A COMPARATIVE ANALYSIS OF ACOUSTICAL SIGNALS IN PIED WOODPECKERS (AVES, *PICOIDES*)

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ABSTRACT

The avian genus *Picoides* with 33 species is the largest of the nearly worldwide family of woodpeckers (Picidae). *Picoides* is the subject of vocal analysis involving field, literature, and audiospectrographic studies. Analyzable data were available for two-thirds of the species. The analyses were conducted using quantitative and qualitative techniques, in a manner attempting isolation of descriptive, functional, motivational, and homologous aspects of acoustical signal communication. Vocalizations include Call Notes, Scolding Call, Double Call, Rattle Call, Short Rattle Call, Mistle Thrush Call, Mutter Call, Kweek Call, Wicka Call, Twitter Call, Wad Call, Soft Notes, Distress Trill, Chirp Call, Loud Chirp Call, Squeak Call, Screech Call, and Distress Cry, and there are several instrumental signals (Drumming, Tapping, Wing Rustling). These are described and many are illustrated sonagraphically for species represented by tape-recordings.

Summaries are provided for all vocal and instrumental signals that have several or more species represented. Most sounds made by these woodpeckers are formed of three major elements: clicking, squeaking, and ascending sounds. When further data become available, these elements may provide a productive means of analyzing the vocalizations. Aspects of the repertoire briefly discussed are the number and quality of calls, their discreteness, overall tendencies in structure, relative frequency of different calls, and combinations. Each major acoustical signal is discussed functionally, in terms of its "meaning" and the biological advantages it affords.

The array of such signals includes calls that may overlap in function, but differ in occurrence, the distance at which they are effective, and other parameters. Drumming and the Rattle Call are the most important long-distance signals. Call Notes chiefly are contact calls. Rattle Calls function in territorial announcement and defense, but may serve as a contact call in some species. Sexual interactions of various kinds are accompanied by Kweek Calls, with special functions in *P. medius* and *P. borealis*. Wicka, Mutter, and Twitter calls mark encounters between individuals and often accompany visual displays. Wad Calls commonly occur between members of a pair. Various nestling and fledgling calls are ascribed functions. Drumming has diverse and often subtle functions, and may differ in structure and function seasonally. It differs from most avian signals in communicating over a distance, aspects of environmental features, e.g., the occurrence of suitable trees for Drumming or nesting. Motivation of the signals is discussed in a framework based on a general arousal scheme and dominance behavior that is directly equivalent to "aggressive" behavior ethologically. The Call Note indicates arousal, Scolding—alarm, and Rattle Calls—aggression, in this context. Kweek Calls of one type usually are submissive; those of another, as well as Wicka Calls, are aggressive. Conflicts between fleeing and aggression find expression in the Mutter and the Twitter Calls, and between aggression and submission in the Wad Call. Hunger, the motivation to flee, or to stay in place usually seem involved in the Squeak Call.

Drumming seems related to a special category of motivation with a low threshold that may be elicited by extraneous noises or the presence of a Drumming substrate. An attempt is made to ascribe likely meanings to the signals, based on their information content. Call Notes indicated the location of the sender, and particularly are noted with changes in position. The Rattle Call is self-assertive or aggressive and transmits that information plus the location of the signaler. Scolding and Short Rattle Calls indicate alarm, and convey that meaning. The complex of Mutter, Twitter, Kweek, and Wicka calls give varied information about the sender's motivational state during interactions. Further analysis is necessary to decipher exact meanings, which depend in any event on the social relations existing between interacting individuals. Other calls and instrumental signals are discussed in a similar manner. Homologies are treated, based on similarities in form and the relation of calls to other calls, displays and situations; evolutionary and ontogenetic effects are related to homology within pied woodpeckers, and to some degree with other picid groups. Some acoustical signals, notably Drumming and Scolding, but even Rattle Calls and Call Notes are effective interspecifically in *Picoides*, between pied woodpeckers and species of diverse woodpecker genera, and occasionally between pied woodpeckers and birds of other families.

Taxonomic applications of the data include as major points the monophyly of the genus *Picoides sensu* Short (1971a), close relationship of *arcticus* and *tridactylus* to the *villosus* subgroup, monophyly of the American group of *Picoides*, the distinctness and derived state of *medius*, and of the *major* group, and the likelihood that the most primitive members of the genus are to be found in Asia among relatives of the *moluccensis* and *canicapillus* groups. Vocalizations are described for two hybrid combinations, *major* × *syriacus* and *scalaris* × *nuttallii*, and are more or less intermediate between those of the parental species.

INTRODUCTION

There are few acoustical analyses of entire genera of birds, and none treating such communication in woodpeckers. Woodpeckers present excellent animals for acoustical studies because they tend to be noisy and conspicuous, and widely distributed. Their sounds are simple, yet show some complexity in arrangement and correlation of different calls. They also employ drumming and tapping sounds that, if not unique in birds, are most fully developed in woodpeckers. The pied woodpeckers, genus *Picoides*, include some of the most familiar of birds, e.g., the Downy Woodpecker (*Picoides pubescens*) of North America and the Great Spotted Woodpecker (*P. major*) of Eurasia. Further, this genus is by far the largest in the Picidae, with 33 species distributed in South America, Middle America, North America, Eurasia, Africa, and reaching Japan, Indonesia, the Philippines, and Ceylon. Because they are rather common and so widespread, more is known of more of them than of any large genus of woodpeckers (e.g., *Picumnus*, *Picus*, *Melanerpes*). The species of pied woodpeckers, and the status of our knowledge of their acoustic communication is indicated in Appendix 1, where the reader will find both scientific and vernacular names of all species treated herein.

We have been studying woodpeckers for more than a decade, the senior author in Europe, North Africa, and North America, and the junior author on all the continents where woodpeckers occur. We have observed 24 of the 33 species and have conducted studies of most of these. Through our efforts and those of our colleagues we have been able to obtain recordings on tape of vocalizations and instrumental signals of 25 species. The especially poorly known species are indicated in Appendix 1; we would welcome any recordings of these species. There are at least literature references to vocalizations of all species, but many vocalizations are unknown in the less-studied species, and even the best-known species require further investigation.

The rarity of such an analysis as we have undertaken is chiefly because information is lacking about many species. While we do not pretend that our analysis is complete or more than tentative, we hope that it may serve as a model for similar analyses of other woodpecker groups and, indeed, of other birds. We believe that our main contribution is in the bases of our analysis, that is, we have attempted a quantitative and reasonably objective analysis of pied woodpecker acoustic signals in a manner that avoids the usual confusing blending of functions, meanings, and homologies with descriptions of calls. To the extent that we have been successful in isolating and considering these aspects, a basis has been provided for future studies and for progress in understanding signal communications in animals.

The organization of the present report has been indicated in the Contents. Note that summaries are given section by section, and therefore no attempt has been made to summarize the entire contents except in the Abstract.

METHODS AND MATERIALS

The recordings we analyzed came from various people listed below. Most recordings were made with Uher Report tape-recorders, using 24-inch parabolic reflectors equipped with one of the following microphones: Sennheiser MKH 405, Uher MD 514 Dynamic microphone, AKG D-19 Dynamic microphone. On occasion these microphones were used without the reflector (young, distress calls, recordings at the hole, and of caged birds), and several recordings were made using an AKG directional microphone. All tapes were sonagraphed by us using a Uher or a Revox tape-recorder, a Kay Electric Sonagraph 6061-B in New York, and a Kay Electric Vibralyzer 7030A in Vienna.

During the analyses it became clear that for the type of vocalizations found in *Picoides* woodpeckers, use of the wide-band filter on the sonagraph (band width 300 Hz.) was the preferable method for demonstrating the important aspects of the calls. These aspects are more clearly portrayed with wide-band analysis, which has better time-resolution than has narrow-band (fig. 1). We decided to illustrate tracings of sonagrams instead of photographs of the original sonagrams. This technique permits us to exclude noise from poor recordings and to include data from very noisy recordings; this is important, for such recordings represent the only analyzable sounds available for some species. It also allowed us to illustrate minor features that are apparent only after detailed study of many sonagrams. This necessarily involved interpretation, which was based on the analysis of the sonagrams and our experience with the vocalizations. The capability to exclude noises, sounds of other birds (and other animals), echoes, and other extraneous sounds through the use of drawings more than makes up for the slight subjectivity required to render drawings from sonagrams. We hope that these drawings are sufficiently complete and detailed to make it possible to identify individual sonagrams obtained from field recordings of undetermined woodpeckers. Our decision as to rendering a drawing always was reached after critical examination of all the sonagrams available for a given vocalization. All drawings were made by Winkler, and are based on wide-band sonagrams unless otherwise stated. Measurements are in millimeters with an accuracy of 0.5 mm. from both narrow-band (pitch) and wide-band (time features) sonagrams. The data were analyzed by computer; the Standard Deviation was computed from the original data in millimeters and then converted into the particular dimension (kilohertz, milliseconds). We emphasize that measurements of this type give only rough approximations of the "true" values; minor inaccuracies arise from the accuracy of the tape recorders and the sonagraph. These "machine" errors are permissible because they are small, and also because they are inconsequential given the variation in biological systems. For the demonstration of characters not to be seen on the sonagram under normal analyzing procedures we slowed down the tape recorder to a quarter of the original speed. By doing so we accomplished most of the analysis of amplitude behavior (using the built-in device on the sonagraph), as well as the "enlargement" of certain calls (fig. 20) by setting the Scale Magnifier of the sonagraph to the range from 0 to 5.9 kHz.

Field notes are the source for the analysis of the usage and behavioral context of the vocalizations. For obtaining quantitative data in the field by this method a stopwatch is handy. The best general time unit for counting call frequencies and noting interactions is the minute; for fast series of Call Notes (p. 9) an interval of 15 seconds is the most practical. Information about the vocalizations recorded on tape was spoken by us during the recording; additional information was written in a notebook immediately after a particular "take."

