

Fig. 2.11A. High See series, by M3 disturbed by presence of observer as he approached nest to feed young. 21 May 1967.

Fig. 2.11B. Tseet note, by an unidentified chickadee visiting a feeding station. 10 Feb. 1966.

Fig. 2.11C. High See series, by F2, apparently disturbed by a Tufted Titmouse which joined her on a feeding platform. 14 Oct. 1966.

Fig. 2.11D. Tseet note, given by the 1965 male as he perched near the observer immediately after being banded; then he flew away. 7 Mar. 1965.

Fig. 2.11E. Tseet note, by an unbanded chickadee near a feeding station. The bird looked down at the observer and gave this call. 9 Oct. 1966.



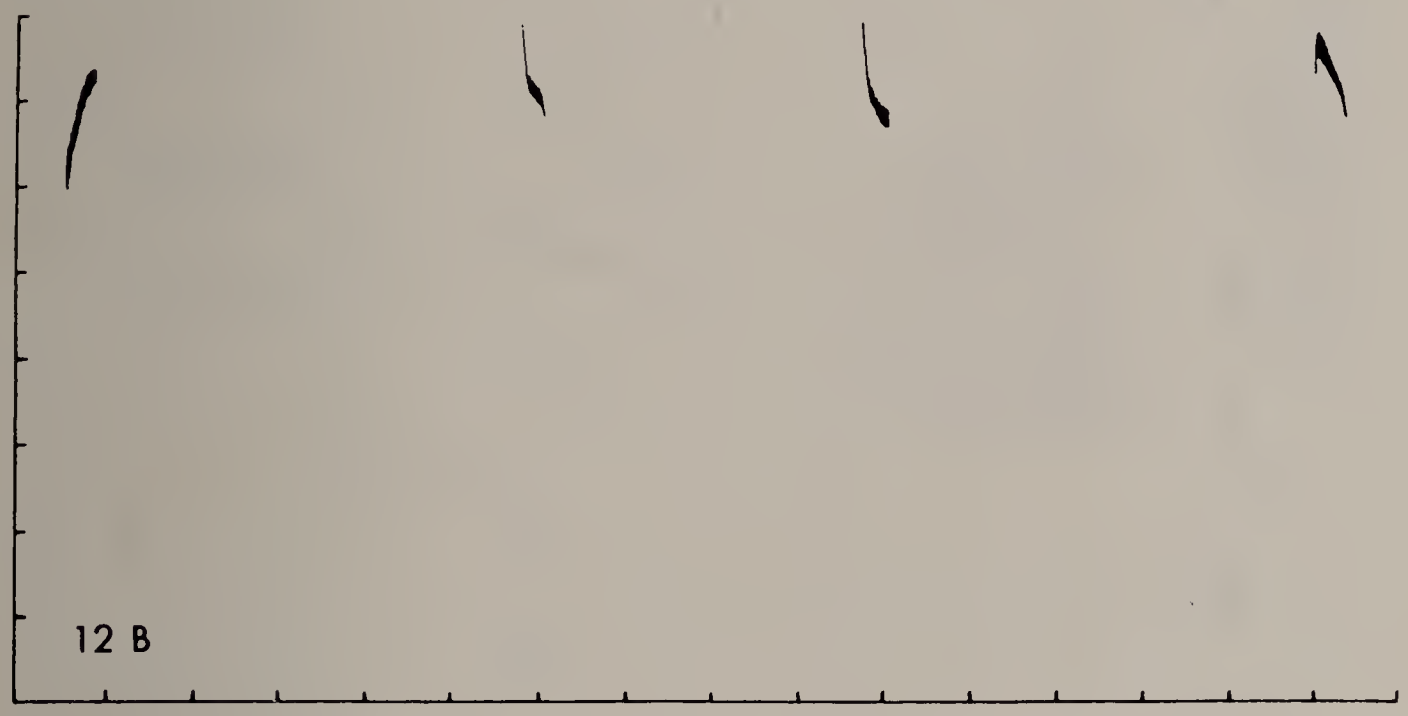




FIG. 2.12A. Tseet notes, given as M2 hopped close past M1; no attack followed. It is not known whether M2, M1, or both males called. 14 Oct. 1966.

FIG. 2.12B. Tseet notes, given as F2 landed close behind her then mate, M2, on a feeding station. It is not known if one or both called. 9 Oct. 1966.

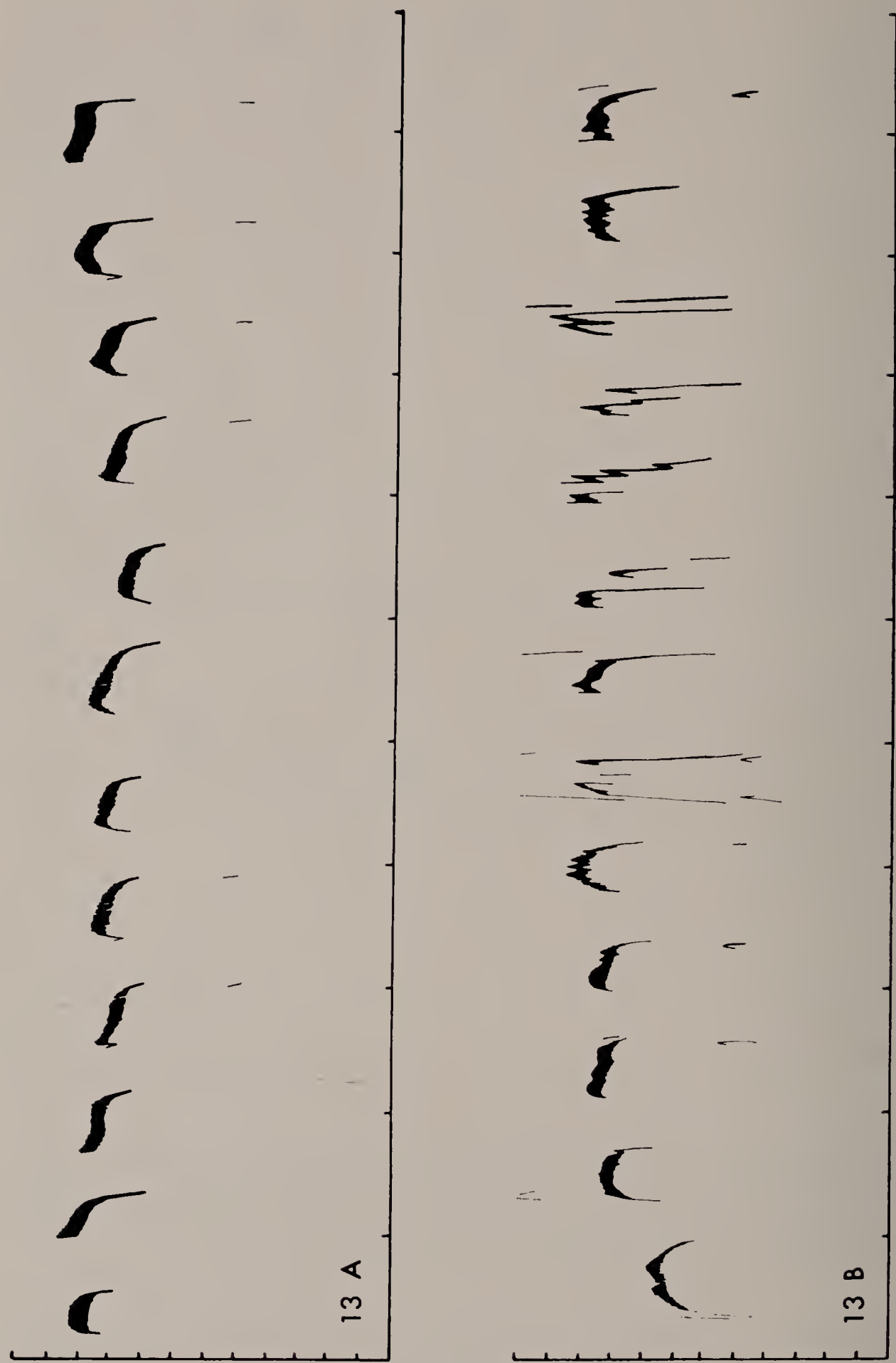
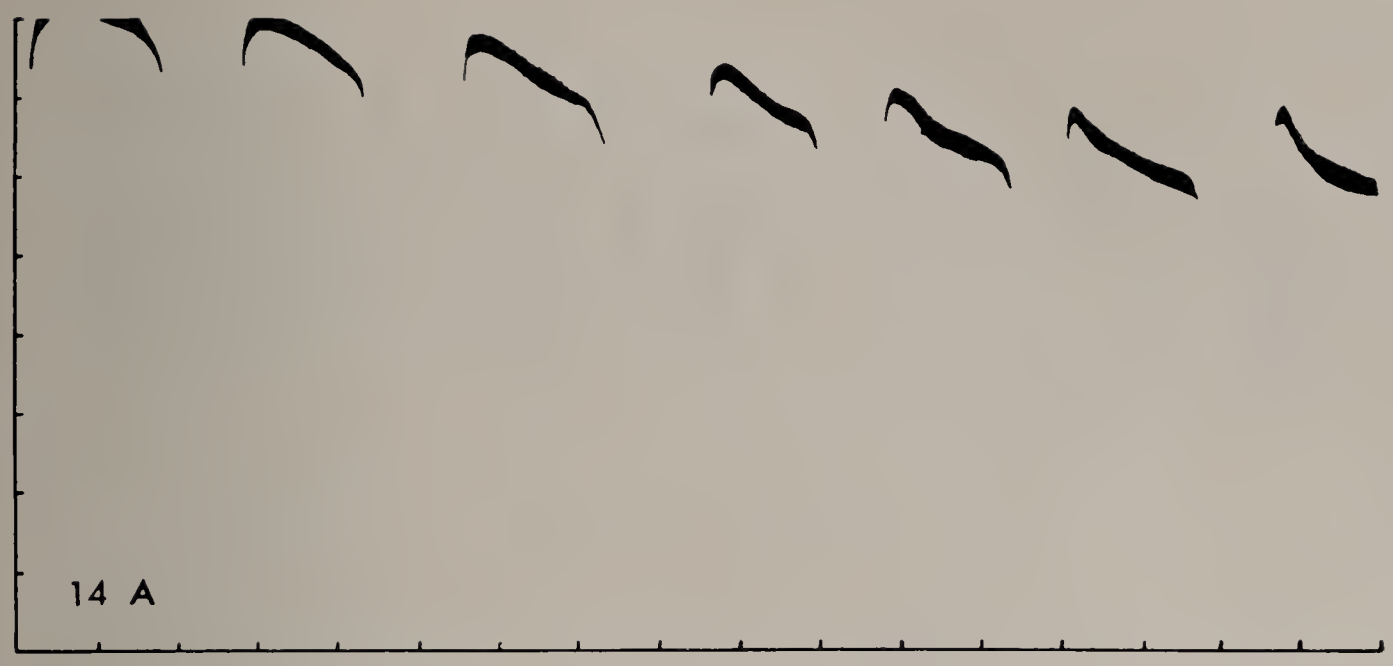



FIG. 2.13A. Variable See series, by M3, near his nest and mate. 15 Apr. 1967. (Vertical scale 0–12 kHz.)
FIG. 2.13B. "Broken" Variable See, part of the same burst of calling as in 2.13A.



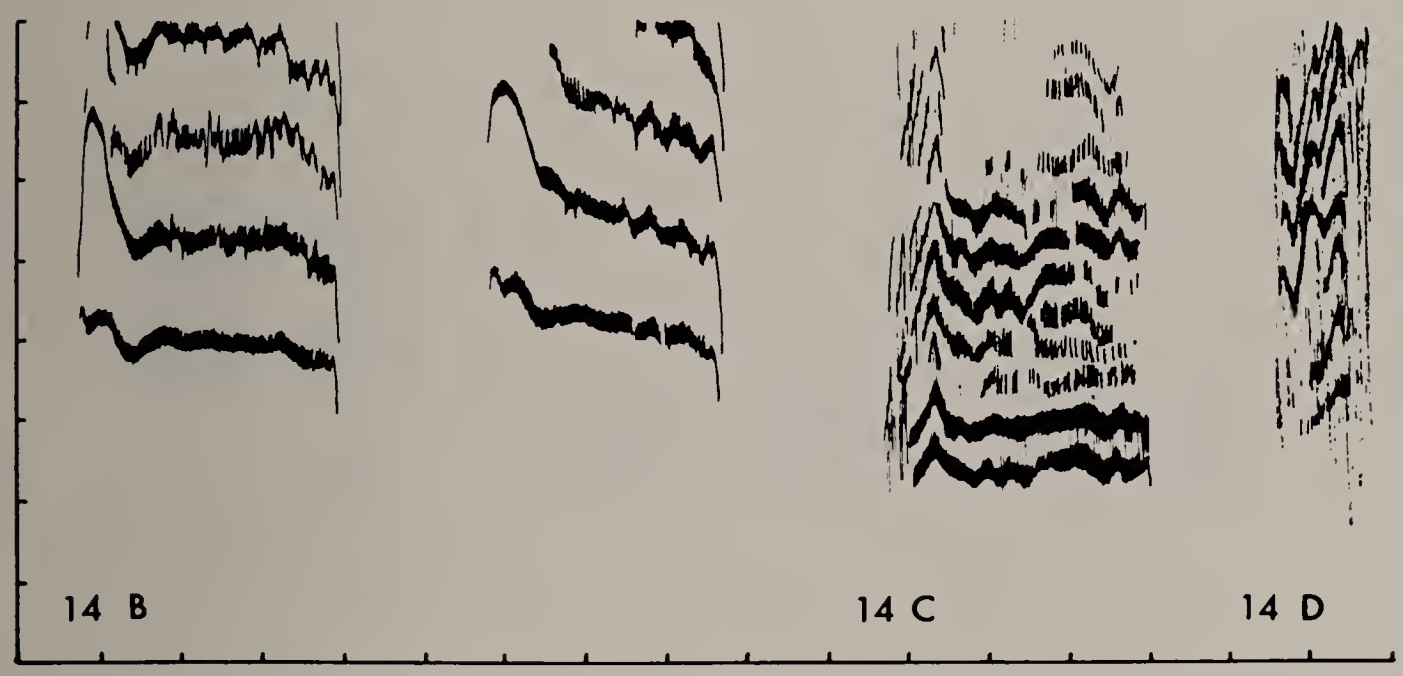
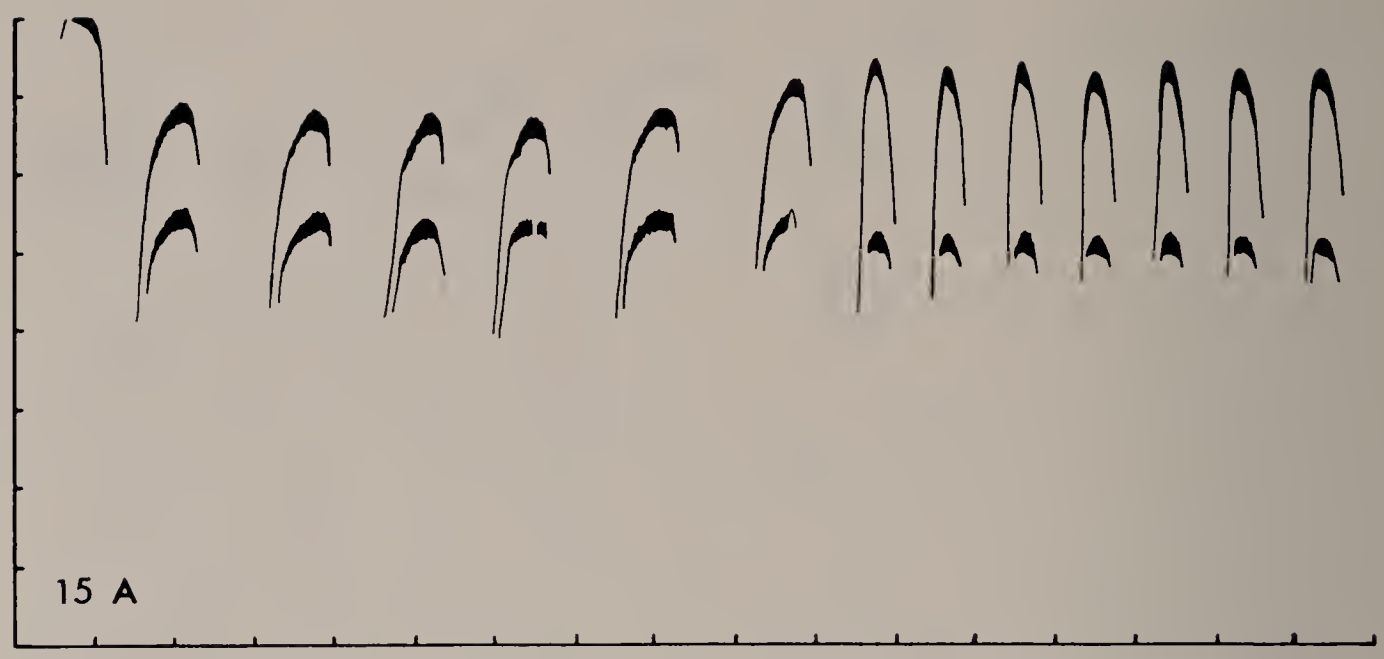




Fig. 2.14A. Series of Squeal notes, given by a chickadee in a box trap with a Tufted Titmouse. 11 Dec. 1965.