Abbreviations used throughout the text include m. for meters, cm. for centimeters, mm. for millimeters, sec. for seconds, msec. for milliseconds, Hz. for Hertz, and kHz. for kilohertz.

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Many persons, too numerous to mention, helped us in the course of our studies. Some of those assisting Short in the field have been cited in his previous publications. Our colleagues Walter J. Bock and Wesley E. Lanyon aided us in numerous ways. The senior author conducted some of the research while a Frank M. Chapman Fellow of the American Museum of Natural History, and he received two grants from the Frank M. Chapman Memorial Fund to assist in his work. He also received support from the Kulturamt der Stadt Wien. Various tape and other supplies, tape-recorders, microphones, and a sonagraph were provided by the Ornithology Department of the American Museum of Natural History, the Chapman Memorial Fund, the Phonogrammarchiv der Österreichischen Akademie der Wissenschaften, and the Komission für Schallforschung of the same Akademie. The junior author was supported in part by grants from the United States National Science Foundation (grant no. GB-5891), the

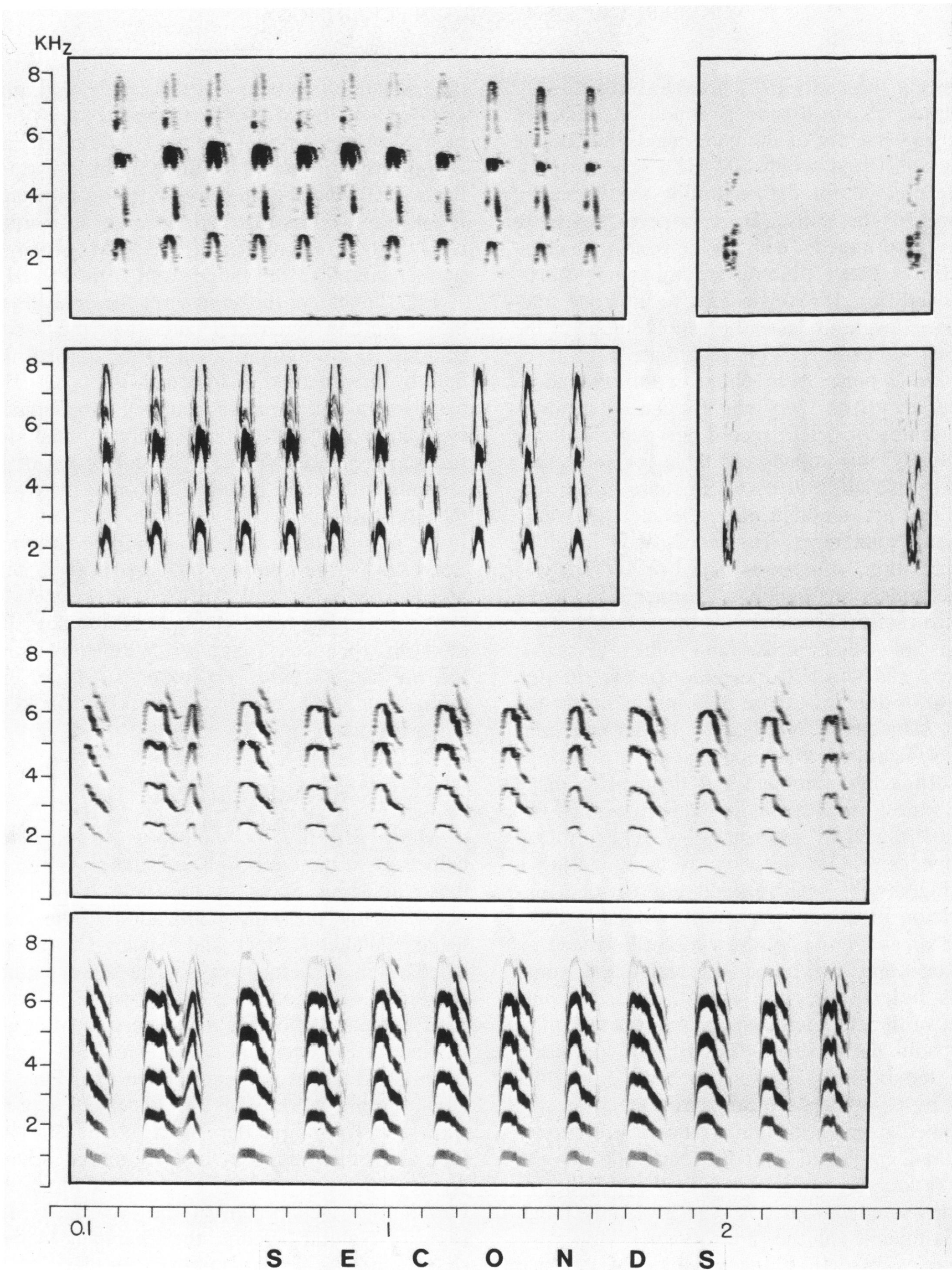

FIG. 1. Three call-types of *P. major*. First row: narrow-band sonagram of begging young (left) and narrow-band sonagram of a Wad Call (right). Second row: same as first row but wide-band sonagrams, cf. fig. 31K and fig. 28G. Third and fourth rows: narrow-band, then wide-band sonagrams of the Distress Call of a hand-held female (cf. fig. 35D). See text for discussion.

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Tapes were provided by our colleagues A. Aichhorn, D. Blume, C. Chappuis, K. Conrads, M. Gochfeld, A. Jilka, B. King, H. Mensendieck, W. Scherzinger, G. Thielcke, and W. Weber, and by Short's summer students J. J. Barry and K. Fiala. We are very grateful to these individuals and agencies. Figures based on sonagrams made from recordings provided us by others are as follows: 5A (Aichhorn); 2T and 3G (Barry); 31A and B, 33A, B, and I, and 36A (Blume); 23A (Chappuis); 5B, 22C, and 33E (Conrads); 22N, 28 O and P, 32A, 33J and K, and 35F, G, H, and I (Fiala); 22E (Jilka); 2B and 37B (Mensendieck); 16 and 35C (Scherzinger); 21A (Thielcke); 3M, 18A, 30 O, and 32 I and J (Weber). Additional figures were based on sonagrams made from these records: Blume, Ruge, and Tilgner's Die Sprache unserer Spechte (fig. 23B); Institut Echo (figs. 17E, 22F, 28B, and D); Japanese Bird Songs, volume 1 (figs. 2M, 5D, 37F); Gunn and Kellogg's Field Guide to Western Bird Songs (fig. 22 I); and Sveriges Radio Radions Fögel Skivor series, numbers 235 and 236 (figs. 2G, 22G, and 37C). It is more than appropriate that we acknowledge these sources, which we do with pleasure—without the data so provided our analysis would have been curtailed greatly.

DESCRIPTIONS OF VOCALIZATIONS

GENERAL NOTES

In this part of our study we try to give reasonably detailed descriptions of the vocalizations of the pied woodpeckers, insofar as known. Wherever possible we present examples of sonagrams of the particular vocalization. We stress the importance of describing and depicting the variation that occurs within diverse categories of vocalizations. There exist many verbal descriptions of calls of species of *Picoides*, but many such descriptions lack sufficient detail to enable us to infer correctly what call is meant. We mention such verbal descriptions only in cases where no other information is available, and when it seems clear what call is meant. For better known calls we summarize the names that seem to have been applied by the various authors. In the interest of brevity, references are omitted where calls have been designated similarly by several authors and seem to be well known.

An important descriptive aspect of the calls is their relation to other behavior and stimuli. For easier comparison this information is coded in table 1, and details about the categories are provided below. For all categories of table 1 we may use "(1)" or "(2)," meaning: (1) bird at a signaling site, i.e., treetop, exposed branch, or other such site to which the bird moved before signaling (site may be used several times independently); and (2) the call is accompanied by a visual display. The seasonal occurrence of a call is indicated by numbers from 1 to 12 representing the months of the year in which the vocalization is given. When observations are incomplete through the year, the numbers are placed in parentheses. Peak months are italicized where known.

If it is not possible to categorize fully a vocalization, only the letter of the code is noted. We hope this scheme will merit use in further studies of these woodpeckers and that gradually more details will be added.

The names and groupings of the various vocalizations are preliminary, and represent a first rough attempt to classify the calls according to their physical aspects. Later we shall review this scheme, modifying the classification of calls under the aspects of function and phylogeny.

CALL NOTE

maculatus. K. C. Parkes (personal commun.) noted that the "pik" call of this species is higher pitched than that of the Downy Woodpecker (*P. pubescens*).

canicapillus. The Call Note of the Gray-capped Woodpecker (fig. 2A, table 2) is a short, sharp but soft note (Short, 1973), appearing on the sonagram as a symmetrical, inverted U- or V-shaped note with emphasis almost equally on the fundamental tone and the first harmonic. Short (*op. cit.*) stated that the Rattle Call (p. 23) is uttered more often than the Call Note (as compared with *P. macei*). The birds,

TABLE 1
Codification of Behavior and Stimuli in Relation to Vocalizations

A. "Non-social" activities

1. Feeding
2. Flight
   a. At takeoff
   b. During flight
   c. At end of flight, alighting
3. Preening and other comfort activities
4. Excavating of cavities

B. Signaling and receiving signals at a long distance

1. Receiving; remaining in place
2. Receiving; approaching signal source
3. Receiving; withdrawal from signal source
4. Move to a behaviorally significant place (drumming tree, hole)
5. Move from a behaviorally significant place

C. Contact with other individuals

1. Potential predator or competitor
   a. Remain in place
   b. Withdraw
   c. Approach
   d. Attack
2. Potential mate
   a. Remain in place
   b. Withdraw
   c. Approach
3. Intrusion upon strange territory
   a. Halt in place
   b. Withdraw
   c. Intrude farther
4. Reaction to intruder
   a. Remain in place
   b. Withdraw
   c. Approach
5. Combat
   a. Approach
   b. Approached

TABLE 1 — (*Continued*)

   c. Attack
   d. Attacked
   e. Pause near opponent (s)
   f. Pause at distance from opponent (s)
   g. Withdraw from conflict on the wing
6. Pursuits on the wing
   a. Pursuing
   b. Pursued
7. Approaching or leaving mate
   a. Approaching
   b. Leaving
8. Remaining at distance from mate
   a. Long distance
   b. Closer
9. Copulation
   a. Signaling before copulation, male
   b. Signaling before copulation, female
   c. Approaching before copulation
   d. Approached before copulation
   e. Copulation
   f. Postcopulation

D. Activities around the nesting cavity or prospective nesting cavity

1. Approaching, at long distance
2. Approaching, nearby
3. At the hole
4. Leaving the hole, in proximity
5. Leaving the hole, at long distance
6. In the neighborhood of the hole
7. Relieving mate

E. Disturbance at the hole

1. Remaining at a distance
2. Attacking
3. Fleeing
4. Approaching
5. Remaining in or near the hole during disturbance or attack

F. Nestlings

1. Parent not present
2. Parent close or approaching at short distance
3. Being fed
4. Pain, etc.
5. Relief of pain, etc.

G. Fledglings

1. Parents at long distance
2. Approached by the parent, or parent nearby
3. Approaching the parent
4. Withdrawing
5. Being fed

H. Other situations

(Specified in text)

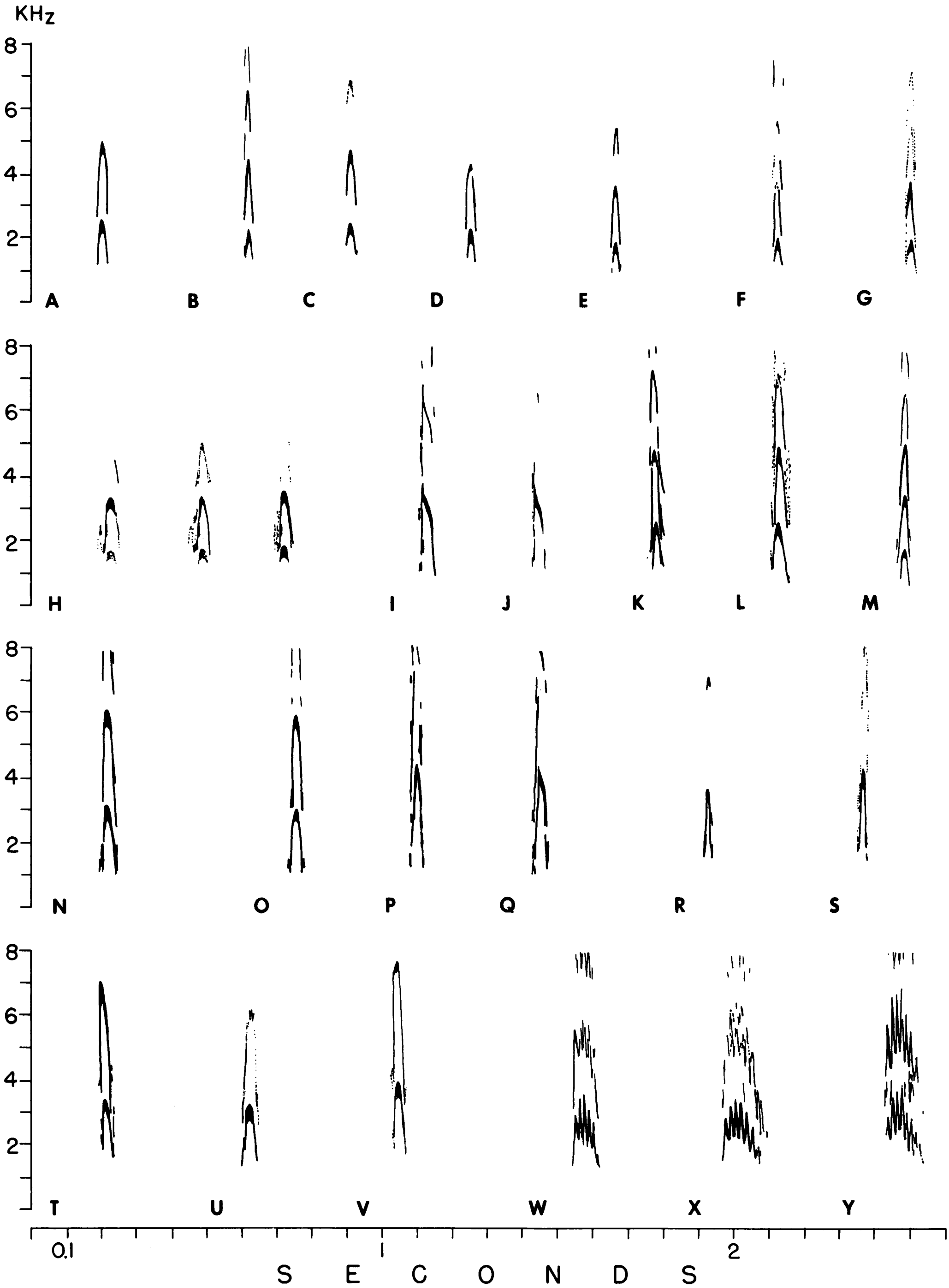


FIG. 2. Sonagrams of Call Notes of pied woodpeckers. A. *P. canicapillus*; India. B. *P. minor*; Germany. C. *P. macei*; India. D. *P. cathpharius*; India. E. *P. darjellensis*; India. F. *P. leucotos*; Austria. G. *P. leucotos*; Sweden. H. *P. medius*; Austria. I. and J. *P. syriacus*; Austria. K. *P. major*; Austria. L. *P. major*, adult female with food in the bill; Austria. M. *P. major*; Japan. N. *P. major* × *syriacus*, imm.; Austria. O, P, and Q. *P. scalaris*; Baja California. R. *P. nuttallii*; Baja California. S. *P. scalaris* × *nuttallii*; Baja California. T. *P. pubescens*; New York. U. *P. pubescens*, adult male with food in the bill; New York. V. *P. pubescens*; St. Catherines Island, Georgia. W, X, and Y. *P. borealis*; North Carolina. All are wide-band.

according to Short, were disturbed by the presence of the observer or of a *P. macei* or involved in agonistic encounters, when giving Call Notes. Often this call was associated with Rattles (p. 23).

Situations: C, D, E, H
Seasonal occurrence: (4, 5)

minor. The note is short and clicking, without being very shrill or loud. On the sonagram it shows as a symmetrical, inverted V-shaped note with the emphasis on the first harmonic tone (fig. 2B, table 2). Because of the call's low amplitude it is seldom heard in the field (see also Witherby et al., 1938). This call was loosely associated with Scolding (p. 19) during disturbance at the breeding hole. From caged birds this call was heard only when there was a strong disturbance (human moving objects in the cage; introduction of a Syrian Woodpecker into the cage). Therefore, it was very seldom heard, and was by far rarer than the Rattle.

Situations: A1, 2c; E1; H
Seasonal occurrence: 1-12

macei. Short (1973) described the sound of the call as sharper than that of sympatric *P. canicapillus*, but less sharp than the Peek Call of *P. scalaris* or the Kix Call of *P. major* (fig. 2C, table 2). The first harmonic of this regularly formed note is of about the same strength as the fundamental tone (calls in which one or the other is slightly stronger can be found). The call is given singly or in very loose, irregular series.

Situations: C1, 4, 7 Seasonal occurrence: (5)

mahrattensis. According to Smythies (1953) a feeble peek is given by this woodpecker. Ali and Ripley (1970, p. 227) wrote that such notes are uttered when observers approach the nesting hole, and that between members of a pair a "chuck" is exchanged.

Situations: C8; E
Seasonal occurrence: Unknown

dorae. "The call is reminiscent of that of the greater spotted woodpecker . . . . . a fairly loud *ka ka ka*" (Meinertzhagen, 1954, p. 304).

cathpharius. Similar to but shorter than the call of *P. macei*, the fundamental tone dominating; this call does not much resemble the calls of the *major* group. It is given in situations involving disturbance by the observer (Short, 1973) and during feeding (Cranbrook, cited in Ali and Ripley, 1970) (fig. 2D, table 2).

Situations: A1, H Seasonal occurrence: (5)

darjellensis. The call was described by Short (1973) at length (see also Diesselhorst, 1968, p. 185). It is sharper than the calls of the previously mentioned small species and of regular, arrowpoint shape on the sonagram, having the first harmonic tone more pronounced than the key-tone (fig. 2E, L, table 2). The Brown-throated Woodpecker called when disturbed by the observer or when the mate flew overhead or perched nearby.

Situations: A1, C8, H
Seasonal occurrence: (5)

leucotos. The call is a soft, low note of regular, symmetrical shape on the sonagram (fig. 2F, G; 4K). Franz (1937) noted that the "Kjück" of the White-backed Woodpecker is two tones lower than that of the Great Spotted Woodpecker (table 2). The call is seldom heard except during disturbance at the nest hole.

Situations: A1; D3, 5; E1, E3
Seasonal occurrence: (4, 5, 6, 12)

medius. This uncommon call is low and on the sonagram is of an inverted U-shape, with an introductory element (fig. 2H, table 2).

Situation: A1 Seasonal occurrence: (1, 4)

himalayensis. A recording obtained by Thielcke at a nest of the Himalayan Woodpecker contains loose, irregular series of calls, apparently uttered by the alarmed parents. The calls show a slight asymmetry at the peak like the one in *syriacus* (table 2).