Fig. 2.14B. Two Scream notes, part of a longer series, by the same bird as in 14A.

Fig. 2.14C. Nestling distress call, given as the bird was taken in the hand for banding. 25 May 1967.

Fig. 2.14D. Nestling distress call, given during a short flight. 25 May 1967.



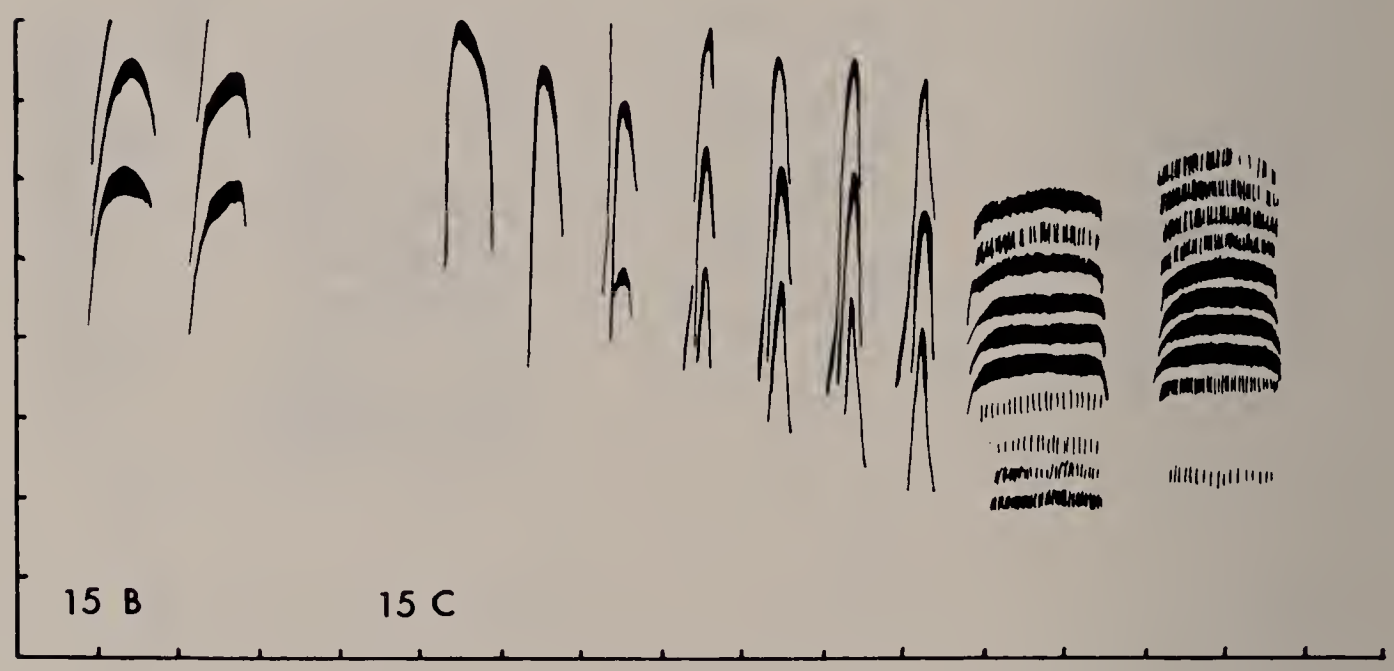
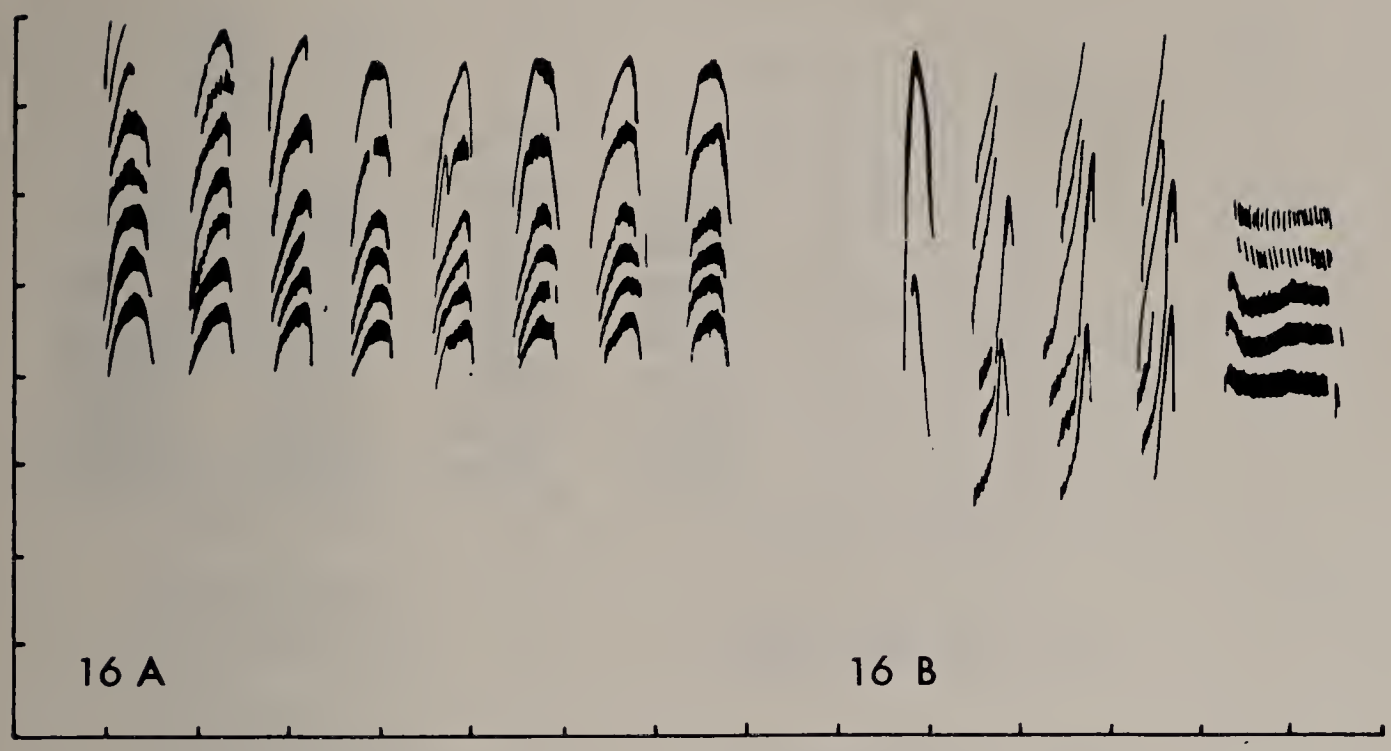




Fig. 2.15A. Loud Tee followed by High Tee, given by M3. The Loud Tee notes were given in flight, the High Tee notes after landing. 16 Apr. 1967.

Fig. 2.15B. Two Loud Tee notes, by F1, pausing before going to a feeding station. 6 Oct. 1966.

Fig. 2.15C. Two High Tee notes, a High Tee-Chick intermediate, 4 Chick notes, and 2 Dee notes. Given by the 1965 male while in a box trap, prior to banding. 7 Mar. 1965.



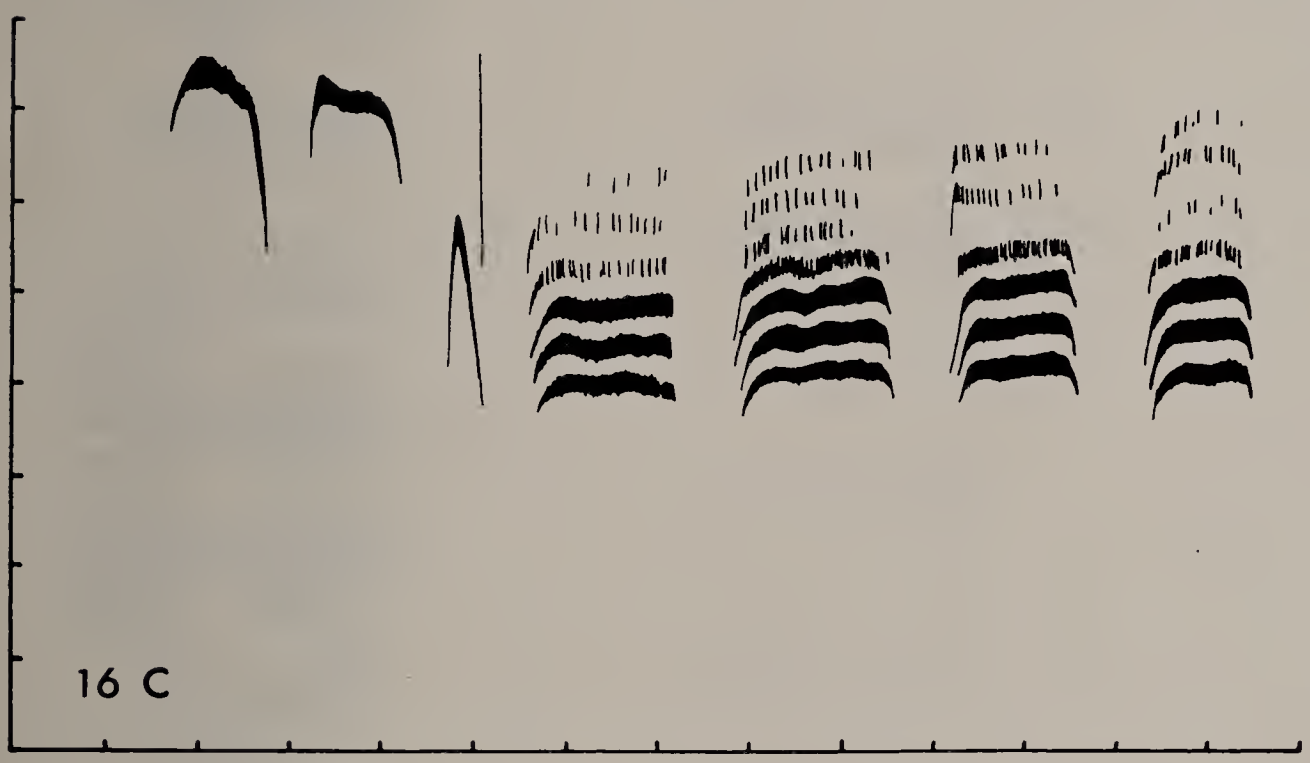
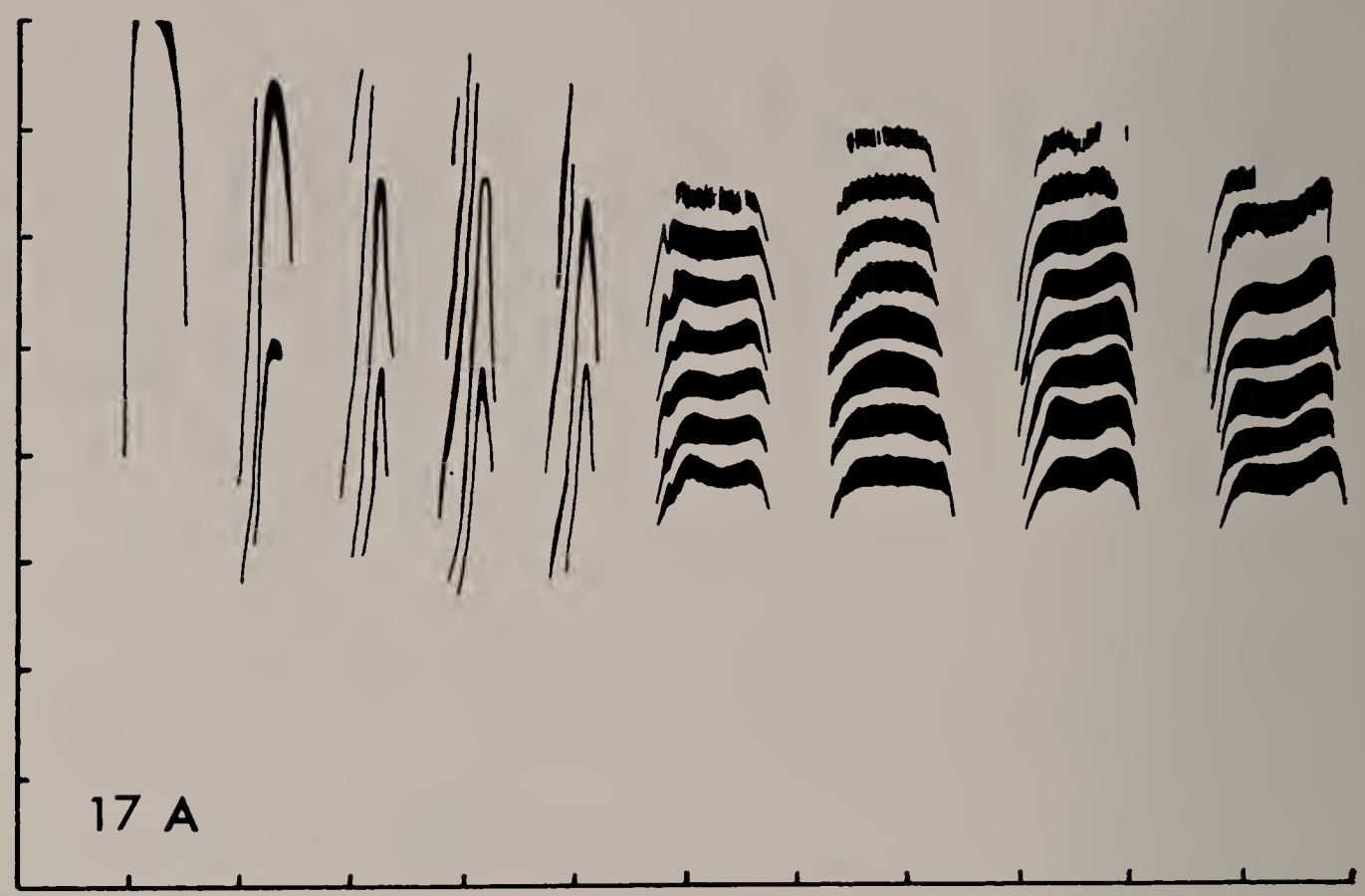




Fig. 2.16A. Rapid Dee series, given by F5 visiting a feeding station while the rest of the flock disputed nearby with a neighboring flock. 9 Nov. 1966.

Fig. 2.16B. High Tee note, 3 Chick notes, and a Dee note. The narrow chevron at the beginning of the Dee note suggests a Chick note. Given by Fl, alone, foraging, and apparently patrolling. 12 Dec. 1966.

Fig. 2.16C. Two High See notes, a High Tee note, and 4 Dee notes. Given by M3 just before approaching Pair 6–5 and engaging them in a dispute. 26 Mar. 1967.



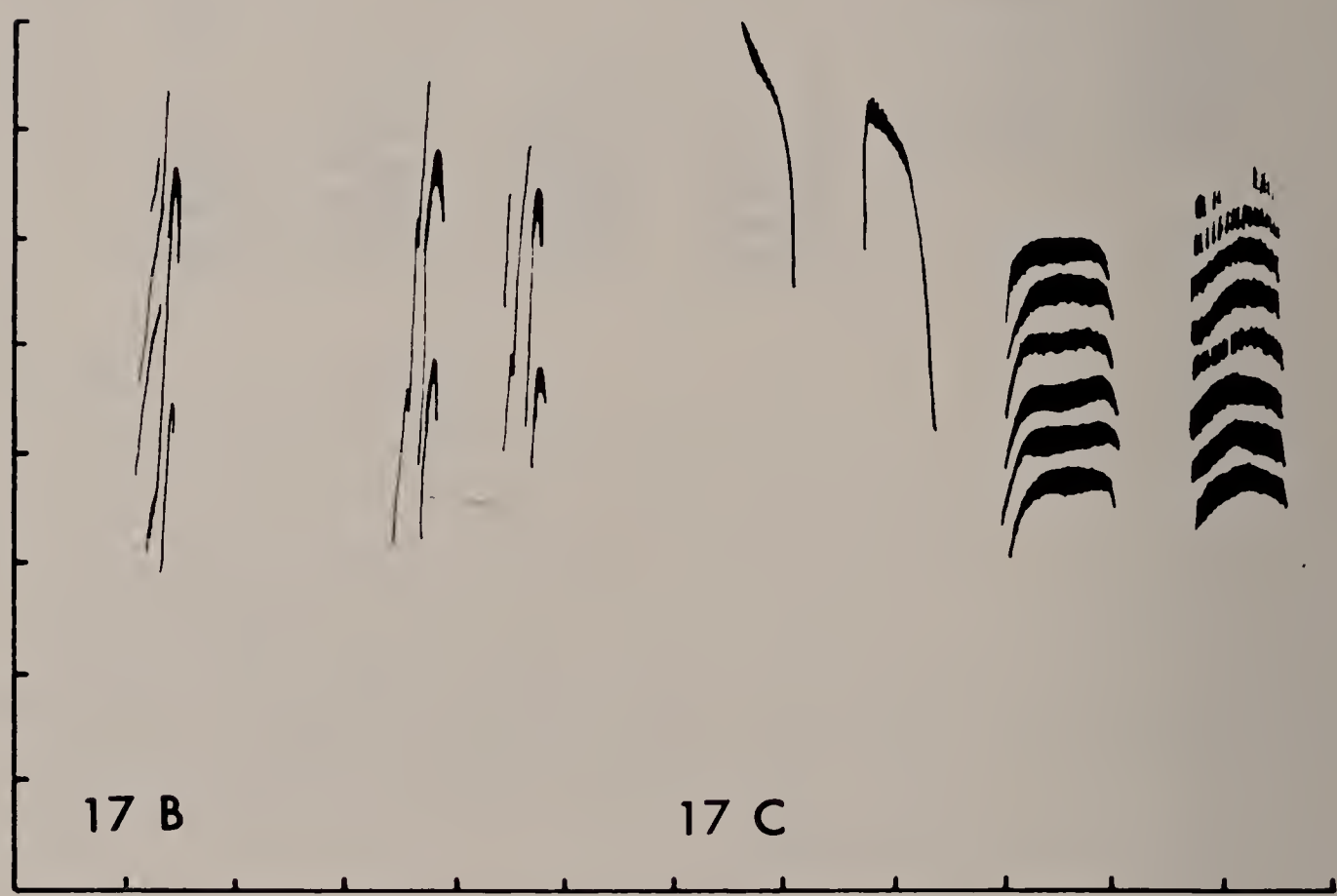
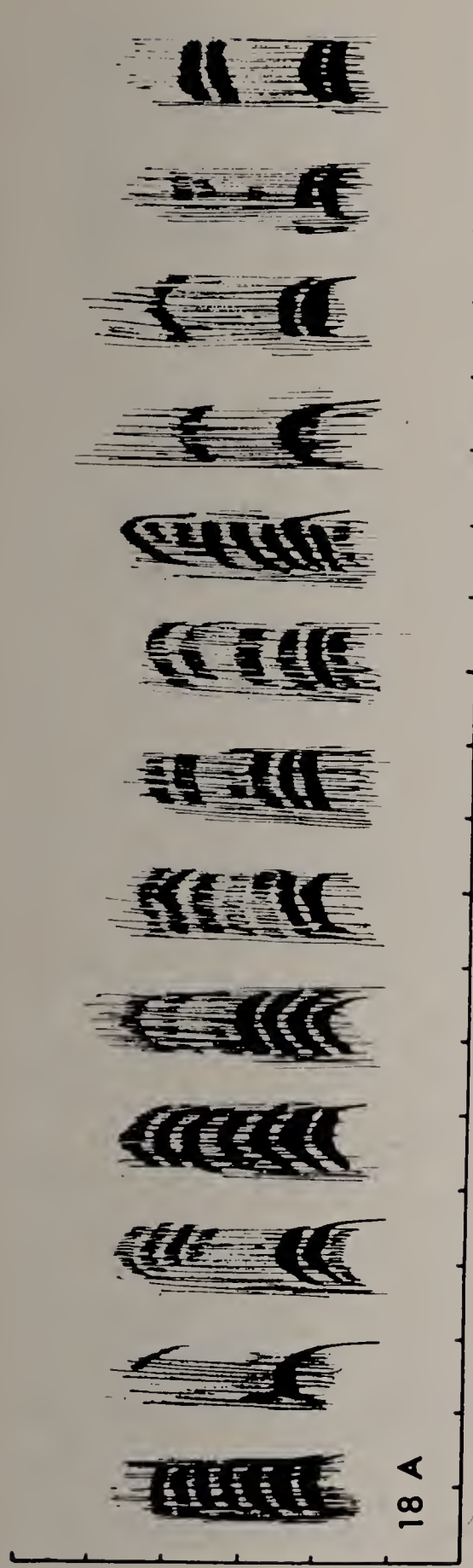




Fig. 2.17A. High Tee note, 4 Chick notes, and 4 Dee notes, given by F5. She scolds near her nest excavation as her mate skirmishes with Pair 3–3 about 50 feet away. 26 Mar. 1967.

Fig. 2.17B. Chick series, given by an unidentified chickadee shying away from a feeding station. 3 Oct. 1966.

Fig. 2.17C. Two Lisping Tee notes followed by 2 Dee notes. M3 gave these on alighting after flying from his nest entrance where he had fed F3. 1 May 1967.



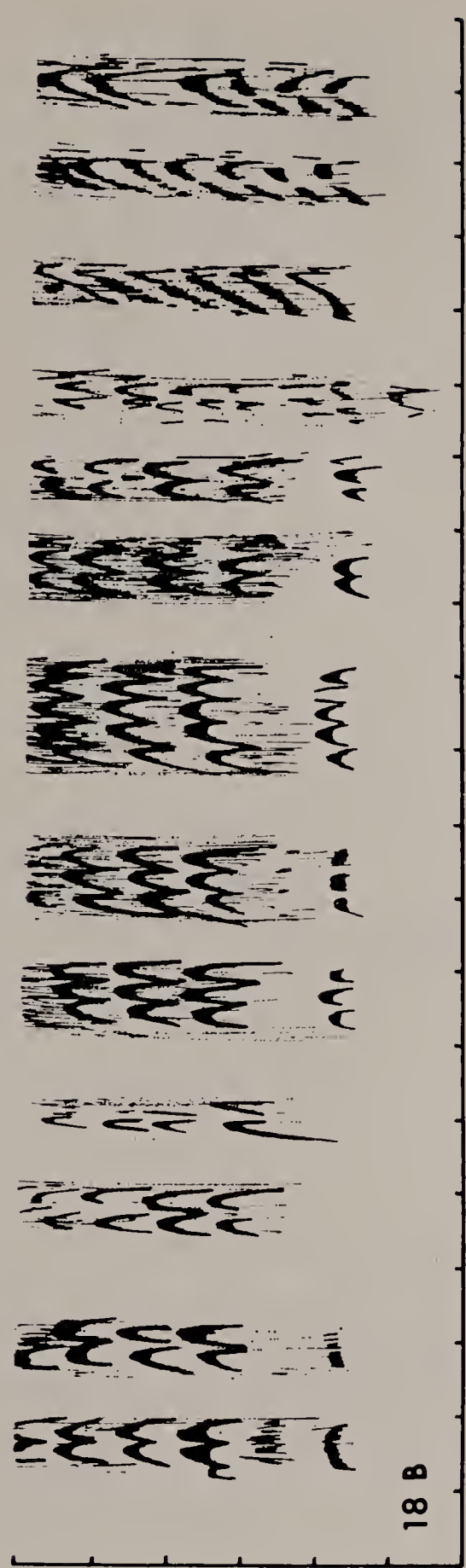
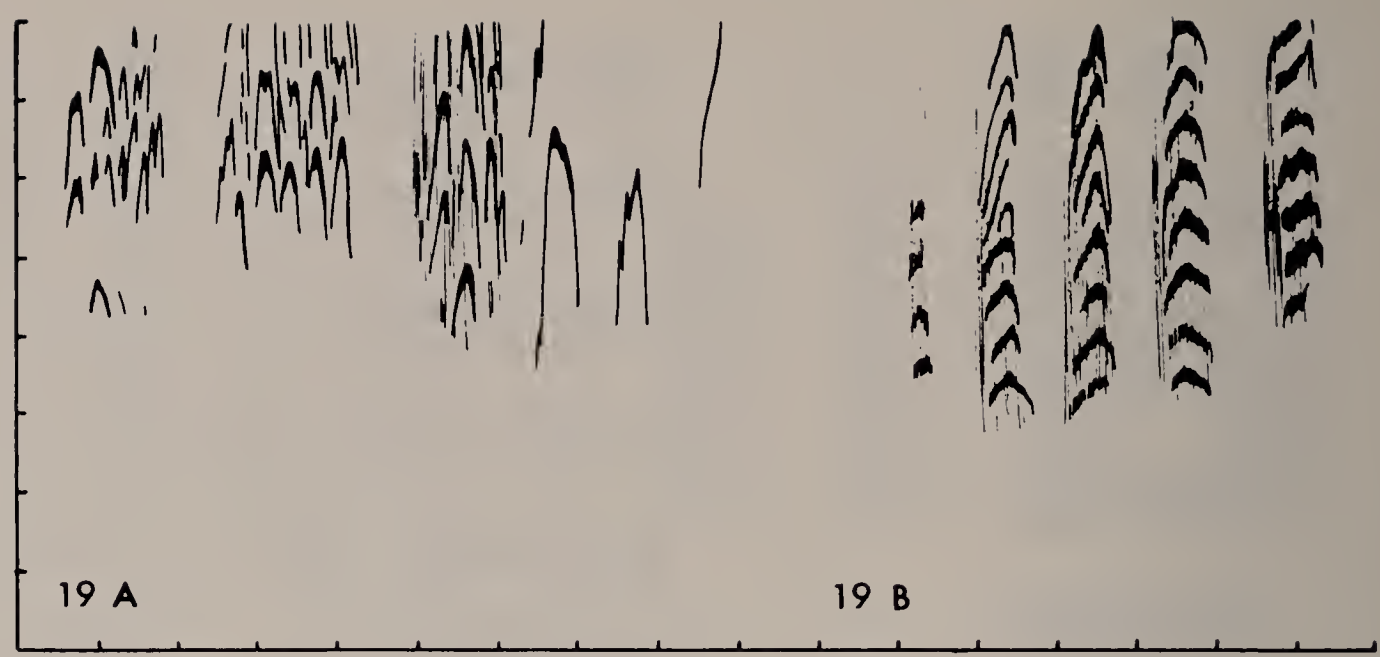




FIG. 2.18A. Harsh Dee series, given by an unbanded bird; M2 approached this bird immediately after these calls and the two engaged in a stand-off dispute. 30 Oct. 1966. (Vertical scale 2–8 kHz.)

FIG. 2.18B. Begging Dee series, by the mate of the 1965 male. 1 May 1965.



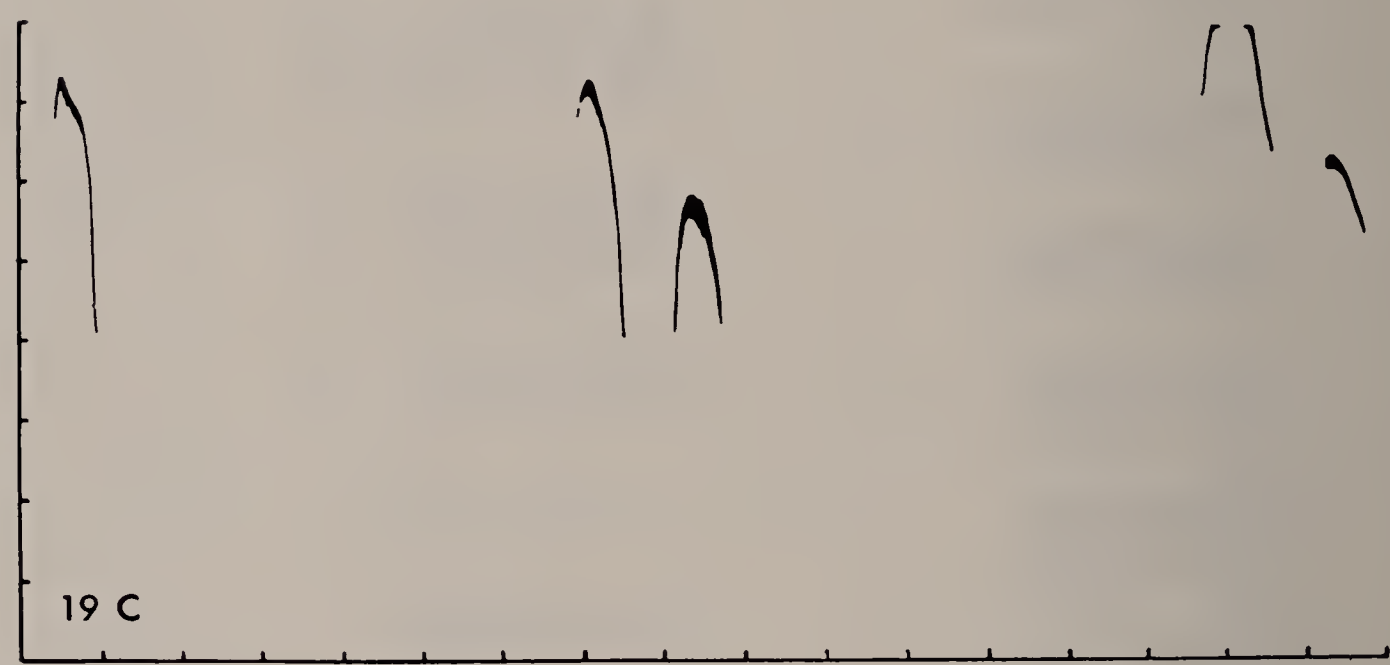
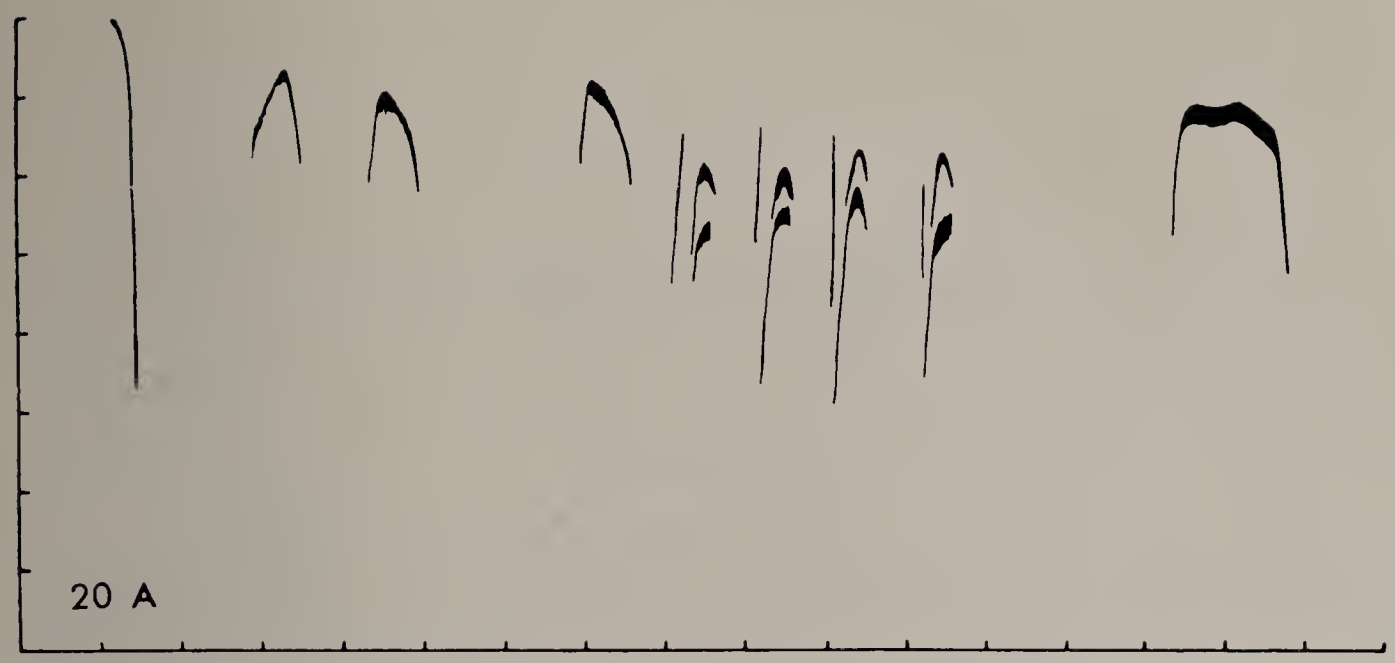




Fig. 2.19A. End of a Begging Dee series terminating in a trill. Given by F3 as her mate approached to feed her. 24 Apr. 1967.

Fig. 2.19B. Begging Dee notes, given by a large nestling. 24 May 1967.

Fig. 2.19C. Lisping Tee notes, given by an unidentified chickadee flying away from his companion, which then followed the caller. 14 Oct. 1966.