Situation: E Seasonal occurrence: Unknown

syriacus. Ruge (1969) referred to the Syrian's Call Notes as Kixen, and Winkler (1972) as Püg-Ruf. This call, the most frequent acoustical signal of this species, is of considerable loudness and has a hard clicking quality (fig.

TABLE 2
Call Notes of Species of Picoides[a]

	Pitch					Duration				
	Mean	Range	S.D.	C.V.	N	Mean	Range	S.D.	C.V.	N
canicapillus	2.4	2.3-2.6	0.46	19.2	9	31.9	30.2-37.7	1.00	3.1	9
minor	2.2	2.0-2.4	0.25	11.5	10	35.5	26.4-53.1	1.97	5.6	10
macei	2.3	2.2-2.5	0.35	15.5	8	30.7	26.4-34.0	0.88	2.9	8
cathpharius	2.1	2.1-2.2	—	—	2	24.5	22.6-26.4	—	—	2
darjellensis	1.7	1.4-2.2	0.73	42.7	13	25.3	22.6-30.2	0.87	3.4	13
leucotos	1.8	1.7-2.0	0.32	18.3	9	28.5	22.6-34.0	1.21	4.2	9
medius[b]	1.6	1.6-1.7	0.22	13.6	3	39.0	37.7-41.5	0.79	2.0	3
himalayensis	3.0	—	0.14	4.7	6	27.9	26.4-30.2	0.75	2.7	5
syriacus[c]	3.1	3.0-3.2	0.34	10.8	11	37.1	34.0-45.3	1.72	4.6	11
major, Austria	2.6	2.3-2.7	0.40	15.6	27	34.4	26.4-41.5	1.39	4.0	27
major, Sweden	2.0	1.9-2.2	0.54	26.6	3	32.1	30.2-34.0	0.79	2.5	4
major, Japan[d]	1.5	1.4-1.5	0.22	15.0	5	27.2	22.6-34.0	1.79	6.6	5
mixtus	3.5	—	—	—	1	37.7	—	—	—	1
scalaris[e]	3.2	2.6-4.3	1.72	53.2	27	37.5	30.2-45.3	1.66	4.4	27
nuttallii	3.4	3.2-3.5	0.37	10.8	9	23.1	18.9-26.4	0.83	3.6	9
pubescens	3.6	3.2-4.0	0.79	21.8	41	33.1	26.4-41.5	1.21	3.7	41
borealis[f]	2.8	2.6-3.0	0.12	4.3	32	103.2	71.7-128.3	15.26	14.8	32
stricklandi[g]	3.0	2.8-3.2	0.39	12.9	13	67.0	56.6-75.5	1.94	2.9	13
villosus[h]	3.0	2.9-3.0	—	—	2	61.0	49.1-75.5	3.26	5.4	13
tridactylus, N.A.	2.8	2.7-2.9	0.43	15.4	3	30.2	—	—	—	3
tridactylus, C. Europe	1.9	1.6-2.1	0.45	24.0	14	48.25	45.3-56.6	1.23	2.5	14
arcticus[i]	—	—	—	—	—	42.2	37.7-45.3	1.35	3.2	11
major × *syriacus*	2.8	2.6-2.9	0.43	17.5	4	37.7	—	—	—	4
scalaris × *nuttallii*	3.9	3.8-4.0	0.09	2.5	4	26.4	—	—	—	4

a. Symbols: S.D., Standard Deviation; C.V., Coefficient of Variability; N, sample size; N.A., North America; C, Central. Pitch is in kilohertz, duration in milliseconds; *b.* clear introductory element; *c.* peak of the note asymmetrical; *d.* lumped data of two sources, see text; *e.* peak symmetrical or asymmetrical; *f.* peak of long duration and with strong frequency modulation (see text for measurements); *g.* peak of long duration, flat; *h.* values for pitch of first harmonic: 6.0, 5.5-6.6, 1.13, 18.7, 10. Keynote usually missing. *i.* see text for more measurements. Central element of the note is missing.

2 I, J, N). The most characteristic feature on the sonagram is its asymmetrical peak: after the fast-rising introductory note (theoretical rising time 10 msec.) the middle part falls down, leading smoothly to the relatively slowly falling end part (20.4 msec.) of the call. The measurements of the pitch of this note were taken at the beginning (the higher-pitched portion) of the middle section. The call has a very variable rate of delivery (see Scolding, p. 19). This rate is correlated with other activities: birds that show many movements, displays, and intention movements also utter this call more frequently. At high rates of delivery the call becomes shriller but in all the analyzed cases the fundamental tone is by far the most powerful component. The Call Note is regularly combined with the Rattle Call (p. 28) and the Short Rattle (p. 38). Transitions to the Squeak Call are common. Field notes also indicate that transitions to the Kweek Call occur, but this remains to be proved by sonagrams, especially in this case in which both calls are relatively similar to the human ear. A loud sharp call, sounding like some Call Notes given by flying Syrian Woodpeckers carrying large food items, is to be heard from nestlings as young as 10 days old. In the late nestling stage this call is delivered

frequently by young looking out of the entrance, and no transition to the Chirp Call (p. 63) could be found (see also *major*, below). Fledged young give this call and transitions to the Squeak Call frequently, especially when adults (or a human provider) are visible. Birds often call many times in the neighborhood of the roosting hole before entering for the night. Syrian Woodpeckers perched on branchlets in treetops within their territory deliver Call Notes regularly. This call is used all year round; only during the periods of copulation, egg-laying, incubation, and small nestlings is the call less likely to be heard (see fig. 21 in Winkler, 1972). Playback experiments before nesting time attract mated pairs, which react by approaching closely (to within 2 to 3 m.) and calling. Breeding birds react to playback by exiting from the nesting cavity, perching at the entrance, or (sometimes) leaving the hole in the direction of the signal source. The mate, especially the male, reacts by approach with food, searching flights and calls.

Situations: A1, 2b, 2c, 3; B1, 2; C 1b, 2, 8; D3; E1, 3, 5; F1; G1 Seasonal occurrence: 1-12

major. This most common call of the Great Spotted Woodpecker was named "Kix-Ruf" by Blume (1968) and its sound was described as "tschick" by Witherby et al. (1938). It is a sharp, shrill, and quite short call in European birds (*anglicus*, *major*, *pinetorum*) (figs. 2K, 2L, 4M). There is, however, noteworthy geographical variation. Schüz (1959) and H. Steiner (personal commun.) noted that birds from Asia Minor have a lower-pitched and softer call. So too are the calls of Japanese Great Spotted Woodpeckers (fig. 2M, table 2). The calls of the subspecies *numidus* of northern Tunisia and Algeria are a bit softer than those of the Central and North European birds; the pitch is about 2.0 kHz. and the duration 41 msec. It would be interesting to analyze also the calls of other such remote subspecies, and their sympatric congeners of similar wide range (*leucotos*; see also *tridactylus*, p. 16). The note on the sonagram shows a regular, symmetrical shape like an arrowpoint. Harmonics are well developed and receive more emphasis when the rate of delivery increases, becoming shriller, too. A short introductory element is more or less developed (e.g., *numidus* shows this element often, some other populations less so).

This call is heard in a wide range of situations. Among other instances, Great Spotted Woodpeckers regularly call before entering the roosting hole, usually at a place nearby, preferring high vantage points (Blume, 1968). Generally, birds that utter this call at rapid delivery rates are found perched in treetops or in other exposed sites. Fledglings are easy to find because of their frequent calling.

As already described for the Syrian Woodpecker (see above), Great Spotted Woodpeckers also react to playbacks of the Call Note with calling, approach, searching flights, and (when breeding) leaving the nesting hole or at least looking out of it.

Situations: A1, 2b, 2c, 3; B1, 2; C; D; E1; F1; G1; H Seasonal occurrence: 1-12

major × *syriacus*. Sonagrams of Call Notes of three hybrids show an intermediate form compared with the father (*syriacus*) and mother (*major*) (fig. 2N, 4 0). The slightly longer duration (table 2) of the call probably is due to the juvenile state of the birds recorded. The Call Notes resemble those of the Syrian Woodpecker more than those of *major* (see also Winkler, 1971a).

mixtus. Short (1970) noticed a "peek" call that was similar to the calls of *scalaris* and *pubescens*. The spectrographical analysis of the one recording available (courtesy of M. Gochfeld) confirms this statement (table 2). The note resembles that of the Downy Woodpecker, being symmetrical and having a rounded peak. Birds disturbed by the observer when feeding, and a male which also occasionally drummed, delivered these notes.

Situation: H Seasonal occurrence: (9)

lignarius. This species, too, has a "peek" call, sounding similar to the last species and *scalaris* and *pubescens*, but lower and less harsh. It is uttered in similar situations as in *mixtus* (Chapman, 1917; Short, 1970).

Situation: H Seasonal occurrence: (11, 12)

scalaris. As a verbal description of the sound Short (1971a) used the word "peek." It denotes the length of the call (compared with *nuttallii*) and its quite high pitch (table 2). Sonagrams reveal considerable variation in this call not only in pitch (see table 2; the Coefficient of Variability is the greatest of all species analyzed) but also in the form of the peak that can be of symmetrical or asymmetrical form (fig. 20P, Q). We were not able to correlate this variation with environmental or geographical data. The variation of the duration of the call, however, is within the limits of the other species.

Call Notes are often associated with Rattles (Short, 1971a) and are heard frequently. A female, alarmed by the presence of the observer, gave 32 notes per minute. Call Notes may be answered by Drumming and Rattles (Short, 1971a).