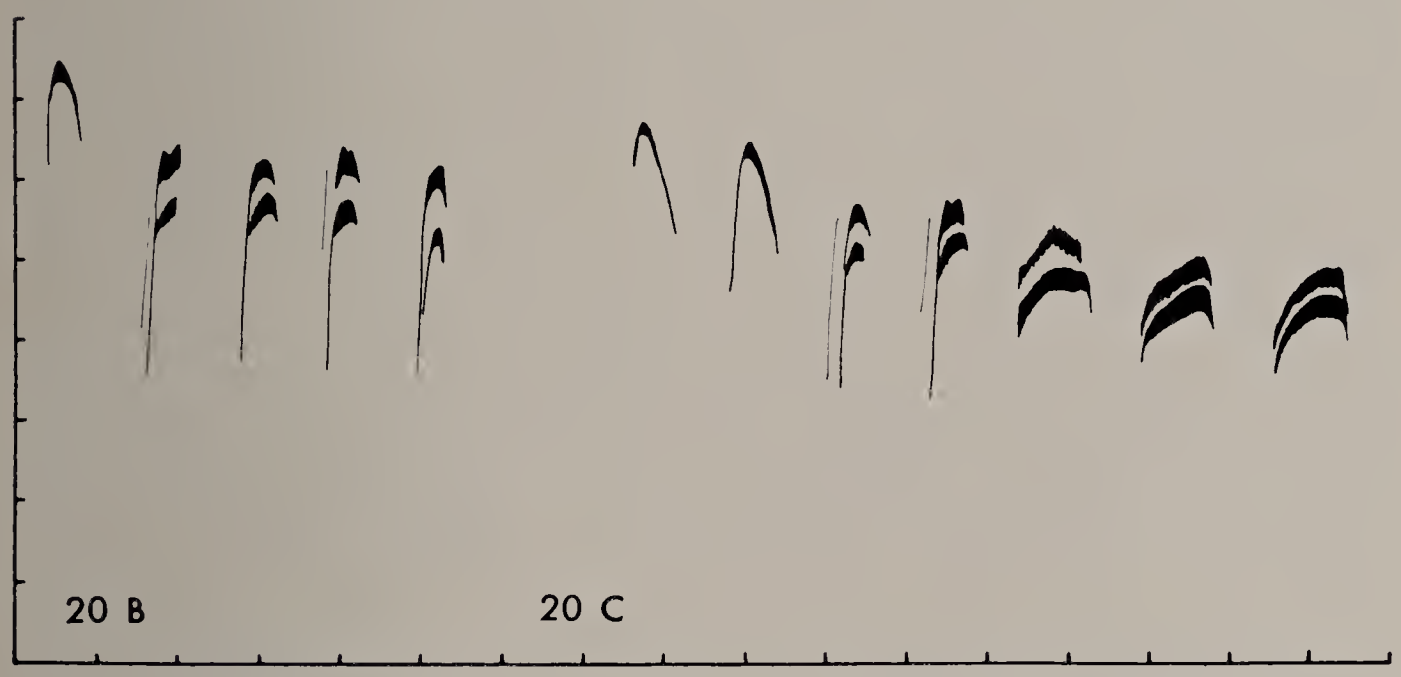




Fig. 2.20A. Four Lisping Tee notes, 4 Soft Dee notes, and one Song note, part of a longer series of these notes given by M6 as he flew away from F5 shortly after a probable copulation. 25 Apr. 1967.

Fig. 2.20B. One Lisping Tee note followed by 4 Soft Dee notes. Given by M6 flying away from F5 after feeding her. 24 Apr. 1967.

Fig. 2.20C. Two Lisping Tee notes, 2 Soft Dee notes, and 3 notes intermediate to Soft Dee and Dee notes, probably given by F1. 24 Oct. 1966.

# 3

# NON-VOCAL DISPLAYS

## Introduction

In the field, primary attention was directed to vocalizations and relatively little to non-vocal displays, many of which are not obvious unless the chickadee is very close by or under inspection through binoculars. Gathering information about non-vocal displays usually required single-minded attention to their performance, to the exclusion of gathering other important information, for example, the identity, location, and activities of other chickadees. The latter kinds of information usually were regarded as sufficiently important to warrant the sacrifice of detailed information on non-vocal displays. Consequently, little information was gathered on all but a few rather flamboyant ones.

It seems likely that for Carolina Chickadees there is no category of message that is encoded by visible displays that is not also encoded by one or more vocal displays. Visible displays have some additional advantages over vocal displays in that the signalling chickadee may attract less attention to himself, and can direct the displays rather specifically to particular recipient(s) by assuming a particular orientation of his body. On the other hand, visible displays are less good for broadcast "advertising" and are useless if the recipient is not looking at the communicator.

Anything a bird does must be informative in some sense. However, only those activities that have been specialized through evolution to function primarily in signalling are labeled "displays." Some activities are easily recognized as displays, while for others it is not clear whether or not they have undergone evolutionary specialization. The latter category is made up of activities that differ only slightly from non-display behavior, but are used in such a way as to suggest that they may be displays, i.e., they are functionally like displays. While vocalizations are obviously displays and many visible displays are also easy to recognize, some activities are of uncertain status and may or may not be visible displays. Displays and activities that function like displays are here called "signals."

The recognizable visible displays are made up of special postures, special body movements, special plumage movements, and combinations of these.

## Displays

### 1. Bill-up and Wing Droop

*Description:* A chickadee giving the Bill-up display tilts its head so that the bill points vertically or nearly so. Its body is usually stretched upright; sometimes the wings are drooped, but the carpals remain close to the body. Occasionally a bird gives a Bill-up from a crouched or cowering position. Two-note Song, T-slink, Click-rasp, and High Tee-Dee series may be used with Bill-up, but often the display is silent.

*Usage:* Bill-ups are always given in direct, close confrontations between two birds. The displayer may or may not face his intended recipient but no cases have been observed in which there was any ambiguity about who was interacting with whom.

The display was given by a bird under actual or potential threat. The most commonly observed usage was for a bird on a feeder to Bill-up when it was joined by another. Several such cases were observed in Pair 2–2; F2 gave most of the Bill-ups. Usually the bird that Bill-upped on a feeding platform waited for the other to feed first, and sometimes even retreated slightly. This may, in part, have been because so many Bill-ups were given by females toward their mates, and such deference was the rule by a female to her male. No cases were observed in which attack followed a Bill-up display.

The recipients gave a variety of responses, including: sitting quietly; retreating; taking seed and leaving; advancing, but not attacking; and giving Body Ruffling, but not attacking (Body Ruffling is discussed below). In a few cases the recipient also Bill-upped; these amounted to standoffs.

*Message:* A chickadee giving Bill-up seems to be in a mood of defensive aggression or, in other words, is prepared to fight if attacked. Since Bill-upping individuals never were attacked, the meaning of Bill-up to recipients is clearly that one should not attack, unless, perhaps, the recipient is in a very aggressive mood.

### 2. Wing Flick

*Description:* In the Wing Flick the wing tips are very rapidly lifted over the back and then returned to rest position. The carpals remain close to the body. One to many Wing Flicks may be given at a time and these usually are spaced at least a second or more apart. It is a very commonly used display. It is associated with Tseet, High Tee, Chick, and Dee notes, if any calls are used, but often it is performed silently.

*Usage:* Wing Flick is used primarily when a bird is making a hesitant approach, e.g., to a feeding station or to another bird, or is uncertain about continuing some activity, such as remaining on a feeding platform vs. flying from the feeding station or remaining near an aggressor vs. retreating. The uncertainty of the bird in making

approaches in which Wing Flick is used is expressed in various ways. The bird may take an indirect route, stop frequently along the way, make some flight intention movements before actually flying, make hovering touchdowns on landings, and shy away from perches. A bird pursuing an activity and Wing Flicking may look around more than usual, bill wipe, and make flight intention movements, or do all three. Usually one can easily identify some feature of the situation that would make the bird hesitant—the observer, another chickadee, or another species.

*Message:* Wing Flicking is probably an expression of an escape tendency interfering with nearly any other type of behavior (general set).

### 3. Tail Flick

Tail Flicking is seen much more rarely than Wing Flicking, although it is used in much the same sort of situations. A Tail Flicking bird sometimes also Wing Flicks. It is not certain whether the motion is up-down, or down-up, or whether both are used.

### 4. Wing Quiver

*Description:* In the Wing Quiver the wings are drooped slightly, then rapidly fluttered in and out from the body. The wings may also open and close slightly with each quiver. Wing Quivering birds sometimes also crouch slightly and often orient directly toward their intended recipient.

*Usage:* Wing Quiver has been observed in four types of situations.

1. By birds losing badly in fights. Most chickadee squabbles do not result in one bird being badly beaten during a direct encounter, since losers usually withdraw before reaching that stage. Rarely an individual is badly defeated but remains near his opponent rather than fleeing immediately. Such birds may crouch and Wing Quiver, usually also with Variable See calling. In one such instance M2 was badly beaten by another male in the Club (31 December 1966). He Wing Quivered silently, facing his opponent, before withdrawing. On 7 January 1967 a prolonged two flock dispute involving several chickadees broke out. One bird retreated with Wing Quivering and Variable See calling, ending with long high notes probably intermediate to Squeals. This bird was attacked again.

2. By females begging for food from their mates. During the period of egg laying, as well as early incubation, females beg food from their mates and are fed by them. The females use Broken Dee notes and sometimes Wing Quiver. Probably fledglings also Wing Quiver while begging for food, but this was not seen. Since fledglings often stay in dense evergreens or high in deciduous trees, very few direct observations were made of their begging.

3. In periods of copulation. During the period when copulations are occurring, males watch their females working around the nest and use prolonged bouts of Variable See and T-slink calling. During

the loudest portions of this calling the males Wing Quiver. During the final approach for copulation one or both pair members Wing Quiver and call Variable See.

4. In agonistic encounters between members of pairs. Wing Quiver was seen twice between mates with families.

On 9 June 1967 two adults at the Newtown Square site, north of the study area (see Chapter 5), were making frequent trips to feed young that were probably newly fledged. On two occasions both adults arrived at the same spot simultaneously. Each time the female crouched slightly, orienting towards her mate, and silently Wing Quivered. There had been no obvious threat by the male and no attack followed. Possibly both parents were in a mood of defensive aggression owing to their newly fledged young and the Wing Quiver helped avert attacks between them.

On 13 June 1967 a two family encounter was observed north of the study area. The adults squabbled while the fledglings begged continuously, until one family abruptly withdrew 200 feet or more. The parents of this family then briefly challenged an onlooker that had approached to the edge of his territory to the west of the dispute area. They then returned to their youngsters and foraged near them as they begged. Twice one adult silently approached the other while Wing Quivering, then made a brief chase on it. Very likely the members of this pair still had some aggressive tendencies owing to the recent squabbling. The Wing Quiver was probably an indication that the attacker was strongly inhibited from attack; however, in this case, attack tendencies gained the upper hand.

*Message:* Wing Quiver is used with the Variable See and Broken Dee calls, and like both of them apparently indicates a readiness to engage in bond-limited activities. In some of the examples, it is clear that agonistic tendencies were simultaneously present, and that they sometimes gained the upper hand (both attack and escape). But it is not clear that agonistic tendencies are *always* present when Wing Quiver is used.

### 5. Gape

Gaping was observed only once. F1 landed on a feeding station with an unbanded bird. The unbanded bird stood upright, fluffed all its body feathers, leaned towards F1, and silently opened its bill several times. F1 crouched with sleeked plumage and head drawn in, not facing the other bird. The Gape, together with other aspects of the unbanded bird's behavior, were clearly recognized as a threat by F1.

### 6-11. Plumage Displays

General Sleeking of all head and body feathers probably indicates the presence of an escape tendency. Sleeked birds often cling to the edge of a feeding platform rather than going directly onto it. They

sometimes use High See calls, and may lean away as well as look away from a nearby chickadee which is threatening them. The fact that the sleeked individuals did not retreat suggests the simultaneous presence of some inhibiting or conflicting tendency. General Sleeking was not seen often.

General Fluffing of head and body feathers is probably the agonistic opposite of General Sleeking. The head feathers, notably the white cheeks, are often especially fluffed and conspicuous. Fluffed birds usually face their opponents more or less directly, sometimes leaning toward them, and are likely to use Click-rasp or Dee series. Very few cases of General Fluffing were seen.

Ruffled Crown, a momentary ruffling of the feathers on the top of the head is a relatively common display. Chickadees sometimes momentarily ruffle the crown after taking a perch or going onto a feeding station. It is often directed towards a human observer near a feeding station. Birds in mist nets often alternately sleek and ruffle their crowns. Ruffled Crown is also used by aggressive chickadees in disputes. Observations on this display are inadequate to make firm conclusions on its message, but probably it encodes a sudden brief rise of aggressive tendencies.

Ruffling the black "bib" feathers has been observed in aggressive Click-rasp calling birds in disputes, but was not seen often.

Another very common plumage display is to sleek the top of the head while erecting a crest along the length of the nape at the midline (Nape Crest). The Nape Crest is used by birds that appear to be hesitant about their activities or intended activities. It is used in approaches to a feeding station, just before taking flight, or while searching out a seed on the feeding platform. Often a bird with a Nape Crest gives other indications of his uncertainty, such as frequently looking over his shoulder or making hovering landings, even if not near another chickadee. In one instance (23 June 1967) two unbanded chickadees, apparently a wandering pair, were seen foraging in Apple Bough. One gave several T-slink calls while his back was toward the other, which was sitting nearby with a Nape Crest and giving Tseet notes.

Nape Crest seems to indicate the presence of a mild escape tendency that is conflicting with the performance of some other, non-agonistic activity.

Tail Fanning has been seen rarely, and an adequate description of its usage was obtained only once. During a dispute involving several chickadees, on 7 January 1967 a chickadee fully fanned his tail, then made an attack-chase on another individual.

### 12. Body Ruffling

In the Body Ruffling display the chickadee ruffles the rump and flank feathers extremely, so that he assumes the size and shape of a

small apple. In addition the wing tips are usually drooped down and slightly outward, although the carpals remain close to the body. The bird may Bill-up, or lean towards his intended recipient. He may bill wipe, hop, forage, or even fly while giving this display. At times a less extreme form of the display is given in which both the ruffling and the Wing Droop are more modest. Birds are usually silent when giving this display but Tseet notes, or very rarely High Tee-Dee series, have been given with it.

*Usage:* Body Ruffling is seen most frequently in the autumn, usually in direct encounters between two birds within a few feet of each other. It is also given in disputes between two pairs, probably by the males, but this has never been confirmed.

In an encounter involving Body Ruffling the usual outcome is for the recipient of the display to retreat, with the displaying individual following (probably chasing). Sometimes the displaying bird makes an outright attack. In one case a chickadee apparently repulsed another's approach by Body Ruffling towards it. Occasionally the encounter is a draw, with both the displaying and non-displaying birds withdrawing. Once two birds, probably males, both gave the Body Ruffling as they hopped apart, bill wiping. Sometimes the recipient merely sits quietly and the displaying bird withdraws. In one case a Body Ruffling bird retreated from an individual giving a Bill-up display. Very rarely does the recipient choose attack as his course of action.

One display has been seen only three times in the study area and may be an extreme variation of the Body Ruffling display. The bird ruffles the feathers as in the Body Ruffling display, but lifts the carpals out from the body. In one case observed by W. J. Smith, two unidentified chickadees faced one another across a feeding platform with these poses. Both then made small rowing motions with the outlifted carpals. A more extreme case occurred when one unidentified chickadee approached a second from behind and landed near it. The second opened his wings and lifted them out from the body, then tilted from side to side. A similar display was given by one member of pair 3–3 towards a human that was removing its young from the nest box for banding. The bird was clinging to a vertical branch as he gave the display, and was briefly silent in an otherwise very noisy bout of mobbing. In this last example the ruffling of the flanks was minimal, and the rump was not seen.

A probably homologous display was directed by a White-Breasted Nuthatch (*Sitta carolinensis*) towards a Tufted Titmouse on a feeding platform. The nuthatch ruffled at least the rump during this. The uplifted carpals and fanning motion of the body are conspicuous, exaggerated movements that are probably indicative of strong aggressive tendencies. Kilham (1968) has described this as a "distraction display"; he observed it only near nests.

### 13. Nest Site Showing

Nest Site Showing is a complex and variable behavior performed by males at nest sites, in the presence of their mates. It was described in Chapter 1.

### 14. Snake Display

Brooding female Carolina Chickadees, when disturbed on the nest, sometimes give a Snake Display in which they produce a hissing sound strongly reminiscent of the noise produced by the Copperhead Snake (*Agkistrodon mokasen*). Pickens (1928) describes it as follows: the bird rises up on its legs slightly and lifts its head high up over the shoulders. Then it brings the head sharply down, moves the tail, and expands the wings and at this moment gives a vocal hiss which sometimes ends in a vocal squeak. The banging of the head and feathers against the nest material and sides of the box, together with the hiss, give the impression of a snake strike.

Two unsuccessful attempts were made to elicit this display from F3. She sat tight when her box was lightly scratched and a finger tip inserted at the entrance hole.

Sibley (1955) pointed out that a similar display is known from several other American and European parids, as well as other non-parid, hole nesting species.

### 15. Wing Whirr

The chickadees occasionally gave a faint Wing Whirr in flight, usually at the moment of suddenly veering from some potential trouble. Wing Whirrs have been heard from chickadees taking flight on release from banding operations. Wing Whirrs were also given by birds when flying near the observer on their way to a feeding station, and by individuals in two-bird chases.

Wing Whirrs are faint and can be heard only if given close to the observer. Hence, they are undoubtedly more common than observations indicate. No tape recordings were obtained.

It is possible that Wing Whirr is not a display, but merely the accidental by-product of a particular kind of wing movement being used for the purpose of quick flight. However, chickadees are often observed making quick, veering flights in which Wing Whirrs are not given. The message of Wing Whirr, which probably *is* a display, may be similar to that of the Chick call—a sudden rise in ambivalence about whether or not to proceed with some activity.

## *Activities of Uncertain Status*

Some activities of Carolina Chickadees differ so slightly from non-display behavior that it is uncertain whether they are displays or not. The following types of behavior fall into this category:

1. Falling leaf flight. Two males were observed during the breeding

season making odd, fluttery flights resembling a falling leaf, in which they dropped several feet. On 24 March 1967 following a boundary dispute with Pair 3–3, M6 made such a flight near his mate's excavation site. His mate was in the immediate vicinity. On 2 April 1967 M3 made a similar tumbling, fluttering drop in the midst of a singing bout. His mate was not seen in the immediate area. Although M3 was not near his nest, he was in a sort of "preferred" area of his territory, where he often sang and called Variable See-T-slink. It is possible that the odd flights were nothing more than awkward fly-catching flights, but the circumstances in which they were seen suggest that they *may* have been displays.

2. Extremely bobbing flight. Chickadees often fly with a slightly bobbing flight. In hesitant approaches the bobbing is often exaggerated. Whether or not such bobbing flight is a display is unknown. Extremely exaggerated bobbing, with very slow forward progress, was seen in two cases involving hole inspection. One such flight was seen in March 1966, when a chickadee approached in this manner a cavity behind peeling bark. The other observation of such flight was on 20 September 1966. Two unbanded, apparently wandering chickadees that were probably a pair, moved around in the study area inspecting holes and cavities, and flying with greatly exaggerated vertical bobbing. Such flight may encode readiness to perform certain bond-limited activities. A possibly similar type of flight was described for the Blue Tit (*Parus caeruleus*), where it is also associated with hole inspection (Hinde, 1952).

3. Moth Flight. Another type of flight, the Moth Flight, described for several other parids (Hinde, 1952, cites several authors) was seen only once in the study population. On 3 April 1967, M3 alternated between Song and Variable See-T-slink, given with Wing Quivering, in his early dawn singing. From time to time he made short flights to another perch in which the wing beats were rapid and of small amplitude, as if he were trying to Wing Quiver in flight. At least once he gave Variable See notes while making the flight. Otherwise Variable See notes usually preceded, followed, or occurred both before and after the Moth Flights. Moth Flight may not be a distinct display in Carolina Chickadees, but rather a continuation of Wing Quivering into flight.

4. Freezing. Chickadees rarely remain still for more than a second or two. Chickadees have been seen very still for periods of several seconds in situations where they apparently anticipated a potentially aggressive approach from another chickadee.

5. Extremely rapid foraging. This displacement-like behavior is seen in birds in disputes, at a moment when they are undecided whether to continue the fight or to withdraw (agonistically motivated). The behavior is used by both aggressor and aggressee, and either attack or escape may follow.

6. Rapid bill-wiping. This behavior was seen rarely but, like rapid foraging, it occurred in disputes. In one interesting case, two birds which were Body Ruffled hopped apart from one another for several feet along a branch, each bill-wiping rapidly.

7. Pivoting on the perch. Birds that appear undecided about taking flight often twist from side to side on the perch. Flight may or may not follow immediately.

8. Crouching. A crouch position was seen rarely. The crouching bird usually faced his opponent and sometimes even made slight, lunging intention movements. Crouches were always received as threats by other chickadees. Crouch position may be merely an intention movement of attack in chickadees, but in many species it is a ritualized threat display.

### *Especially Informative Non-display Behavior*

Some non-display activities of chickadees are especially good indicators of a bird's tendencies, motivations, or "mood." They act as highly relevant context to some displays, and probably sometimes heighten the impact of a message on a recipient.

Many of these activities are indications of hesitation about doing something. These include flight intention movements, indirect approaches with many intermediate stops, hovering in front of a perch before touching down, clinging to the side of a perch rather than standing on top of it, especially at feeding stations, and bill-wiping. Birds anticipating trouble often look around a great deal. The impact of a message may be especially affected by the orientation of the signalling bird. Facing another bird, and even leaning toward it, usually means the signaller is fairly likely to act in an aggressive manner. Averting the head, turning the whole body sideways or even backwards, and leaning away from another chickadee all indicate that the bird is not aggressive, and may even be about to flee. The message of a Click-rasp call would be more threatening in the former orientation and less threatening in the latter.

# 4

# COMMUNICATION AND SOCIAL ORGANIZATION

## Messages and Social Organization in *Parus carolinensis*

Some hypotheses can be offered about how the display repertoire is suited to the social system of the chickadees. More precise hypotheses will require an exhaustive study of meanings and more detailed information about vocal repertoires of other American parids, especially those with slightly different social systems. The following is a preliminary attempt to find correlations which may be causal, i.e., social system and repertoire peculiarities which are, evolutionarily, each other's causes and effects.

Moynihan (1970) and W. J. Smith (1969) find that most species have 20 to 40 displays. Rarely 40 to 50 displays are recognized and then usually by authors using a relatively loose definition of the term "display." Also, there is probably some tendency on the part of those who have concentrated intensely on one species to name variations of one display as distinct displays. Carolina Chickadees fall toward the upper part of the range, with 35 displays recognized here (20 vocal, 15 visible and other). It is likely that species that have close, persistent social relationships, which fluctuate daily and seasonally, have some need for, and the ability to employ, a relatively large number of displays.

It must be useful to express the variety of aggressive states encoded by T-slink, Slink-rasp, Click-rasp, Tee-rasp, and Chip because a chickadee's relationship to other conspecific individuals shifts frequently during the year, and sometimes even during one day. This is to be contrasted with birds that are solitary during much of the year, but which during the breeding season have two basic sorts of relationships, viz., acceptance or tolerance of mate and young (with only occasional lapses) and, secondly, antagonism toward all other conspecific individuals. The chickadee aggressive displays are used in a large variety of situations, including hard fights with territorial neighbors, dominance interactions with flock-mates, patrolling breeding territory or flock range, and squabbles between members of a pair.

There are nine calls which encode some sort of escape tendency. These vary from a weak tendency, as in Tseet, to a strong one, as in Chip or High Tee, to a thwarted tendency, as in Squeals. In addition, these same calls encode different conflicting tendencies. As is the case for attack tendencies, it is probably useful for such persistently social birds to be able to express relatively fine degrees of difference of escape tendency in many situations, and thus adjust to shifting relationships

with one another. Also, it has been pointed out (see especially Moynihan, 1962) that flocking is probably selective in large part owing to its value as a predator detecting device. It follows that the sighting of a predator must be communicated to the other flock members and calls encoding escape tendency, especially High See and Loud Tee, are used for this.

The 35 Carolina Chickadee displays encode a relatively small number of messages (11), and of message combinations, and there is considerable overlap between some displays in types of messages encoded. However, displays encoding the same set of behavioral tendencies differ in the *probabilities* they encode, in two ways. First, they differ in the strength or level of the tendencies encoded, i.e., the likelihood of performance of *any* of the kinds of behavior specified in the display. Second, they differ in the *relative* strengths of the tendencies encoded *within* each display, i.e., if any action at all is taken, the likelihood of performing A vs. B. The ability to encode the same behavioral combinations at different levels of probabilities is another means by which Carolina Chickadees can achieve a fine tuning of their complex social interactions.

Many of the displays encode very general messages, such as general set, non-agonistic subset, and locomotory activities. These are the displays used in the largest number of different situations. Since Carolina Chickadees know one another as individuals over long periods of time and also are familiar with the area in which they live, they are able to make extensive use of contextual information in interpreting what would otherwise be uselessly vague statements by their companions (Table 4.1).

There is no season when Carolina Chickadees are solitary; every individual is always associated with at least one other bird. During molting periods the association is weaker and it is fairly common to see a chickadee patrolling, foraging, or preening alone, but it always rejoins one or more companions after a while. During the summer wandering birds, apparently juveniles, are occasionally seen alone, but presumably they soon join family groups or flocks. This strong tendency to remain in association is reflected in the repertoire by two vocalizations, Lisping Tee and Soft Dee. They reflect the persistently social nature of the chickadees even more than the six vocalizations encoding bond-limited behavior, because the latter are used primarily in the breeding season.

In some bird species song may be used more during actual fighting than it is by Carolina Chickadees. However, these chickadees are associated in a flock during part of the year and it may be helpful at the start of the breeding season for a bird to be able to announce with Song that its relationship with its companions has changed from a flock companion to that of breeding and territorial rival. Closely related *P. atricapillus* has a very similar social system and its Song usage closely parallels that of *P. carolinensis* (see Dixon and Stefanski, 1970).

TABLE 4.1

List of Vocalizations and Corresponding Message Types

The identification and location messages are present in all displays and are not listed here. Probability is also indicated by all displays but is only mentioned where it is helpful in distinguishing two otherwise similar messages.

| | |
|---|---|
| T-slink | Attack vs. general set. |
| Click-rasp | Attack vs. general set; probability that attack will occur is higher than for T-slink. |
| Slink-rasp | Attack vs. general set; probability that attack will occur may be intermediate to those of T-slink and Click-rasp. |
| Chip | Attack vs. escape. |
| Song | Readiness for agonistic and bond-limited behavior (possibly low level frustration?). |
| Song Variant | Same as Song but thwarted by lack of opportunity. |
| Faint Song | Readiness to perform association and other bond-limited behavior. |
| Faint Song Variant | Same as Faint Song but (probably) thwarted by lack of opportunity. |
| Variable See | Agonistic vs. bond-limited, or escape vs. bond-limited. |
| Broken Dee | Readiness to perform bond-limited behavior. |
| Lisping Tee | Association vs. locomotory activities. |
| Soft Dee | Association vs. general set? |
| High See | Escape vs. general set excepting some bond-limited behavior. |
| High Tee | Escape vs. locomotory activity. |
| Chick | Intermediate to High Tee and Dee. |
| Dee | Escape vs. general set. |
| Loud Tee | Escape vs. non-agonistic subset (levels of both tendencies probably high). |
| Tseet | Weak escape vs. general set. |
| Squeals | Thwarted escape. |
| Scream and Hiss | Thwarted escape and attack. |

## Messages of *Parus carolinensis* and Other Species

The "message" approach described in Chapter 1 has previously been used to study communication of rather few species. Among birds these species are all members of the family Tyrannidae and all are relatively solitary. Among mammals, only captive prairie dogs and gorillas have been investigated at all thoroughly, and more restricted observations have been made on humans (W. J. Smith, in press). *Parus carolinensis* is the first parid, and the first persistently social bird, to be investigated with this approach. It is of special interest to compare the number and kinds of messages encoded in its display repertoire with those of dissimilar species.

A list of all kinds of messages known from all species investigated with this approach was presented in Chapter 1. Carolina Chickadees encode no messages not used by other species and do not use three that are found in some other species, viz., play, social interaction

hesitance, and copulation. The play message is apparently restricted to mammals. Social interaction hesitance is so far known only in gorillas and man, and in one recently investigated tyrannid flycatcher. The copulation message is apparently more widespread, occurring in at least some birds, but probably many displays thought to encode this narrow message will be found to have wider usage and be the broader, bond-limited message.

The messages encoded in the Carolina Chickadee display repertoire thus fall entirely within the range of messages known already from other species. The conformance of the basic communication pattern of this socially and phylogenetically different species with that of other taxa increases the likelihood that the message list will be found to be common to a large and heterogeneous group of animals.

# 5

# VARIATION IN THE DISPLAY REPERTOIRE OF *PARUS CAROLINENSIS*

## Variations in Repertoire Usage

### *Distribution of Calls in Various Situations*

Table 5.1 summarizes the uses of all the vocalizations in a large variety of situations. Not enough is known about visible displays to make such a table for them. The table indicates very roughly the commonness of each vocalization within a given situation. It does not indicate the commonness of the vocalizations relative to the total number of utterances of the birds; some calls may invariably be used in a given situation, but the situation itself may be quite rare. A special category is included for calls for which usage is qualified by additional circumstances not specified in the table. For example, Song is used very frequently during patrolling in spring, but rarely in patrolling at other times.

Table 5.1 shows at a glance that some calls have very broad usage, while others are restricted to only a few situations. W. J. Smith (1969) suggested that because the number of displays that can be used by a species is limited, evolution has favored the development of messages that can be used in a large number of situations. The recipient of the display then makes considerable use of contextual sources of information when interpreting the information he has received in the display. More precise and limited messages have evolved, Smith argued, when communication must be rapid and a large degree of ambiguity cannot be tolerated. Other reasons he suggested for evolution of precise messages, such as low availability of contextual information and limited social interaction, do not appear to apply to Carolina Chickadees.

There are two reasons it is impossible to give any reasonable estimate of the absolute frequency of calls. First, when recording and editing field tapes one tends to preserve only the best examples of the most common calls but to save every example, no matter how badly recorded, of rare calls. Second, the absolute frequency of calls depends upon the frequency of occurrence of appropriate situations; this must surely change from year to year and from flock to flock. For example, in some winters territoriality is much more in evidence. With the resulting rise in squabbling between pairs, Click-rasp, T-slink, etc., would be used more often than in other years.

TABLE 5.1

RELATIVE FREQUENCY OF VOCALIZATIONS IN SEVERAL SITUATIONS

| | T-slink | Click-rasp | Slink-rasp | Tee-rasp | Song | Song Variant | Faint Song | Faint Song Variant | Chip | Variable See | Tseet | High See | Abrupt Tee | High Tee | Loud Tee | Chick | Dee | T-Chick-Dee | Broken Dee | Lisping Tee | Soft Dee | Squeal, Scream, Hiss |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Patrolling | 4 | 4 | 2 | 2 | 5 | 5 | | | 5 | 5 | | | | 2 | 2 | 1 | 2 | 4 | | | | |
| Countercalling challenge | 4 | 4 | 2 | 2 | 5 | 5 | | | 5 | | | | | 2 | 2 | 1 | 2 | 4 | | | | |
| Fighting (participant) | 2 | 4 | ? | ? | 1 | 1 | | | 5 | 5 | | | | 2 | 2 | 2 | 2 | 4 | | | | |
| Fighting (onlooker) | 4 | 1 | ? | ? | 1 | | | | | | ? | 2 | | 2 | 1 | 1 | 2 | 4 | | | | |
| Direct 2-bird encounter | 4 | 4 | 4 | 4 | 1 | | | | 1 | | 4 | 2 | | 1 | | 1 | 1 | 1 | | | | |
| Approaching feeder | | | | | | | | | | | 4 | 2 | | 3 | 2 | 2 | 3 | 4 | | | | |
| Leaving feeder | | | | | | | | | | | 4 | 2 | | 3 | 2 | 3 | 3 | 4 | | | | |
| Foraging, eating | | | | | | | | | | | 4 | 2 | | 3 | 2 | 2 | 3 | 4 | | | | |
| Predator sighting | | | | | | | | | | | | 4 | 1 | | | | | | | | | |
| Predator mobbing | 2 | 2 | ? | ? | | | | | 1 | | | 2 | | 3 | 2 | 2 | 3 | 4 | | | | |

TABLE 5.1 (*Continued*)

| | T-slink | Click-rasp | Slink-rasp | Tee-rasp | Song | Song Variant | Faint Song | Faint Song Variant | Chip | Variable See | Tseet | High See | Abrupt Tee | High Tee | Loud Tee | Chick | Dee | T-Chick-Dee | Broken Dee | Lisping Tee | Soft Dee | Squeal, Scream, Hiss |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pair formation | 3 | 3 | ? | ? | | | | | 1? | | 4 | ? | | 3 | 2 | 1 | 3 | 4 | | | | |
| Nest site prospecting | | | | | | | | | | | ? | ? | | 3 | 2 | 1 | 3 | 4 | | | | |
| Copulation approach | | | | | | | | | | 4 | | | | | | | | | | | | |
| Begging food | | | | | | | | | | | | | | | | | | | 4 | | | |
| Accompany mate at nesting activity | | | | | 2 | 1 | 4 | 2 | | 3 | 2 | | | 2 | 1 | 1 | 2 | 3 | | 4 | 2? | |
| Leave mate (in spring only) | | | | | | | 4 | 1? | | | 2 | | | | | 1 | | | | 4 | 2? | |
| Leave flock | | | | | | | | | | | 2 | | | | | 2 | | | | 4 | 2? | |
| Approach to feed mate or young | | | | | | | 4 | 1? | | | 2 | | | | | 1 | | | | 4 | 2? | |
| Accompany family of young fledglings | | | | | | | 4 | 1? | | | 2 | | | | | 1 | | | | 4 | 2? | |
| Trapped bird | | | | | | | | | | | | | | | | | | | | | | 4 |

Code: 1 = rare, 2 = infrequent, 3 = frequent, 4 = very common, 5 = special circumstances: (a) Song and Song Variant are very common in spring, rare otherwise; (b) Chip is restricted to use primarily by alpha males and at flock boundary areas; (c) Variable See is used in patrolling only by males ready for copulation, and in disputes only by badly defeated birds.

However, it is possible to give a rough estimate of the relative frequency of calls. Probably High See, High Tee, Chick, Dee, Loud Tee, and Tseet are the most common by a large measure. Second to that group are T-slink, Click-rasp, Slink-rasp, and Tee-rasp, followed by Song. Song Variant, and the faint versions of song, plus Lisping Tee, Soft Dee, and Variable See comprise the next most frequent group, with Broken Dee, Chip, and Squeal, Scream, and Hiss least frequent. It must be stressed that this estimate is based on intensive study of only one small population. However, in brief observations of other populations nothing was seen that would contradict any conclusions based on analysis of the observations of the Apple Bough birds.