Situations: A1, 2b, 2c; C 1a, 3a, 4a, 5a, 5e; H
Seasonal occurrence: 1-12

nuttallii. This call, described by Short (1971a) as Pit, is short and high-pitched (fig. 2R, table 2). The variation of this note does not exceed normal limits as in the previous species. The harmonics are less stressed than is the fundamental tone.

The Call Note is frequently associated with Double Calls, which usually are uttered more commonly and are associated with Rattles. The Call Note may evoke Rattles and Drumming (Short, 1971a).

Situations: A1, 2; B1, 2; C 1a, 1c, 3a, 4a, 5a, 5e, 7, 8 Seasonal occurrence: 1-12

scalaris × *nuttallii*. Short (1971a) discussed the calls of a hybrid male and stated that these Call Notes are intermediate between those of the parent species, although strongly tending toward *scalaris* (fig. 2S, table 2).

pubescens. Kilham (1962) described the Call Note of the Downy Woodpecker as chip or kick, Short (1971a) as Pit (fig. 2T, U, V). The call of this species is the highest pitched in this genus (table 2). Only the calls of *villosus* which lack the fundamental tone (see below) are still higher in pitch.

The Call Note regularly is combined with the Rattle and with the uncommon Double Call, and strongly associated with Scolding. Between the latter and the Call Note all sorts of transitions may be recognized.

The call is not so uncommon as the corresponding call of *minor* but is more restricted to situations involving "excitement from any cause" (Kilham, 1962) than the very common but more specialized Rattle (p. 29).

Situations: A1, 2b, 2c, 3; C1, 3, 4, 5; E 1, 4, 5
Seasonal occurrence: 1-12

borealis. The Call Note of this species and that of *arcticus* are the most derived such calls within the (known species of the) genus. The pitch of this call can be defined only by viewing the middle part of it as a strongly frequency-modulated signal, and considering the zero-level of the oscillation, the carrier-frequency, as the pitch of the call. Such analysis shows that the call is pitched near those of *stricklandi* and *villosus* (figs. 2W, X, Y; 3A; table 2). The modulation frequency ranges from 64 Hz. to 88 Hz. (Mean, 76 Hz., N=32) and the band width is about 1.2 kHz. Besides this outstanding feature the call also is the longest Call Note of the genus (table 2). The sound of this extreme call is "szrek" or "shrit" (Ligon, 1970, p. 256).

The Call Note is not only the most common call of the Red-cockaded Woodpecker (Ligon, 1970, p. 256), but it probably also is the most often uttered vocal signal of all pied woodpeckers. Although the rate of delivery does not become great, the call is commonly heard because it is uttered incessantly. The observations on which these statements are based include birds that live in groups. The only single bird observed (Winkler, personal observ.) never gave a Call Note even when deliberately disturbed.

Nestlings near fledging gave Call Notes at the hole entrance, and fledglings called quite frequently at the place where they were waiting to be fed.

The Call Note occurs all year (T. H. Carter III, personal commun.).

Situations: A1, 2b, 2c, 3, 4; D 1, 3; E 1, 4, 5; F1; G1 Seasonal occurrence: 1-12

stricklandi. The long note, sounding like peep, is characteristic for all subspecies of this woodpecker (Davis, 1965). It bears some similarity to the Hairy Woodpecker's note and might even be confused with it initially (fig. 3 B, C, D, E, H, I; table 2). One very high note (fig. 3C) was recorded from a female, which called frequently in the normal fashion but gave this call only once. The ratio of the pitch of this call to normally pitched calls is three to two. The fundamental note of the Call Note is the one most stressed, showing a flat peak not found in any of the previously described species.

This is the most common call of this woodpecker, associated with many situations and regularly interspersed with the Rattle Call.

The Call Note can be evoked by the observer when following a silently feeding bird. The call is often given spontaneously and is a common response to Rattles or Call Notes. Playback of Drumming, among other effects, elicited many Call Notes when we approached a female that was maintaining a considerable distance at a time when the territory was well established. Birds relieving a mate at the nesting hole regularly gave one or more Call Notes when close to the site. On the other hand, the relieved bird flew off and gave Call Notes and sometimes Rattles from a greater distance. In some cases calling birds perched in the top of a tree or on other exposed perches.

Situations: A1, 2b, 2c, 3; D1, 2, 3, 5, 6; E1
Seasonal occurrence: (3-5)

villosus. Its well-known, high-pitched peeping call has the peculiar feature where in most cases the fundamental tone is missing, its place indicated only by the corresponding "legs" of the note (fig. 3F to K, table 2). Rarely, this tone is present, sometimes with a "distorted" sound (fig. 3H) that is detectable to the human ear. On the other hand, notes can be heard that seem to consist only of the introductory and ending clicks (fig. 3K), therefore resembling the Call Notes of *arcticus* (fig. 3N, see below). There are some indications of geographical variation, as demonstrated in the figures; but more systematically collected vocal data have to be obtained to evaluate this variation.

The Squeak Calls of young Hairy Woodpeckers are somewhat similar, hence transitions to it are to be expected, although these have not been recorded yet (the senior author has heard them). The most common association of this note is with the Rattle Call.

The Call Note is uttered spontaneously and in answer to other Call Notes. Fledglings call very often and increase the tempo at sight of an adult bird.

Situations: A1, 2c; B; C1, 2, 3, 4, 5; E1, 2, 4, 5; G1
Seasonal occurrence: 1-12.

tridactylus. The Call Note was described by Verthein (1935) as güg, by Thibaut de Maisières (1943) as ptuk or ptik, and by Scherzinger (1972) as Kjüb. The Call Note of Central European birds (Germany, Austria) is shaped like a broad arrowpoint, with the fundamental tone emphasized and possesses significant introductory and ending elements (fig. 3L, M, table 2; see Ruge, 1975). Swedish birds have essentially the same calls. North American birds (New York) are different in all their measurable characters. Unfortunately, our recordings are insufficient for comparison of these geographical groups. This species, the only Holarctic woodpecker, would be an ideal subject for the study of geographical variation (see p. 19).

All previously cited authors noted that this is the most commonly heard call.

Situations: A1; D3; E; F1
Seasonal occurrence: 1-12

arcticus. The Call Note of the Black-backed Woodpecker is essentially a fast double click (fig. 3N, 4J), sounding in the field like a sharp, single click-note. The second of them shows a needle-like form on the sonagram. The pitch of this needle is 2.55 kHz. (2.30-2.91 kHz., Standard Deviation 0.677, Coefficient of Variability 26.5, N=14) and its duration is about 8 msec. (N=13, table 2).

Situations: A1, 2; B; C 1a, 1c, 1d, 3a, 3c, 4a, 4c, 5a, 5b, 5d, 5e, 5f, 8a; D1, 2, 3, 6; E1, 2, 4
Seasonal occurrence: 1-12

Summary of Call Notes. Call Notes generally are the most common and simply structured of pied woodpecker vocal signals. Sonagraphically the basic form of this call is an

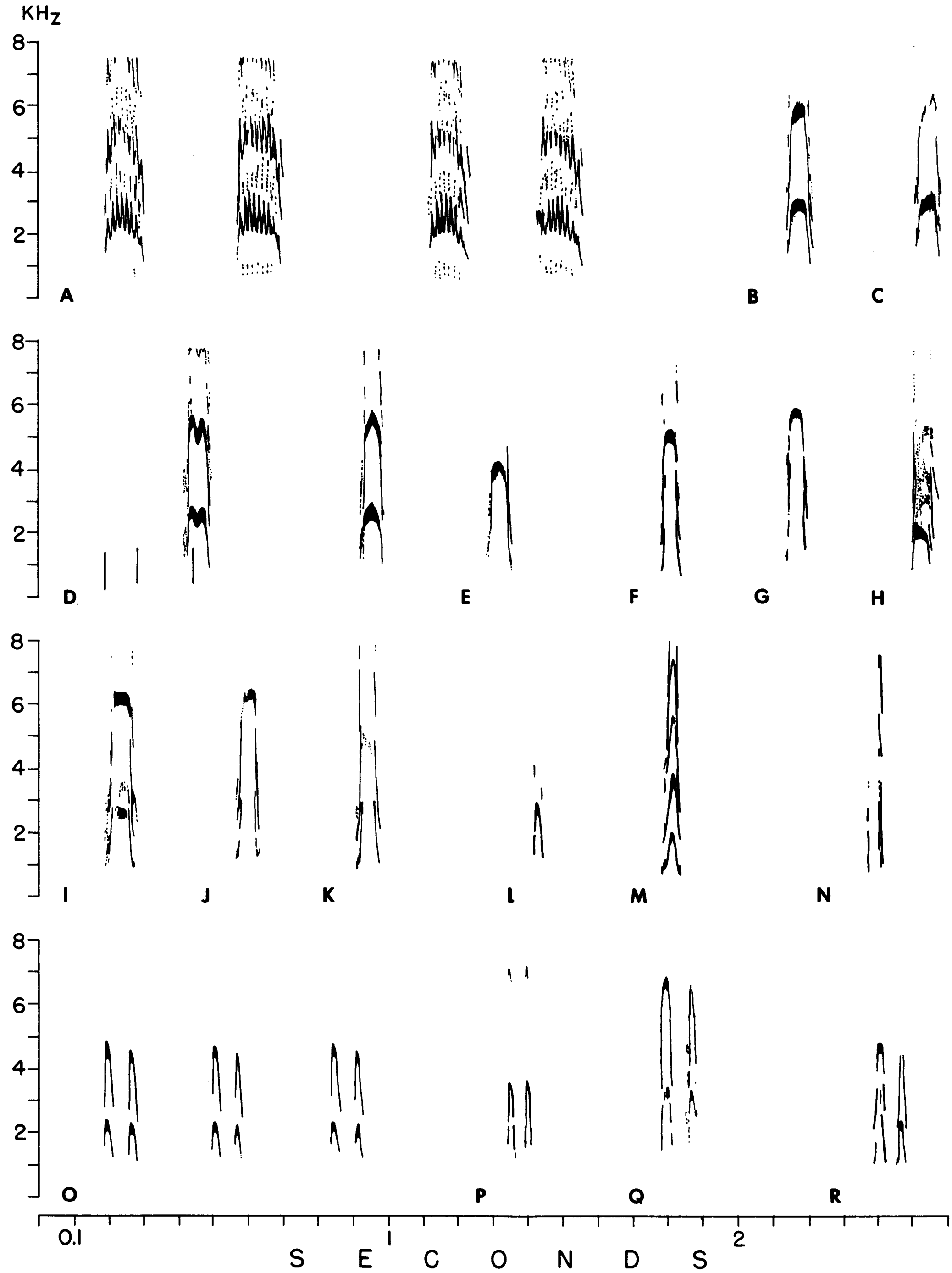


FIG. 3. Sonagrams of Call Notes and Double Calls of pied woodpeckers. A. *P. borealis*, adult before feeding fledgling; North Carolina. B, C. Adult male and female *P. stricklandi*; Arizona. D. *P. stricklandi*, adult bird flying off, the vertical lines mark wing beats; Arizona. E. *P. stricklandi*, female; Arizona. F. *P. villosus*; Adirondacks, New York. G. *P. villosus*; Long Island, New York. H. *P. villosus*, distorted call (see text); Long Island, New York. I, J, and K. *P. villosus icastus*, two female and one male calls (extremes chosen); Chiricahua Mts., Arizona. L. *P. tridactylus*; New York. M. *P. tridactylus*; Austria. N. *P. arcticus*; New York. O. Double Calls of *P. canicapillus*; India. P. Double Call of *P. nuttallii*; Baja California. Q. Double Call of *P. pubescens*; Georgia. R. Double Call of *P. albolarvatus*; California. All are wide-band.

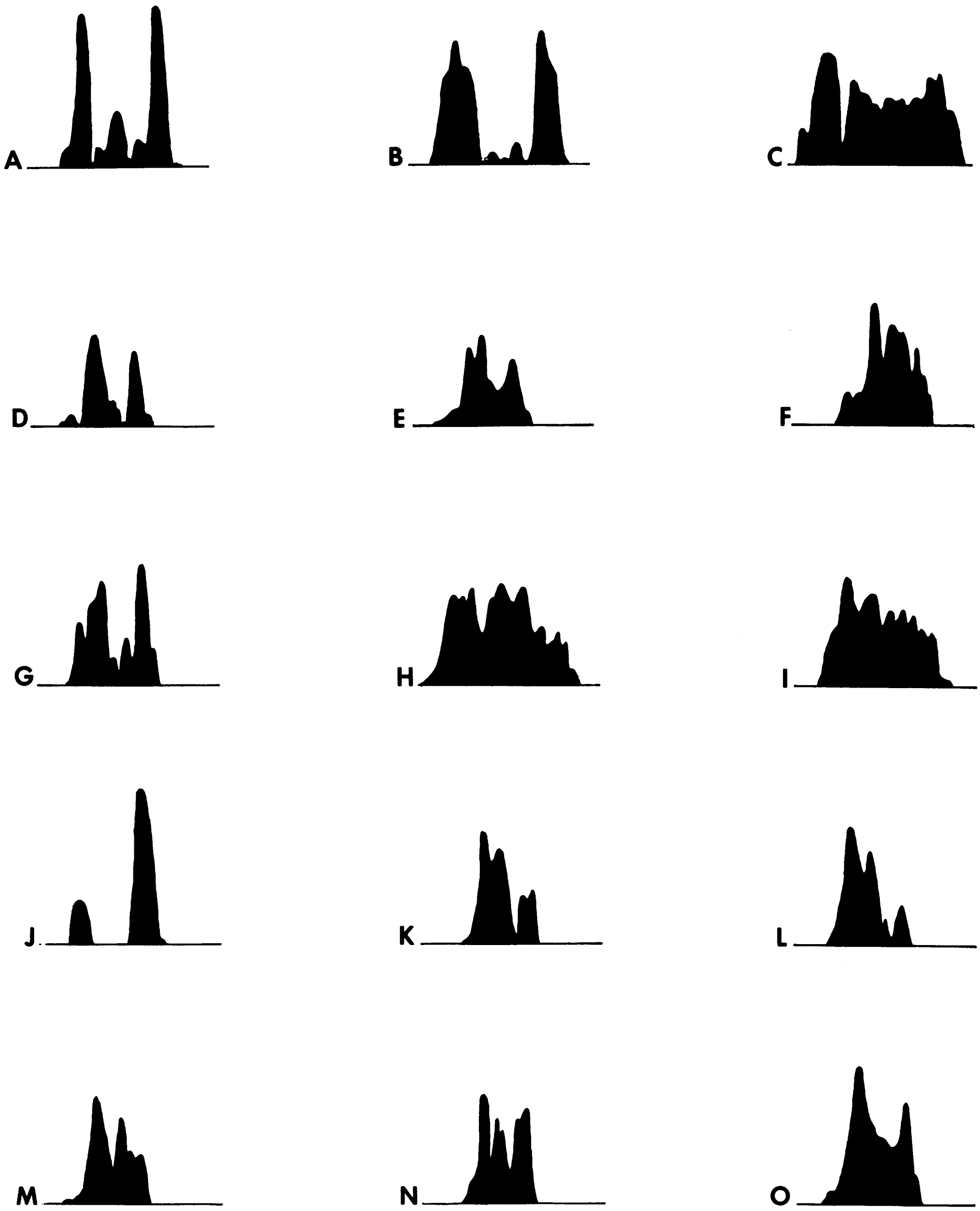


FIG. 4. Amplitude characteristics of pied woodpecker Call Notes. The baseline represents a time interval of 0.1 second. The amplitude is given at a relative rate. A. *P. villosus*, female; New York. B. *P. villosus*, female; Chiricahua Mts., Arizona. C. *P. villosus*, male; Chiricahua Mts., Arizona. D. *P. tridactylus*; Germany. E. *P. tridactylus*; Austria. F. *P. albolarvatus*, first note of a five-note Short Rattle; California. G. *P. albolarvatus*, male, first note of a three-note Short Rattle; California. H and I. *P. stricklandi*; Arizona. J. *P. arcticus*; New York. K. *P. leucotos*; Austria. L. *P. darjellensis*; India. M, N, and O. Female *major* (mother), male *syriacus* (father), and immature (hybrid young) *major* × *syriacus*; Austria.

inverted V- or U-shape; however, the bulk of the energy is embodied in the rising and the falling, fast, click-sounding legs. Variation of several types occurs, such as geographic (e.g., in *major*), and that caused by brief external stresses (e.g., carrying of food by *major*, *pubescens*, and others; or due to flight, as in *stricklandi*). Hybrids of *major* × *syriacus* and of *scalaris* × *nuttallii* show intermediacy between the parental species in the structure of their Call Notes. The central (peak) part of the Call Note can be very weak, as in *villosus* and to some extent in *albolarvatus*; the peak is lacking entirely in *arcticus*. The form of the Call Note is asymmetrical, with a falling central portion in *syriacus* and *scalaris*. There is a marked, regular frequency modulation in the Call Note of *borealis*. The last-mentioned call, together with those of *villosus* and *stricklandi*, is exceptionally long. Call Notes occur singly or in loose series, and sometimes are given over extended periods of time; we found no consistently regular series. This call is associated with a wide range of situations, and very often is uttered along with Rattles and Scolding. Despite its variation, mentioned above, this call is the most constant in the repertoire of pied woodpeckers. Hence it is ideal for comparative and taxonomic studies.

SCOLDING

minor. Scolding (fig. 5A) consists of a burst or fast series of Call Notes. The notes are slightly higher pitched than the Call Notes (table 3). These calls were uttered during flight-attacks against a female *P. major*, which had opened the hole of a pair of *P. minor* (recording by Mensendieck), and as a person climbed up to the nest (recording by Aichhorn).

Situations: E1, 2 Seasonal occurrence: (5)

darjellensis. "Alarm a rapid titititititi" (Fleming, Fleming and Bangdel, 1976, p. 144).

leucotos. When disturbed at the nesting hole White-backed Woodpeckers utter unremitting series of Call Notes. These series are less regular and organized than those of *minor* or *medius*, so they might not represent a typical Scolding, which might be found in future investigations.

Situation: E1 Seasonal occurrence: (5, 6)

medius. Scolding is a clear fast series of elements that are like Call Notes, but are shorter and slightly higher pitched than Call Notes (fig. 5B). Without the introductory part the duration of the notes is 29.6 msec. (see table 3).

Situation: E1 Seasonal occurrence: Unknown

syriacus. Disturbance at the breeding hole elicits frequent Call Notes. Models of woodpeckers presented at the breeding hole can evoke fast series (120-180 calls per minute, Winkler, 1972) and attacks. The same vocalization was employed by a female whose mate had been caught and held; she encountered a strange male a half-hour after this transpired, and uttered Scolding Calls at him (Winkler, unpubl. data).

Situations: C4; E1, 2
Seasonal occurrence: (2, 4, 5)

major. Attacks against a Starling (*Sturnus vulgaris*) inspecting a hole were accompanied by Scolding (fig. 5C). This consists of elements like Call Notes, but of a higher frequency than the Call Note. The call series on the Japanese record probably also represents a Scolding Call (fig. 5D). This is commonly a reaction of a pair to a human observer near their nest. However, there seems to be variability between pairs, some of which do not call at all. When a human is near the nest one of the parents detects the disturbance and starts to call. The mate soon comes near, the Scolding climaxes for a moment, then the partners separate and continue to scold at a distance of 30 m. from the nest, and more from each other. The nestlings reduce their Chirps or stop calling altogether (Poulsen, 1949). These reactions, approach by the adult and suppressing of the Chirps by the nestlings, also were obtained by us in play-back-experiments (four experiments with one pair). Both Scoldings are somewhat organized in bursts (for instance the interburst intervals have a Coefficient of Variability of 11.2, from the Japanese record).