### *Seasonal Variation*

Similarly, it is not possible to give an exact picture of seasonal variation in the usage of calls, especially for those used in skirmishing, because, as explained above, the frequency with which various kinds of situations arise varies from flock to flock and from year to year. However, a rough picture can be drawn with respect to seasonal variation.

Loud Tee, High Tee, Chick, Dee, High See, Tseet—uniformly common all year except that Tseet may be slightly more common during flocking than at other times, and all of these calls are less common than usual during the nesting cycle when birds are moving about in pairs using Lisping Tee, Soft Dee, Broken Dee, and Faint Songs.

Song, Song Variant—very common in early spring patrolling, fall off in frequency to a low point during the summer, slight recrudescence in late summer and early autumn, then another low.

Click-rasp, Slink-rasp, Tee-rasp, T-slink—very common in early spring, fall off somewhat in summer except for use by patrolling (probable) juveniles, then quite common during autumn as birds move about and settle into winter associations.

Chip—most common in autumn, but also occurs anytime when bird experiences sufficiently extreme motivation.

Lisping Tee, Soft Dee—used in flocks all winter, especially Lisping Tee, but more common during breeding season, especially when males are accompanying females up to the time of incubating.

Faint Song and Faint Song Variant—used primarily during early nesting through fledging stages.

Broken Dee—almost never occurs outside of the nesting season; used only by females and juveniles; females start using it during egg-laying (possibly before egg-laying according to reports in the literature) and continue into early brooding; young use it before leaving nest and for several weeks after fledging.

Variable See—very common during early breeding season, falls off during incubation, rare at other times.

Squeals, Screams, Hisses—no seasonal variation.

### *Distribution of Calls Among Males, Females, and Juveniles*

Song Variant, Faint Song, and Faint Song Variant were thought to be given rarely by females but these cases were not definitely confirmed. Otherwise, females are known to use the entire vocal repertoire. They probably also use the entire set of visible displays excepting Nest Site Showing. However, many calls are used by them infrequently, especially when compared with male usage of the same calls. These include Song, Song Variant, Faint Song and Faint Song Variant, and Chip. Click-rasp and T-slink, and probably Slink-rasp are used slightly more often, but still much less than by males. The primary reason for the difference between males and females is that males usually assume the burden of territorial defense and fighting. Whenever females did become involved in fighting they used appropriate calls. Loud, harsh Click-rasps were used by at least two females when encountering another pair near a potential nest site. One of these females even took the lead briefly in attacking the other pair. There are instances when, in the absence of their males, females used two-note Songs when intruders came within their territories or flock ranges. They did not undertake vigorous defense. However, females were not observed to be alone and contending with intruders during the nesting season. Dixon and Stefanski (1970) observed female Black-capped Chickadees using song in absence of their males; some of these cases were soft, "signal" song (Faint Song homologue). In one case a female with a non-aggressive mate sang at a boundary. Similarly, a female Great Tit was seen to undertake vigorous defense of territory while her mate was ill (Gompertz, 1961). Probably female Carolina Chickadees also would undertake adequate defense once nesting were underway if their males were indisposed or absent. Normally, however, females are primarily observers at disputes.

Two females are known to have used Chip while alone and patrolling. F4 used it when entering a flock dispute point west of the swimming pool (23 September 1966) and F1 used it at the north end of the Club woods (12 December 1966). What prompted these females to patrol is not known; female patrolling was rare and never occurred in the breeding season. Patrolling females use the full range of calls normally used by males, except that well-developed (loud and continuous) singing was never heard from a female.

T-slink and Click-rasp were used by females in occasional direct encounters. Most notably these were used by F2 in repulsing repeated aggressive approaches from her then mate, M2. Usually, however, females retreat from, or side-step, attacks.

Adult males use the entire vocal and visible display repertoire, with the single exception of Broken Dee. Presumably adult males never assume any role of dependency to which Broken Dee is appropriate.

It is possible that a disabled chickadee might use Broken Dee, but this has not been seen.

When a parent enters the nest cavity, young nestlings beg with faint, clear "peeping" sounds. No tape recorded examples of this call were obtained. When nestlings are several days old they beg with Broken Dee, which probably is ontogenetically derived from "Peep," but this is not known. Large nestlings of Pair 3–3 used Screams and Hisses when handled during banding.

For the first 15 days after fledging Broken Dee was the only call heard from the youngsters of Pair 3–3. During the next few days occasional faint amateurish, i.e., poorly formed and poorly controlled, Click-rasp and T-slink notes were heard interspersed among Broken Dee notes, but it was not definitely confirmed that the calls were by the young; they might have been made by the adults as an inhibited expression of aggressive tendencies. By this time Pair 3–3 was leaving its young alone for brief periods and quietly foraging alone.

On 7 July 1967, three days after Pair 3–3 was observed traveling with a "family" group which contained two of their own color-banded offspring and two unbanded "extra" juveniles, an apparent juvenile moved through Apple Bough, calling High Tee-Dee series, rapid Dee series, and T-slink, jumbled together with Broken Dee's. The adult calls were all very amateurish. The youngster flew away with Lisping Tee-Soft Dee series. It was unbanded and alone, and foraged constantly. Perhaps such lone wandering fledglings join family groups when they encounter them, contributing to the tendency of "families" to contain mixed broods.

On 23 July three unbanded apparent youngsters and M3 moved through Apple Bough foraging. Each of the youngsters in turn gave a burst of calling including Song, Click-rasp, and T-slink. The calls were given rapidly and jumbled together, and were very amateurish, with the exception that one youngster was proficient at one Click-rasp variant. The others always appeared to ignore the calling bird, except that two never called at the same time. M3 also did not call and did not take offense at this patrolling-like behavior in his territory. The obviously amateur quality of the calls may help youngsters to avoid eliciting aggression from established residents, at least at this season.

The use of particular variants of complex calls by different individuals is discussed below.

## Variations in Form of Vocalizations

### *Variation Within the Study Area*

Several calls are quite variable in form. Even in calls with a relatively simple form, such as series of short similar notes, there may be variation in frequency, frequency spread, length, and exact shape of

each note, as well as in the interval between succeeding notes and the total number of notes in a series. Such variation as occurred in simple call notes was shared by all of the individuals in the study population; no bird showed obvious preferences for particular variants.

Although Song and Song Variant are made up of clear whistled notes, they are also somewhat variable at least in frequency and the number of notes. Song Variant has a number of different patterns of high and low notes.

One very unusual song-like vocalization was heard rarely, and then only at a distance along the northern boundary of the Apple Bough flock range. In the one tape recorded example (September 19, 1966) the caller was not seen but seemed to be in a countercalling dispute. The basic unit consisted of a short introductory note which was the peak and downsweep of a narrow chevron, followed immediately by a clear, flat, song-like note. This unit was repeated two, and sometimes three, times in rapid succession. Ordinary Song and Song Variant were heard during this bout of calling; the Song Variant sometimes overlapped the unusual call and was, therefore, given by a different individual.

There is a variety of possible interpretations of this vocalization. First, it might be a distinct display, one which is being newly evolved, or one which is disappearing from the repertoire. This hypothesis is not too likely but cannot be ruled out at this time. The evolution of display repertoires is discussed by Moynihan (1970). Second, the call may have been an odd version of Song. An individual recorded near Winfield, Kansas (see below) gave Songs similar in many respects to the odd Apple Bough vocalization. In these Songs the second and third high notes were short and chevron-shaped. However, the chevrons were much broader than the ones in the unusual Apple Bough call. Also, no other use was made by the Apple Bough population of short, chevron-shaped Song notes. The possibility that the odd vocalization was an unusual Song also cannot be ruled out but does not seem likely. Finally, the call may have been an odd T-slink, or Slink-rasp. A Slink-rasp, actually Slink-rasp-slink, was recorded eight miles north of Apple Bough (see below) in which the introductory portion comprised two brief chevrons and the "slink" note was fairly long; this was followed by a rasp and another "t-slink." Rasps do not usually carry over long distances, so the odd song-like call may have been an unusual "T-slink-t-slink," or even a "T-slink-rasp-t-slink," the rasp portion of which was not heard at a distance. Since the vocalization was not heard from the Apple Bough flock during the study it was apparently a peculiarity of some member of a nearby flock, or of some wandering individual.

By far the most conspicuously variable calls are those which are made up of several different kinds of notes. In such a call there can be variation in the number and order of different kinds of notes, as well as in their length, shape, rapidity, etc. Click-rasp, Tee-rasp,

Slink-rasp, and T-slink fall into this category (see Figs. 2.1A-2.6B). Variation in a call can be minor or major. Conspicuously different arrangements of components in, say, two Click-rasp calls can be easily recognized as two distinct variants. But where two calls differ by the omission of one or two introductory notes, or by a slight change in shape (frequency/time) of a note, it is not clear whether they should be considered one variant or two. Such minor variations are not taken in this study as constituting distinct variants, although they might be so considered if one were to conduct a more detailed study of variation.

The emphases of this study precluded a systematic examination of individual preferences for particular variants. In the field priority was given to obtaining good behavioral information along with the best tape recordings that could be made under the circumstances. Concentrating on perfect, "clean," tape recording would have cost needed data on the birds' activities. At the end of the study the clearest recordings from each individual were sonagraphed and inspected for individual peculiarities. The extent of variation produced by each individual might easily be underestimated by this method.

M3 had a minimum of two Click-rasps, one Tee-rasp, two T-slinks, and two Slink-rasps. Each variant had its characteristic introduction, with the exception that the introduction to one variant of Click-rasp was once used with the "rasp" characteristic of the other variant. This same introduction occasionally included an extra note. One of the variants was sometimes doubled (T-rasp-t-rasp). The two Slink-rasp forms were sometimes alternated during long bouts of calling.

M6 used at least three Click-rasp variants, each with its own introduction. Two of these were sometimes doubled. No recordings were obtained of Tee-rasp or T-slink. This male used a Slink-rasp variant in common with M3 and M7.

M7 had at least two Click-rasps, both different from the variants used by M6. Both males used an ascending "rasp" note, but the introductions were peculiar to each male. One good example was obtained of Slink-rasp; it is closely similar to one of the Slink-rasp variants used by M6. No examples were obtained of Tee-rasp or T-slink, though this male undoubtedly used at least the latter call.

M2 used at least one T-slink and two Click-rasps. M1 used three Click-rasps, and a double T-slink identical to one used by M3. The introductory portions to the first and second "slink" notes of this variant are different and match in both males.

M5, who was in a flock north of the study area, used at least two different Click-rasps. One had a distinctive introduction unlike anything used by members of the Apple Bough Flock. Whether other individuals in the northern flock used notes of that type is not known.

Females used these calls rarely and only a few good quality recordings were obtained. As with males, the extent of variation in female

repertoires is probably underestimated. F1 and F4 each used one T-slink and one Click-rasp. F5 used a Slink-rasp virtually identical to the one used by M3, M6, and M7; she also used a Click-rasp similar in some respects to the one used by F1.

In the autumn of 1969 the calling of a newly banded male in the study area was sampled extensively for the purpose of examining the variations in his calls. This male used seven, possibly eight, distinct variants of Click-rasp, and two T-slinks; some of these were used both with single and double slinks and rasps. Minor changes were sometimes made by addition or subtraction of a note from the introductory portions. An unbanded male in the area was sampled less extensively during the same period; he used five Click-rasps, of which four were the same as variants used by the banded male. He also used three distinct Slink-rasps.

Excluding the fact that some Click-rasps can be doubled, and that introductions were sometimes varied slightly by addition or subtraction of notes, there were a minimum of 17 distinct Click-rasp variants, two of Slink-rasp, five of T-slink, and one Tee-rasp used by nine members of the study population, of which three were females. Two males in the area in 1969 used eight (or nine), three, three, and zero variants. The seven (or eight) variants of Click-rasp used by the banded 1969 male is the largest number of variants used by a single individual, but he was the most thoroughly sampled individual. Members of the study population probably used more variants than were counted.

Each individual had at least some calls which were uniquely his own. Many shared one or more variants with at least one other bird. One Slink-rasp variant was held in common by three males and one female. The extent of overlap might have proved to be greater if the sampling had been designed to reveal total individual repertoires. There was no evidence that females tended to share their mate's repertoire. Several males shared calls with the final alpha male (M3), but this could have been accidental.

Two reasons can be suggested as to why the 1969 males had more variants than did the 1966-67 birds. First, the samples of their calling were designed specifically to study individual repertoires; males of the study population might also have had comparably large repertoires. Second, the 1969 males were recorded in the autumn and might have been new in the area. It may be that new residents employ a large repertoire, then adapt to the local population by discarding all but elements similar to those in current usage. The persistence of experienced individuals in the area would form a background against which newcomers could measure their vocabularies. Newcomers probably also learn variants from local residents. The limited overlap in usage of some variants in the study population, and more extensive overlap in the two 1969 males, shows that at least some individuals

learn from others. What governs the development of individual repertoires is not known; the present study was not designed to investigate this and only indicates a range of possible answers.

The important part of these calls, as far as individual peculiarities are concerned, is the introductory portion. While "rasp" notes can vary in pitch and quality, there is considerable sharing of "types" of rasp by different individuals. For example, four of six males in the study population used rasps which ascended in pitch (see Fig. 2.4D), but each male's introduction was his own.

It is possible that different kinds of variation might have a different "valence," i.e., pose more of a threat. There is evidence that T-slinks *as a category* are less threatening, that is, indicate lower probability of attack, than are Click-rasps (see Chapter 2). But there is no evidence in my data to test the possibility that particular variants, or particular kinds of variations within each category, e.g., ascending rasps vs. descending ones, indicate different attack probabilities. Dixon (1969) discussed this idea with respect to song exchanges in the Plain Titmouse. But the question there is complicated by the likelihood, in his estimation, that many "songs" of this species are actually derived from "close quarters threat calls," i.e., may correspond to something like T-slink and Click-rasp. The problem for the Plain Titmouse is to decide which types of song fall into which category (some presumably are "true" song), and which songs are variants within each category.

Carolina Chickadees differ from Plain Titmice in that while the latter frequently countercall with identical song motifs, Carolina Chickadees usually adjust to call *differently*. Ward's (1966) recordings of countersinging in several populations of Carolina Chickadees showed there was a tendency for males to adjust their singing so that each used a different variant. My observations of Song exchanges in the study population agree with his finding. Further, I found that if one individual used a "flat" Click-rasp, the other would counter with an ascending or descending one. This argues against a "valence" to individual variants, since if the first male preempted the kind of variation with the particular valence the second male wished to use, the second would be forced to "lie" about his attack probabilities. The reverse also argues against "valence" to individual song motifs in Plain Titmice—except to the extent that they fall into T-slink- or Click-rasp-like categories.

### *Variation in Two Populations Near the Study Area*

In May 1967 brief observations were made on chickadees in and adjacent to the John J. Tyler Arboretum, approximately four miles northwest of the study area, near Lima, Pennsylvania. The Tyler birds (four pairs) sounded very similar to the Apple Bough birds, and virtually no distinctive differences appeared in any sonagrams prepared of their calls. All components of even the most complex Click-rasp

and Slink-rasp calls were similar or identical to those used by Apple Bough birds, and no unusual combinations of them were found. Only one conspicuously different call, a Song Variant, was noted, and it was used by two neighboring males. It had a pattern HLLL, but the high note had a frequency only very slightly higher than the low notes. Other chickadees near these two pairs were not located and recorded, so the extent of this variant in the Tyler population is not known.

In June 1967 brief observations were made on chickadees in woodlots on a privately owned farm eight miles north of the Apple Bough study area in Newtown Square, Pennsylvania. Approximately 10 different birds were recorded in a total of four hours at this site. The Newtown Square birds were similar in voice quality and overall pattern to Apple Bough and Tyler birds, but did have at least three very distinctive variants and one apparently new call not known in Apple Bough birds. Two of the variants were Click-rasp calls, which had introductory notes of a sort not used by Apple Bough birds. The third was a Slink-rasp; it was described above.

The new call, never heard from Apple Bough birds, was a high pitched, emphatic See-eet!, which was used by one apparently patrolling bird, and by another probable male alone in a counter-calling dispute with a neighboring pair. The lone male did not approach the pair closely at first, but called High Tee and See-eet!, and moved parallel to the pair. Finally the lone male changed to Click-rasps and the dispute moved to the point of brief actual combat. From the point at which the lone male changed to Click-rasps, he stopped giving See-eet! Near the end of the dispute the lone male was joined by a bird which was probably his mate, and the two of them withdrew from the dispute area. The message of See-eet! is not at all clear from these brief observations. See-eet! sounds strikingly similar to a call given by *Parus bicolor*.

### *Variation in Two Populations Distant from the Study Area*

Carolina Chickadees were also recorded briefly in May 1965, 1966, and 1967 at a single site in the Pocomoke Swamp near Whaleyville, Maryland, approximately 120 miles south of the study population in Pennsylvania. The Click-rasp calls of the Pocomoke birds sounded rather different from the Apple Bough birds, having a softer, or mushier quality. Sonagrams of some of these Click-rasp calls showed that many of them had longer introductions made up of a great many very short, click-like notes. In some, the rasp notes had very harsh quality, owing to greater spacing in the clicks or oscillations making up the rasp. Harsh rasps were heard from Apple Bough birds but were less extreme and less common than in the Pocomoke birds. Some of the Songs recorded at Pocomoke had a very plosive-sounding beginning—possibly due to the rapid downward sliding in frequency at the beginning of the first note. Otherwise, with one exception, the

Songs were not unusually different from those recorded in Pennsylvania. The Songs and Click-rasps were recorded from apparently patrolling chickadees. No Song Variants or T-slinks were recorded. The only other calls recorded from this population were High Tee, Chick, and Dee, and nothing unusual was noted about them.

In the 1967 recording session an odd three-note Song was recorded from an individual at the usual recording site. Later on the same day the same odd Song was recorded from another individual approximately a mile upstream on the same river. No recordings were obtained of this particular Song, but it had plosive beginnings to the notes, and the second high note had a much lower pitch than the first high note. Both individuals that used this Song were apparently patrolling at the time.

On 2 and 3 June 1967 some recordings were obtained of several individuals and pairs near Winfield, Kansas. Song, Click-rasp, T-slink, Variable See, High Tee, Chick, and Dee were recorded from these birds. Two of the Songs were quite different from anything heard from the Pennsylvania and Maryland birds. In one of these the first high note had a frequency scarcely higher than the low notes, while the second high note had a more usual high frequency. Another individual gave a Song essentially like this, except that he omitted the fourth note. A third individual gave Songs with normal frequencies, but the second, or second and third, high notes were very short and slightly chevron-shaped. Short song notes were never used by Apple Bough birds, but Brewer (1961) speaks of songs comprising both long and short notes as "characteristic."

Introductions to both T-slink and Click-rasps often consisted of very brief, click-like notes. One bird gave what appeared to be two introductions for each slink, i.e., two identical bursts of short notes, each falling in pitch. Another individual repeated bursts of such introductions with no slink or rasp following. None of the extremely harsh rasps found in Pocomoke birds were heard from the Kansas birds.

In all of the observations on populations outside of the Apple Bough area, vocalizations were used in a manner fully comparable to the Apple Bough usages; no behavior observed with any call would contradict interpretations of the communication aspects of the calls. Observations on the other populations were, however, extremely brief. While something could be understood about the behavior of the calling birds, full understanding of each situation could never be obtained, because immediate and past histories of the individuals were never known. The full range of variation of any of the other populations was certainly not approached. Hence, the samples from populations other than Apple Bough are only bare indications of the sorts of variation that occur.

The widespread variation in calls from site to site argues against the possibility that subtle message differences are associated with par-

ticular variants or kinds of variations (see discussion in preceeding section).

### *Variation and Dialects*

Ward (1966), in his geographically extensive investigation of variation in the Song of *P. carolinensis,* defines dialect as a song form distinct from the "normal" and "prevalent in a limited area." Armstrong (1963) takes a constancy of variations, or in limits of variations, in a community to be a dialect. In an essentially identical definition, Marler and Tamura (1964) use "dialect" to describe the properties of song patterns that characterize each separate population of breeding birds.

There are a number of problems that arise in dealing with the above definitions of "dialect"—problems of both a practical and theoretical nature. At the heart of all the problems is the question of how to take an adequate sample.

To begin with, Ward's definition assumes that it is possible to determine what is a "normal" song. This would pose no real problem for a species with a fairly invariant song throughout most of its range. But Carolina Chickadees vary considerably, even on a local scale. Ward, in agreement with most authors, took four-note alternated song as the "normal" song of the species, even though in five of nine regions that he sampled it comprised 1/2 to less than 1/4 of the total songs he recorded. Nevertheless, four-note songs *are* common enough that most bird watchers—and authors of bird books—regard them as "typical."

Second, determining what is "prevalent" or "typical" in an area requires much more sampling than is usually realized. This is especially true if care is taken to distinguish Song from Song Variant; a brief sample may catch a bird in a period of calling Song Variant. Furthermore, Apple Bough birds and their neighbors all used two or more variants of Song, and a brief sample might catch only one of them.

The biggest problem in determining what is a "dialect" is determining what is a "limited area," "community," or "separate population." There is a real danger in taking a sample from one area, taking a sample from another area several miles away, and labeling the two as "dialects" typifying the two areas. If the samples had been taken from two slightly different points, say a mile farther along a road, they would, for Carolina Chickadees, almost certainly be slightly different, yet by this method would also be labeled dialects and assumed to be characteristic of the same two areas.

The problem does not exist where the study population is on an "island" (*sensu lato*). But in the case of the present study, should Apple Bough, Tyler Arboretum, and Newtown Square birds be considered as one population, or three? A region in Ward's study included sites from as close as a few miles and as far away as 80 miles.

Probably a more constructive approach is simply to describe differ-

ences between sampled populations as "dialectal," while avoiding labeling the samples as "dialects." The attempt to determine a "dialect" seems in most cases to be a side issue of a more interesting pursuit —the study of geographic variation. Labeling a sample as a dialect may be one way to attempt to handle some of the findings of variation, but is misleading to the extent that it is typological.

### *Further Studies of Variation and Dialects in* P. carolinensis

Ward's survey of Songs of Carolina Chickadees (1966) included nine regions along the Atlantic coast from New Jersey to Florida. He found some variation from region to region, most notably in "slurring" of frequency within a single note, alternation of high and low notes, and number of notes. Almost certainly he included some examples of what is here recognized as Song Variant, as well as true Songs; and these are two different displays because they have different usages. However, he also had one Song type which may have been an unusual Song, instead of a Song Variant. This form had a high note, a very brief low note, then a low note of standard length. The correct classification of such a vocalization would have to be made behaviorally, by watching the activities of the bird using it over an extended period of time. Ward noted (p. 147) that "There is a definite tendency for a Carolina Chickadee within any one region to sing in a manner consistent with the song of others in the same region. The regional manner of singing may focus on the accepted typical song form of the species, may be typified by a stereotyped but distinct dialect form, or may have fluidity as its common denominator—i.e., a consistent freedom from any stereotypy."

Ward's reduction of all information to statistical measures of physical parameters actually conceals some of the findings which are of interest here. He does mention incidentally some information which indicates some of the pattern of individual variation which he found. For example, all of the six noted Songs from one region were given by one individual and formed its entire repertoire, at least while Ward was recording it. Similarly, in another region four individuals gave the odd Song with the doubled low note, although it is not mentioned whether they were close neighbors or not. Ward also mentions that changing the number of notes in a Song was relatively common. This was also observed in the birds in the Apple Bough population, which showed some tendency to give shorter, odd-numbered Songs as the dawn singing period drew to a close.

Although Ward recorded a large number of Songs in total, a more extensive experience with one local population suggests to me that very many Songs need be recorded in one area over a period of at least several days, in many situations, to get a "representative" sample. His data are useful, however, in providing a minimal estimate of variation both from region to region and in individual birds, as well as showing

in a few instances that "peculiarities" may be favored by a few birds in a region. It would have been interesting to know how many of his birds were close neighbors.

Ward recorded in some areas near Black-capped Chickadees, including sites near Chester, Pennsylvania, about four miles south of the Apple Bough population. He noted that in two of the three regions where Black-capped Chickadees were nearby, including the Chester population, there was a higher degree of stereotypy, while in the third population songs tended to be longer and with less regular alternation (presumably more Song Variant in the sample). Otherwise, Ward could detect no significant changes in the Song given near Black-capped Chickadee country, except that birds very close to the border of the ranges of the two species gave some songs so unusual that he was uncertain as to species.

Tanner (1952), who studied Black-capped and Carolina Chickadees in the southern Appalachians, found no active hybridization. Although he could detect evidence of probable past hybridization in one population, the border region contained no intermediates and was sharply defined. Tanner noted that to his ear Carolina Chickadee calls were higher pitched and thinner than those of Black-capped Chickadees, and the Dee notes of the chick-a-dee call were given more rapidly by the former. He found occasional Black-capped Chickadees in mixed flocks with Carolina Chickadees. He thought that some of the odd songs given by birds which also gave normal Black-capped Chickadee songs were probably learned from Carolina Chickadees by first-year Black-capped males spending a winter in a Carolina flock, rather than due to hybridization. His evidence for this seems to be that all specimens were distinctly in one population or the other, and no mixed breeding pairs were detected. While Black-capped pairs were seen wandering through Carolina nesting territories, they were never found actually nesting at the lower altitudes. These Black-capped birds were ignored by the nesting Carolina Chickadees and, in fact, Tanner never saw any evidence of interspecific antagonism.

Brewer (1961) also noted a number of apparently local variations in Carolina Chickadee songs in some midwestern populations, but made no mention of variations in other vocalizations. For example, birds in one area used a four noted Song in which the last syllable was buzzy sounding. Another characteristic found in many Illinois birds was that the first one or two notes are drawn out and the last two rapidly given. He also heard many kinds of variations which are probably widespread, such as three note Songs, and six, or more, note Songs.

Brewer also studied the Songs used by chickadees in a hybrid zone near Vandalia, Illinois. It is difficult to know without sonagrams what the Songs were like, as phonetic descriptions are especially hard to deal with for whistled notes. He found five types of birds, which gave Black-capped Songs only, Carolina Songs only, Black-capped plus unusual

Songs, Carolina plus unusual Songs, or unusual Songs only. By "unusual" Songs Brewer meant those which were outside the normal range of variation of either species, and because he apparently spent considerable time in the field he was probably familiar with the range of potential variation in normal Song. He remarked that while several unusual Songs were used, one was most common. In a contact zone in eastern Missouri, most of the Songs were of the type which was the most common "unusual" Song in the Illinois overlap zone. Brewer had evidence of active hybridization in at least the Illinois population, so the unusual Songs could have been hybrid versions. The physical attributes of the birds giving the unusual Songs were not stated. Tanner (1952), on the other hand, had evidence that active hybridization was not occurring in the Appalachians, and hypothesized equally plausibly that some "unusual" Songs had been learned by first-year Black-capped males in winter flocks with Carolina Chickadees (see above). Tanner did not say that the odd Songs given by probable Black-capped Chickadees were identical with, or similar to, Carolina Chickadee Songs. However, young birds might be stimulated to experimentation by hearing a (for them) "wrong" Song. The observations needed to determine whether the unusual Songs are innate (hybrid) or learned would be difficult to make; this is a problem which eventually will have to be settled by experimentation.

### *Variation in Song of Other Parids*

The Song of the Black-capped Chickadee is generally thought to be invariant—a mixture of fee-bee and fee-bee-ee. Odum (1941-42) spent over 12 months in close study of a large population of Black-capped Chickadees in New York and mentioned no departure from this type of singing. Brewer (1961), however, cited several authors who have mentioned unusual songs given by birds deep in the Black-capped Chickadee range. Bagg (1958) reported an apparently local variation, a monotonal two- or three-note Song, given by birds on Martha's Vineyard Island, Massachusetts, although occasional individuals gave rare "normal" Song. A similar Song is also reported by Bagg from the Gaspé Peninsula, Quebec. Lawrence (cited by Brewer, 1961) also heard this kind of Song in Ontario. Three- or four-noted monotonal Songs were described for a western subspecies (*occidentalis*) by Dawson and Bowles (1909); the last note may or may not be at a lower pitch. Lumley (1934) also described this Song but felt that it resulted from individuals imitating the Song of the Mountain Chickadee (*P. gambeli*).

Desfayes (1964) reported that Black-capped Chickadees around Anchorage, Alaska use exclusively a Song which is a monotonous repetition of dü-dü-dü-dü-dü (his phonetics), a Song which to his ears is identical to a *Parus montanus* Song from the Swiss Alps. He also said he heard the same type of Song in Alberta, but did not see the bird. The geographical range of usage of the *montanus*-type Song is not

known in any detail, nor is it known whether, in some populations, the same individual uses both *montanus*-type Song and the "typical" fee-bee Song. But the obviously close relationship between *P. montanus* and *P. atricapillus* suggests at least one source for potential variation in the Songs of the latter. Thönen (1962) also discussed the Songs of these two species in respect to the degree of separation of the two populations.

Gompertz (1961a and b) made extensive observations on the vocalizations of the Great Tit (*Parus major*) in Britain. While most of her observations were restricted to one area, she had sufficient opportunity to hear Songs of Great Tits in other areas to gain the impression that "parts of the same dialects may recur in widely separated localities." It was usual for males to have a repertoire of at least four Songs, and the highest number known from one individual was seven. She felt that possibly individuals had an inherited predisposition, or learned very early in life, to use a certain basic pattern, e.g., two-note vs. three-note Songs, but also acquired Songs like, or similar to, those used by its close neighbors in subsequent breeding seasons. The experience of hearing a limited variety of Songs in a small area is partly attributable to the tendency of the Great Tit to countersing with Songs most like those used by its neighbors; aside from this restriction males appeared to use any Song in their repertoire at random.

Extensive studies on variation in vocalizations of other European tits are not available.

Dixon (1961) reviewed the voices of American tits with a view to their geographic ranges and overlap. He concluded that usually congeners which overlap have voices sufficiently different to prevent both interbreeding and interspecific antagonism. He observed (Dixon, 1954, 1960) an interesting exception to this rule around Berkeley, California where the Chestnut-backed Chickadee has recently invaded an area formerly occupied only by the Plain Titmouse. The Plain Titmouse is an unusual parid in that it takes up a territory during its first year, and then holds it, usually without change or interruption, until its death. In its year-round territoriality, it permits only its mate into its territory, with a brief exception during fledgling stage when territoriality is slightly relaxed. While the smaller chickadee has slightly different foraging habits, and takes predominately smaller food particles, its voice is similar enough to elicit aggression from the titmouse. Dixon observed Plain Titmice and Chestnut-backed Chickadees countercalling, countersinging, and fighting, the last being initiated—and won—by the titmouse. The result of these interactions was that the chickadee was excluded from the areas occupied by the titmice, except very briefly when territoriality relaxed during the fledgling period. In 14 of 21 encounters, the aggressive interaction between the two species was initiated by the vocalizations of one or the other.

Further observations were made in the same area in 1961 and 1962

by Root (1964), who found more overlap in territories, and no aggression, between the two species. The situation is an interesting one which should be studied further.

*Factors Contributing to Local and Widespread Geographical Variation*

The study of "dialects" in *P. carolinensis* seems to be a "red herring" which draws investigators away from the trail of a more interesting pursuit—the nature, extent, and causes of variation in vocalizations. The extent to which use of different variants of calls is governed by genetic makeup, and early and later experience, is not known. These are difficult problems to study. Birds in captivity may lack some sorts of important opportunities and consequently fail to perform natural behavior. A study in the wild would be a considerable undertaking, though it could probably be done. A linear, riparian woods surrounded by relatively barren (for chickadees) open farmland would be ideal for a study in variation, especially if it had an occasional narrow gap, and occasional "bridging" habitat to populations outside of the riverbank area. Extensive recording would have to be made of each of several flocks, preferably with color-marked individuals, along a length of the river, across some gaps, and in nearby semi-isolated populations that might influence the riverbank population. The effect of newcomers on the resident population, and of the resident population on newcomers, could be examined. One might learn something about how newcomers in an area adjust their repertoire of variations of some vocalizations. With luck, one might find an individual with a known repertoire shifting along the river to another part of the study area. Or, better, one could collect from a second area birds whose repertoire of form variation was known and introduce them into the study area.

It would be very interesting to know how young birds develop their individual repertoires, but movements of young of the year have never been followed in *P. carolinensis;* it is likely that some of them move a considerable distance. Consequently, it will probably be hard to study in the wild the development of a juvenile whose local origin and parentage are known. It will be of interest to study variation in Song, Song Variant, T-slink, Slink-rasp, and Click-rasp, though of course the study of Song and Song Variant would require far less sonagraphic analysis.

There is no direct evidence that Carolina Chickadees use individually specific variants or individually specific selections of variants for purposes of individual recognition. Judging from the way Carolina Chickadees react to one another at close quarters around feeding stations, it is obvious that they can usually recognize one another as individuals in the absence of vocalizations. Yet in a dispute, when the most active participants may be at close quarters, things may move very rapidly and become confusing; furthermore, the occurrence of disputes and the identity of the disputants is usually of interest to

other individuals that may be at a distance. Similarly, the location and identity of males that are patrolling a territory is also of interest to individuals that are often at some distance from the caller. The identity of the caller is, therefore, frequently useful information for the recipient(s). This, together with the fact that individuals do appear to use unique selections of variants, argues that variation probably serves for individual recognition.

There is available now, from the studies cited above, some rough idea of how variable Carolina Chickadee vocalizations are, both individually and locally, as well as on a wider geographical basis, although there is no detailed mapping of variation. But the relative contributions of genetics and learning are simply not known.

Marler (1960) has discussed a number of points related to variability of song. He pointed out that geographical variation is enhanced by variation in a species' sound environment over its range, by the presence of barriers between populations, and by mechanisms acting to preserve local tradition, e.g., sedentary habits, or migrants which return to the same area, and a tendency for males to countersing with similar song types. Individual recognition should be a primary factor enhancing variation in the repertoire of individuals and in a local population.