Situations: E1, 2
Seasonal occurrence: (4, 5, 6)
(Central Europe)

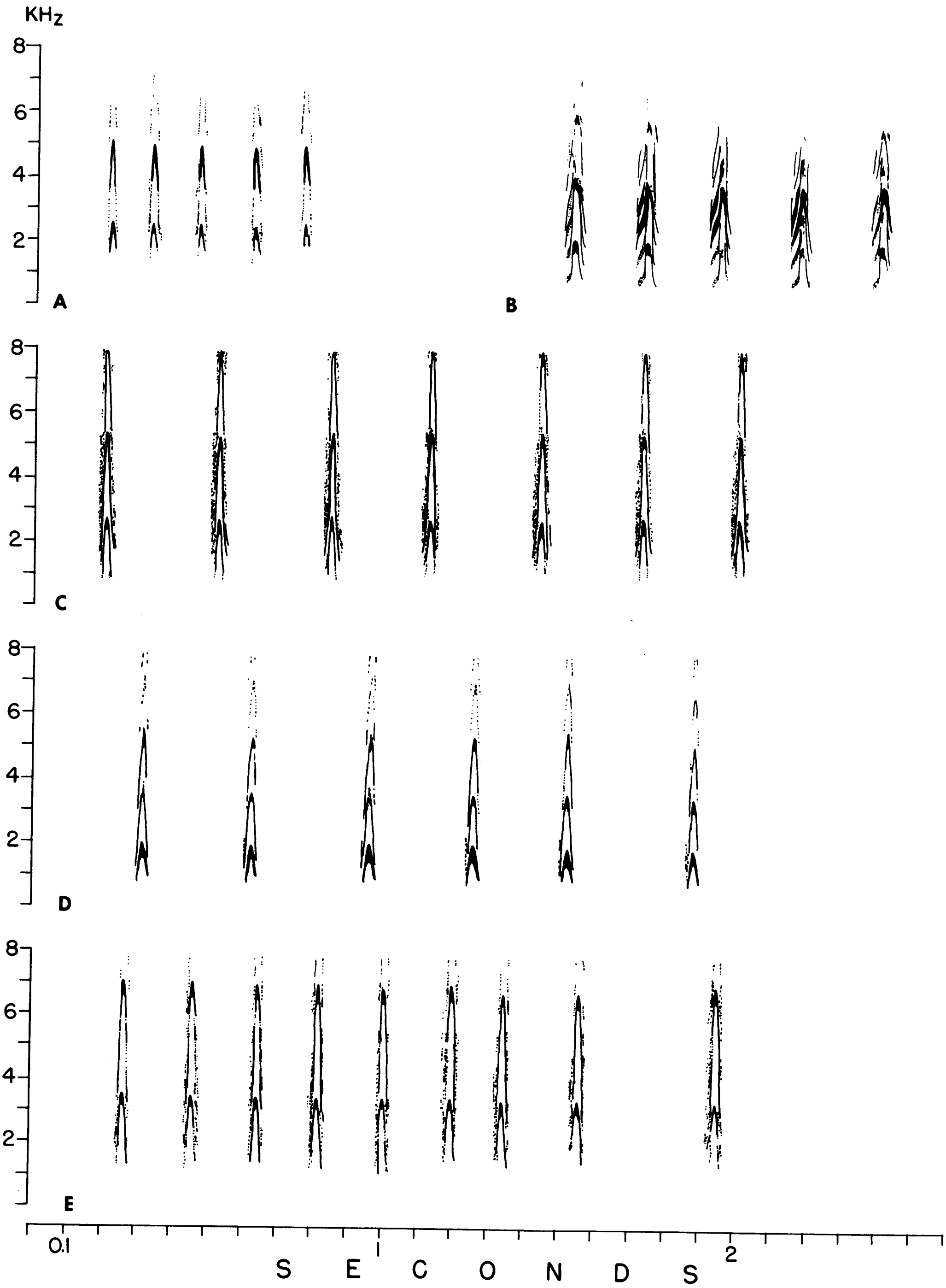


FIG. 5. Sonagrams of Scolding Calls of pied woodpeckers. A. *P. minor*; Austria. B. *P. medius*; Germany. C. *P. major*; Austria. D. *P. major*; Japan. E. *P. pubescens*; New York. All are wide-band.

pubescens. Disturbance near the breeding hole (nestlings close to fledging) caused a female Downy Woodpecker to deliver a series of Call Notes (fig. 5E). When joined by her mate both birds increased the calling to Scolding and remained near the observer. Playback of the Scolding about 200 m. away from the hole attracted the male, which gave Rattle Calls

TABLE 3
Scolding Calls of Pied Woodpeckers[a]

Species	Mean	Range	S.D.	C.V.	N
			Pitch		
minor	2.3	2.1-2.4	0.23	9.8	24
leucotos[b]	1.6	1.6-1.6	0.03	1.6	6
leucotos[c]	2.7	2.6-2.9	0.11	4.1	7
medius	1.8	1.8-2.0	0.23	12.5	6
major, Austria	2.6	2.5-2.6	0.04	1.4	7
major, Japan	1.7	1.6-1.8	0.04	2.5	6
pubescens	3.3	3.2-3.4	0.05	1.6	9
tridactylus	1.9	1.8-2.0	0.04	2.4	19
			Duration		
minor	26.1	22.6-30.2	0.56	2.1	24
leucotos[b]	30.2	26.4-34.0	2.39	7.9	6
leucotos[c]	31.0	24.5-36.8	4.64	15.0	7
medius	54.1	52.8-56.6	0.71	1.3	6
major, Austria	38.8	37.7-41.5	1.84	4.7	7
major, Japan	34.0	30.2-37.7	2.39	7.0	6
pubescens	32.0	30.2-34.0	1.94	6.1	19
tridactylus	45.9	37.7-52.8	4.91	10.7	19

Intercall Interval

Species	Mean	Range	S.D.	C.V.	N	Ratio Duration/ Intercall Interval[d]
minor	188.5	117.0-366.0	62.02	32.9	22	0.138 (0.223)
leucotos[b]	822.0	664.2-913.2	110.1	13.4	4	0.037 (0.05)
leucotos[c]	659.0	547.8-764.5	95.4	14.5	5	0.047 (0.057)
medius	218.9	207.5-237.7	12.80	5.8	5	0.247 (0.260)
major, Austria	298.7	271.7-320.8	21.00	7.0	6	0.130 (0.143)
major, Japan	344.7	264.2-513.21	88.23	25.6	6	0.100 (0.129)
pubescens	206.7	147.2-392.5	63.6	30.8	17	0.155 (0.217)
tridactylus	443.8	226.4-656.6	135.41	30.5	15	0.103 (0.203)

a. Symbols: S.D., Standard Deviation; C.V., Coefficient of Variability; N, sample size. Pitch is in kilohertz, duration and intercall interval in milliseconds; *b*. Salzburg, Austria; *c*. Bayerischer Wald, Germany; *d*. in parentheses is the ratio of the mean duration/minimal intercall interval.

and Call Notes. In both cases a Tufted Titmouse (*Parus bicolor*) also approached the source of the signal. In other cases Downy Woodpeckers disturbed at the hole uttered frequent Call Notes and Scolding. A female near a (probably intruding) male uttered a rapid series of calls before a brief combat took place. Typical Scoldings show bursts that have a quite regular time pattern (e.g., Coefficient of Variability of 7; intraburst interval of one burst is 4.2).

Situations: C2, E1 Seasonal occurrence: (2, 6)

borealis. Scolding as such was not found in this species. When disturbed at the breeding hole, and even when a hand-held fledging bird gave Distress Cries, the adults only responded with frequent Call Notes (to 9 in 5 sec., fig. 3A), and seemed to direct more attention and signals to each other than to the source of perturbation.

tridactylus. As in other species the Scolding consists of rapid series of Call Note elements. The series are slower than in the other species, however (table 3; see also Ruge, 1975). In one instance Scolding was characterized by a switch to higher amplitude and a simultaneous change to a different sound caused by the final harmonic becoming stronger than the fundamental tone.

Situation: E1 Seasonal occurrence: (6)

Summary of Scolding (table 3). In principle this call consists of rapid series or sometimes (*minor*, *medius*) clear groups of such series of elements like Call Notes. Usually the calls are louder, vary less in a given time interval, stress more the harmonic components, and occur in more regular series than do Call Notes. Fast Scolding series can resemble Rattle Calls but may be distinguished by the ratio between element duration and interelement interval (tables 2, 3). In almost all species mentioned above Scolding can start and end in more or less frequent Call Notes. *Picoides medius* might be an exception for it never gives Call Notes when alarmed (Conrads, personal commun.). The most common situation involving Scolding is disturbance at the nest, but in at least two species (*syriacus*, *pubescens*) this call bears relations beyond this particular stimulus. It would be of interest to establish whether this call can be evoked by owls and other such stimuli during the breeding and even the nonbreeding season.

DOUBLE CALL

canicapillus. (fig. 3 O). The first note of the Double Call resembles the Call Note, and the second one is shorter and of lower pitch. The fundamental tone and first harmonic are codominant (Short, 1973; table 4). These notes are uttered occasionally, sometimes interspersed with Rattle Calls, and often in agonistic situations.