Marler (1960) has also pointed out that variability in singing will be better understood when functions of song are better understood. Some of the probable functions of song, in at least some species, mentioned by him are: (1) preventing interbreeding by attracting the right species as a mate; (2) repulsing intruders; and (3) maintaining a pair bond, helping a female to recognize her mate, and synchronizing a pair physiologically.

The data presented for *P. carolinensis* suggest that these functions are contributed to by several vocal and nonvocal displays as well as non-display sources of information. Pair formation in Carolina Chickadees occurs at any season, including those when males are hardly singing at all. Intruders are repulsed by patrolling and disputing, during which a variety of vocalizations is used, including Song, Song Variant, Click-rasp, T-slink, Slink-rasp, and Chip. Song and Faint Song probably aid in maintaining the pair bond and in synchronizing the pair physiologically, and Song is probably useful in helping the female to recognize her mate in circumstances where his distance and direction from her are uncertain. Such would be the case, for example, when the female was in the nest cavity. In most circumstances his identity would not be in question. Dixon and Stefanski (1965, 1970) reached much the same conclusions regarding *P. atricapillus,* for which they present a detailed analysis of usage and function of Song and "signal song" (Faint Song).

# 6

# COMPARISONS WITH OTHER PARID VOCAL DISPLAY REPERTOIRES

Table 6.1 shows probable homologies between the vocal displays of *P. carolinensis* and the three other American parids whose vocal repertoires are known in any detail. Information on visible displays is so incomplete that they are excluded from consideration in this chapter. The following discussion expands a few points related to Table 6.1 and describes the sources of data for each species. For a detailed description of how the table was constructed the reader is referred to S. T. Smith, 1968.

Odum (1941, 1942), Brewer (1961), Dixon and Stefanski (1965, 1970), and Dixon, Stefanski, and Folks (1970) have all contributed to present knowledge of the vocal repertoire of *Parus atricapillus.* Not surprisingly, there appears to be a nearly one-to-one correspondence between its repertoire and that of *P. carolinensis.*

All the authors were in substantial agreement on the number and kinds of calls although there were minor differences. Brewer did not hear all the calls described by Odum and had difficulty interpreting some of his phonetic representations; however, he did hear some calls which Odum missed. An important aspect of Brewer's work is that he studied both Carolina and Black-capped Chickadees, and their hybrid, and found their vocalizations similar in both form and usage.

Dixon, Stefanski, and Folks (1970) published sonagrams showing that the *P. atricapillus* call corresponding to Variable See in *P. Carolinensis* occurs in both broken and smooth, as well as intermediate, forms. The sonagrams of the "male precopulatory call" and "supplanting call" also show close similarity to the Click-rasp, Slink-rasp, and T-slink group of calls of the Carolina Chickadee. Though it would be premature to infer that there is anything like an exact one-to-one correspondence in either form or usage, there is clearly a strongly similar set of calls in the Black-capped Chickadee. Minor differences in the form of the calls used in the precopulatory and fight situations led Dixon, Stefanski and Folks (1970) to name the former as a separate display—"unique precopulatory vocalization." I see no reason to recognize separate displays in either *P. carolinensis* or *P. atricapillus,* at least until variation has been thoroughly studied.

The study of song usage in *P. atricapillus* by Dixon and Stefanski (1965, 1970) did not offer evidence on whether "phoebe" and "phoebe-be" are distinct displays such as Song and Song Variant, or whether these two forms have some other significance. The Black-capped Chick-

adee's usage of whistled songs, both loud and soft, appears to be very similar to the usage of the song group by Carolina Chickadees.

The data on *P. bicolor,* and *P. atricristatus,* are taken mostly from Dixon (1955), plus my own observations in a few instances.

Most of the data on *P. inornatus* are from Dixon (1949); more recent work was also done by Dixon (1969) on singing in this species. One interesting point of the more recent study is that several calls which were apparently variations of song were used as "fighting notes." The relationship between these song-fighting notes and song-like vocalizations which accompanied aggressive acts as described in the earlier study is not clear. Nevertheless, Dixon suggests that Titmouse songs derived, evolutionarily, from "close-quarters threat calls." He notes (1969, p. 100) in support of this a "structural and contextual similarity of some song-types in this species to the fighting notes used in boundary skirmishes by Black-capped Chickadees."

Not all of the song themes were used as fighting notes. Perhaps the group of calls corresponding to T-slink, Slink-rasp, and Click-rasp in this species have converged in form with Song. If so, themes used in ways characteristic of Song usage in other parids could be distinguished behaviorally as "true Song," while the other motifs could possibly be associated with varying probabilities of attack.

There is an overall similarity between the repertoires of the two titmice and those of the two chickadees. They have diverged somewhat in the form of the individual calls, and probably to some degree in details of usage of homologous displays. The extent of the differences between these two groups is not clear yet because neither of the titmice has been studied as thoroughly as the chickadees. Where a particular call (homologue) appears to be missing from a repertoire the most likely explanation, on the basis of current status of the literature, is that it exists but has not been heard. Unless one concentrates specifically on studying vocalizations it is easy to miss rare vocalizations and to fail to differentiate between similar ones.

Published information on other American parids is too spotty to be of use in a repertoire comparison.

The vocal repertoire of *Parus major* was studied in considerable detail by Gompertz (1961a and b) and the repertoire of *Parus palustris* has been reported on by Morley (1949, 1953). *Parus montanus* was reported on by Thönen (1962) who regards the alpine (*montanus*) and lowland (*salicarius*) groups as races. They have distinctive Songs but otherwise their vocal repertoires are indistinguishable in usage and nearly so in sound. Thönen (in litt.) remarked that while the *montanus* group has "on the average" a "somewhat more powerful, rougher call note than the lowland birds," each bird varies the quality of its call notes according to the situation, and there is such great overlap between the two populations that he cannot distinguish individuals of the two groups by their call notes.

TABLE 6.1

A Comparison of Vocal Repertoires in Four American Parids[1]

| *P. carolinensis* | *P. atricapillus* | *P. bicolor* | *P. inornatus* |
|---|---|---|---|
| T-slink, Click-rasp, and Slink-rasp | "Dominance note" probably = Click-rasp; variation with musical notes = Slink-rasp; "musical towill" probably = T-slink[2] | Equivalent calls but perhaps no exact homologues | Several song-like vocalizations |
| Song | Song | Song | Song |
| Song Variant | Either "phoebe" or "phoebe-be"? | May be one of variations described? | May be one of several variations described? |
| Faint Song | Signal Song | None described | May be faint notes identical to Song themes; used Oct.-Jan. in attacks on trapped individuals? |
| Faint Song Variant | Possibly yes | None described | May be one of faint songs? |
| Chip | None described | None described | None described |
| Variable See | "Mating note," twittering | Sit-sit-sit twitter or trill | Sit-sit-sit twitter |
| High See | Tsee "warning note" | See-see-see fear call | See-see-see |

TABLE 6.1 (*Continued*)

| *P. carolinensis* | *P. atricapillus* | *P. bicolor* | *P. inornatus* |
|---|---|---|---|
| High Tee, Chick, and Dee | "General call" and scolding notes | Equivalent of general call and scolding notes | Tsicka dee dee |
| Broken Dee | Begging note | Yes (STS) | Siviva, burry call |
| Loud Tee | Brewer: ditdit-ditdit | None described | None described |
| Tseet | Tseep, tseet "recognition or contact note" | Tsit, tseet | Sip, sisip |
| Squeals, Screams, Hisses[3] | "Distress call" | Squeal | Screech |
| Lisping Tee | Tsleep, tsleet, "flight or restless note," also heard by STS | Yes (STS) | Loud sisip |
| Soft Dee | Brewer: ticket-ticket | None described | None described |

[1] Names of *P. atricapillus* displays are from Odum (1941, 1942), except for those indicated from Brewer (1961). Data on *P. bicolor* (including *atricristatus*) are from Dixon (1955) and from author's observations. Data on *P. inornatus* are from Dixon (1949, 1969). The repertoire of *P. carolinensis* is taken as the standard.

[2] A Click-rasp very similar in form to those of *P. carolinensis* was recorded by the author in Yosemite National Park; sonagrams published by Dixon, Stefanski, and Folks (1970) are also similar. Probably the form and usage differences of these calls in the two species are slight.

[3] Exact equivalents may or may not occur.

Several calls of *P. carolinensis* have clear homologues in the repertoires of all three European parids. These include Song, Variable See, Broken Dee, Tseet, High Tee, Chick, and Dee. *P. palustris* and *P. montanus* both also have homologues of High See and Faint Song. *P. montanus* has homologues of Hiss, Lisping Tee, and probably also of Soft Dee and Loud Tee.

There are also calls present in the repertoires of the European parids which are used in ways strongly reminiscent of other calls of *P. carolinensis*. For example, calls roughly corresponding to T-slink, Click-rasp, etc. occur, but one-to-one equivalents are not identifiable from present descriptions and may, in fact, not occur. For some calls, the homologues appear to be absent. Some of these absences may be owing to incomplete information. Others may be instances where a call has been evolutionarily discarded, its message presumably no longer needed, or subsumed under some other display (see Moynihan, 1970, for a discussion of the evolution of display repertoires).

The extent to which closely related species evolutionarily adapt their display repertoires more to their own ends by shifting the messages which they communicate from one display to another is not known. W. J. Smith is presently undertaking a study of such "message assortment" among displays within genera of tyrannid flycatchers (see W. J. Smith, 1970a, for example). It was hoped that examination of the repertoires of several parids might contribute to an understanding of this phenomenon. However, extensive information on the details of usage of calls which is required to analyze the message content of displays is simply not available for most of them. Hopefully parids will continue to be popular subjects for study and enough will become known about their displays to be useful for such comparative purposes.

# 7

# SUMMARY

1. The subject of this study is communication behavior in the Carolina Chickadee (*Parus carolinensis*). The objectives were: (1) to identify the specialized signals used by this species and the information encoded in each signal; (2) to begin to understand how the communication pattern helps to mediate the species' social organization; (3) to compare, via observations and published reports, the display repertoire of the study population with that of other populations of *P. carolinensis,* and congeneric species; and (4) to compare the information encoded in the display repertoire of this persistently social bird with that encoded by less social species in other avian families, and by mammals. Emphasis was placed on vocal displays rather than on non-vocal displays and unritualized signals.

2. The information encoded in a display (its "message") is that information about the displaying individual that the recipient of the display would know in the theoretical event in which he received only the display, unaccompanied by information from contextual sources. Messages indicate which types of behavior, of the communicator's entire behavioral repertoire, he is doing or is likely to do (see W. J. Smith, 1969). Message statements were derived by examining in detail the usage of each display. The kinds of situations in which each display was used were enumerated.

Those aspects of the situations and of the individual's histories which were thought to be contextual sources of information relevant to the communication events were identified. The meanings of the displays to the recipient birds, as judged by their responses, were studied but in less detail than were the messages. Finally, the apparent functions of each display in various sorts of situations were discussed.

3. The study involved intensive field observations and tape recording of a small population in a residential area west of Philadelphia, through an autumn, winter, and spring; more casual observations preceded and followed this period. Many of the birds were color-banded so that their histories and interactions with one another could be followed for prolonged periods. The tape recorded sounds were subjected to extensive sonagraphic analysis.

4. Communication behavior of Carolina Chickadees was of interest because of the species' social organization. These chickadees flock during the fall and winter, and separate into pairs holding exclusive breeding territories in the spring. They are highly sedentary; many individuals become known to one another and react to each other as individuals. They, therefore, were an interesting point of comparison

with migratory and more solitary birds for which detailed display repertoire studies have been published. In addition to the fact that their strong social tendencies lead to a large number of interactions in which communication is used, they are active, usually easy to observe, and highly vocal. Finally, they could be studied year-round rather than just in the spring breeding season, as is the case with many temperate zone birds.

5. Twenty vocal and 15 non-vocal displays are recognized. The vocal displays and their messages (encoded information) are as follow:

| | |
|---|---|
| T-slink | Attack vs. general set. |
| Click-rasp | Attack vs. general set, probability that attack will occur is higher than for T-slink. |
| Chip | Attack vs. escape. |
| Song | Readiness for agonistic and bond-limited behavior (possibly low level frustration?). |
| Song Variant | Same as Song but thwarted by lack of opportunity. |
| Faint Song | Readiness to perform association and other bond-limited behavior. |
| Faint Song Variant | Same as Faint Song but probably thwarted by lack of opportunity. |
| Variable See | Agonistic vs. bond-limited, or escape vs. bond-limited. |
| Broken Dee | Readiness to perform bond-limited behavior. |
| Lisping Tee | Association vs. locomotory activities. |
| Soft Dee | Association vs. general set? |
| High See | Escape vs. general set excepting some kinds of bond-limited behavior. |
| High Tee | Escape vs. locomotory activity. |
| Chick | Intermediate to High Tee and Dee. |
| Dee | Escape vs. general set. |
| Loud Tee | Escape vs. non-agonistic subset (levels of both tendencies probably high). |
| Tseet | Weak escape vs. general set. |
| Squeal | Thwarted escape. |
| Scream and Hiss | Thwarted escape and attack. |

6. Considerably less attention was given to non-vocal displays in the field and in laboratory analysis. Their messages appeared to be redundant to those of the vocal displays.

7. The 35 displays recognized for the Carolina Chickadee appeared to encode 11 of the 14 basic sorts of messages found by W. J. Smith (1969, 1970b, and pers. comm.) to be common to a large number of birds and mammals. Carolina Chickadees are the first parid, and the first persistently social, i.e., never solitary, bird to be studied with the purpose of determining the message content of the entire display repertoire; this makes their conformance to the basic messages encoded by dissimilar species all the more striking. The three basic sorts of messages not encoded in their display repertoire are Copulation, Play, and Social Interaction Hesitance. The Play message is known only from primates. The Social Interaction Hesitance message is known only in man, gorillas, and perhaps from a tyrannid flycatcher. The Copulation message is known from some birds, but it is argued that in many cases what is thought to be a strictly sexual message is probably a broader, bond-limited message.

8. The use of elements of the display repertoire by different classes of individuals, in different situations, and in different seasons, is discussed.

9. Variability within individual repertoires, among individuals in local regions, and on a broader geographic scale of Song, Song Variant, Click-rasp, and T-slink is considered. Probably all individuals used more than one variant of each of these, though marked preferences for one variant were sometimes shown. Some variants appeared to be unique to an individual, while others were shared; the amount of sharing was probably underestimated by the method used to assess individual repertoires. Factors influencing the use of different variations are discussed. Arguments are presented that individual recognition is a primary consideration. Further arguments are presented against the notion that variations of the types described have different "valences," i.e., have slightly different messages regarding attack probability. Geographic ("dialectal") variation is considered, and it is suggested that the concept of "dialects" as employed in much of the literature is misleading to the extent that it is typological.

10. Several adaptations of the display repertoire to the persistently social life style of the chickadees are discussed.

Seven vocalizations encode a readiness or tendency to perform association or other kinds of bond-limited behavior. Four vocalizations encode attack tendency, nine (possibly 10) encode escape tendency, and two (possibly three) encode both agonistic tendencies. The vocalizations vary in the combinations of these tendencies with each other and with other tendencies, and in the absolute and relative strengths of the conflicting tendencies. Chickadees have long-term relationships

with each other as individuals; these relationships shift from season to season, day to day, and even minute to minute. Hence, the large selection of agonistic displays enables them to adjust rather finely their responses to one another. In addition, the large number of vocalizations encoding escape tendency may have been selected for as predator warnings; in species that form persistent relationships the survival of one's companions is worth some risk to one's self.

Eleven vocalizations encode rather general messages, i.e., messages which do not specify closely the communicator's probable behavior. Because Carolina Chickadees are so persistently social, and know one another as individuals for long periods, they can rely on extensive contextual information in interpreting one another's displays. Compared with other birds and mammals, Carolina Chickadees have a rather large number of displays. Probably persistently social species have some need for, and ability to employ, larger numbers of displays. Although many of the displays overlap in the tendencies or combinations of tendencies which they encode, they differ in the encoded probabilities of performance. This permits a finer adjustment of the communication events to the situations at hand.

11. The vocal repertoires of *P. atricapillus, P. bicolor,* and *P. inornatus* are considered in detail from reports in the literature and compared with that of *P. carolinensis.* Comparisons are hampered by the fact that the entire display repertoires of the other parids have not been studied in as great detail as that of *P. carolinensis.* On the basis of present knowledge, the repertoire of *P. atricapillus* appears to be very similar to that of *P. carolinensis.* The titmice are apparently less similar, but their display repertoires are least well known. Table 6.1 shows probable homologies among the repertoires of the four species.

The display repertoires of the European species *Parus major, P. palustris,* and *P. montanus* are also considered. They are found to differ more from *P. carolinensis* than do other American parids.

12. Detailed examination of the display repertoires of several parids should permit some assessment of how they are adapted to each species' social organization and, in particular, show if messages are shifted or re-assorted from one display to another in different species. However, the entire display repertoires of other parids are not yet known in sufficient detail to accomplish this end.

# 8

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