Situations: A2c; C4, 5a
Seasonal occurrence: (4, 5)

macei. Compared with the previous species, Double Calls are given infrequently (Short, 1973) and remain to be studied in detail.

nuttallii. The Double Call of the Nuttall's Woodpecker was named the Pitit Call by Short (1971a), who described it in detail. The two notes are almost identical and are similar to the Call Note or Pit Call of Short, 1973 (fig. 3P, table 4). There are transitions to the Rattle, represented as "pit-it-it-it" or more rapidly as "prrit," forming a transition similar to that found in *scalaris* among the Call Note, Short Rattle, and Rattle Calls (Short, 1971a). Therefore, especially without recordings available, it is a moot point whether or not to define a Short Rattle Call in *nuttallii* (see p. 38). The finding that this call, compared with the Call Note, is more frequent in late winter and spring and less so in November (Short, 1971a) might be correlated with territorial activity (for a functional explanation see also Short, 1971a, p. 84). The call often is associated with Drumming and Rattles, and may elicit either.

Situations: A1, 2c; B1-5; C 1a, 1c, 2, 3, 4a, 4c, 5a, 5b, 5d, 5f, 7a, 8; D2, 3, 4, 6; E1, 4, 5
Seasonal occurrence: 1-12

pubescens. Double Calls were recorded by the junior author from a Downy Woodpecker

TABLE 4
Double Call of Some Pied Woodpeckers[a]

Species	Pitch Mean	Pitch Range	Pitch S.D.	Pitch C.V.	Pitch N	Duration Mean	Duration Range	Duration S.D.	Duration C.V.	Duration N
canicapillus										
note 1	2.45	2.4-2.5	0.05	1.9	5	27.2	22.6-30.2	3.70	13.6	5
note 2	2.36	2.3-2.4	0.06	2.6	4	23.6	15.1-26.4	4.90	20.8	4
nuttallii										
note 1	3.54	3.4-3.6	0.08	2.3	5	20.7	18.8-22.7	1.89	9.1	4
note 2	3.59	3.5-3.6	0.06	1.7	5	17.4	15.1-18.9	1.56	8.9	4
pubescens										
note 1	3.28	—	—	—	1	—	—	—	—	—
note 2	3.16	—	—	—	1	—	—	—	—	—
albolarvatus										
note 1	—	—	—	—	—	37.7	—	—	—	1
note 2	2.3	—	—	—	1	30.2	—	—	—	1

[a]*Symbols*: S.D., Standard Deviation; C.V., Coefficient of Variability; N, sample size. Pitch is in kilohertz, duration in milliseconds.

on St. Catherines Island, Georgia (fig. 3Q, table 4). They essentially resemble those of *nuttallii*, the notes being very much like the Call Note.

Situations: C 1a, 4a, 4b Seasonal occurrence: (3-6)

albolarvatus. The Double Call of the White-headed Woodpecker is a "peek-it" commonly heard in winter (Short, 1971a). Besides Double Calls, of which only one was recorded, triple calls and calls with more elements occur, forming an even transition to the Rattle Call (see p. 35). The recorded example (fig. 3R, table 4) was given by a flying male after he gave one Rattle and three Short Rattles.

Situation: A3 Seasonal occurrence: (4)

RATTLE CALL

temminckii. Berndt and Meise (1962) mentioned a geegee . . . (German original: gigi . . .) call which probably represents the Rattle Call of this small woodpecker, an important and virtually unknown species.

Situation: Unknown Seasonal occurrence: Unknown

moluccensis. Short (1973, p. 269) heard a weak Rattle, described as "ti-ti-ti-ti-ti-ti-ti." It is softer than the Rattle of *canicapillus* though similar to it.

Situation: Unknown Seasonal occurrence: (4)

kizuki. It frequently gives a call like grating over a comb. This call is especially common in spring together with Drumming and Kweeks (Jahn, 1942, p. 218).

Situation: A2 Seasonal occurrence: 1-12 (?)

canicapillus. Short (1973) described the Rattle of this species in detail, the Rattle Calls mainly being those of fledgling birds he studied. Therefore, a considerable amount of variation in all parameters can be found. Caldwell and Caldwell (1931) described the adult Rattle as a rapid-fire chi-chi-chi-chik on a descending scale. The recordings contain at least one Rattle that probably represents the full adult call (fig. 6A, B, C; tables 5, 6), described by Short (1973) as a fast Rattle. This call had 17 notes. Four calls were closely preceded by Kweek Calls, and probably also were given by adults perched near their fledged young (see also Kweek Call). In these Rattles double notes are found. All Rattles are preceded and followed

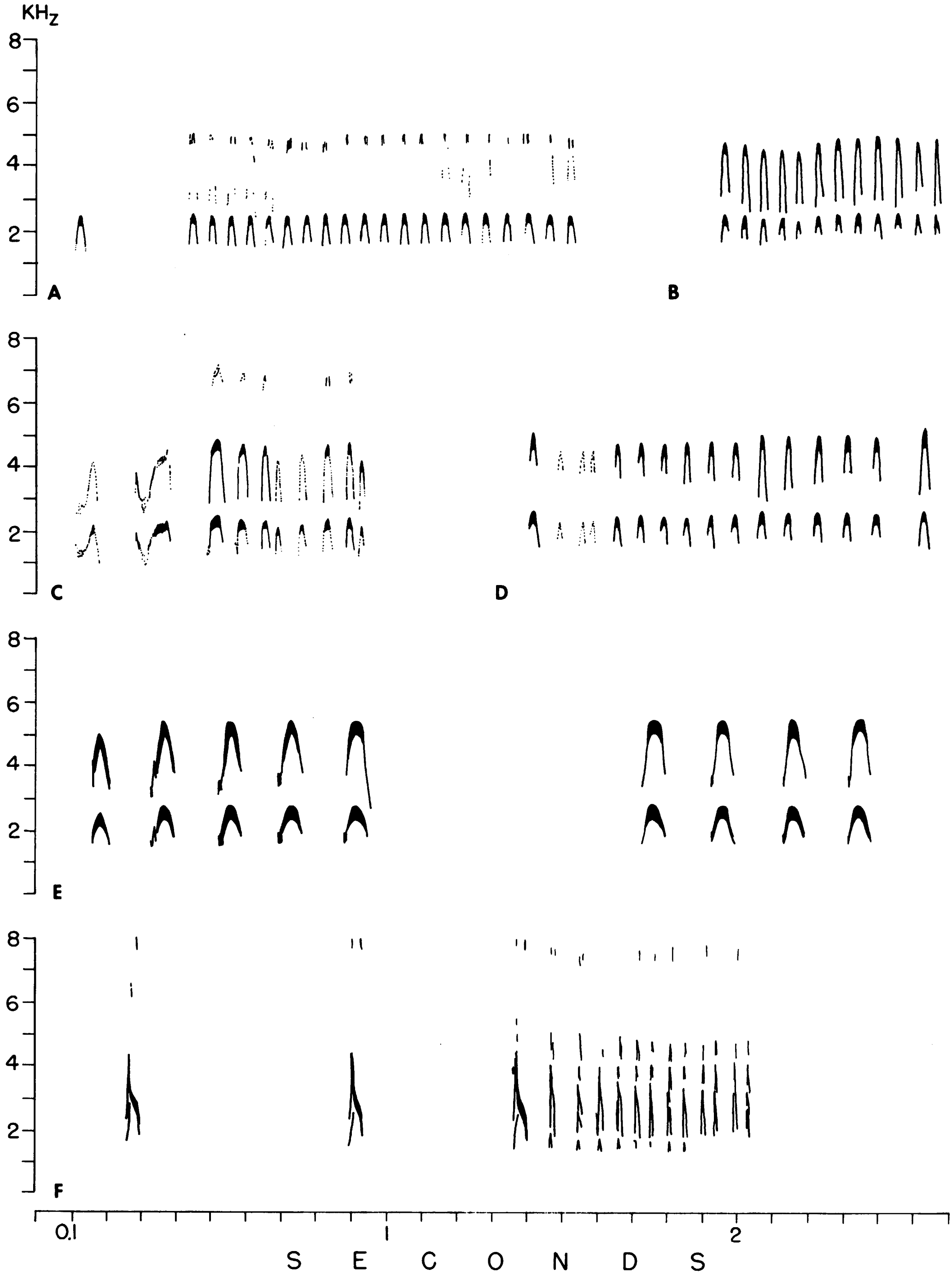


FIG. 6. Sonagrams of Rattle Call of pied woodpeckers. A. *P. canicapillus*; India. B. *P. canicapillus*, fledgling; India. C. *P. canicapillus*, adult, Kweek-Rattle combination; India. D. *P. macei*; India. E. *P. minor*, the first five and the last four notes of a 19-note call; Austria. F. *P. syriacus*, Rattle following Call Notes; Austria. All are wide-band.

TABLE 5
Rattle Calls of Pied Woodpeckers (Introductory note omitted)[a]

Species	Mean	Range	S.D.	C.V.	N	M
			Pitch			
canicapillus	2.4	2.3-2.4	0.02	0.9	16	—
minor	2.7	2.5-2.8	0.09	3.5	46	—
macei	2.3	2.1-2.4	0.07	3.2	30	—
dorae	1.2	0.9-1.3	0.13	10.9	17	—
darjellensis	2.1	2.1-2.2	0.03	1.6	14	—
leucotos[b]	2.3	2.2-2.5	0.09	3.9	8	—
medius	1.6	1.2-2.1	0.27	16.8	70	—
syriacus	1.6	1.4-2.0	0.12	7.6	26	—
scalaris	3.5	2.9-3.9	0.27	7.7	53	—
nuttallii	3.9	3.7-4.1	0.08	2.0	72	—
pubescens	3.4	2.9-3.9	0.21	6.3	62	—
borealis	2.6	1.8-2.8	0.22	8.4	20	—
stricklandi	2.1	1.8-2.3	0.14	6.6	69	—
villosus	1.9	1.6-2.4	0.14	7.1	76	—
albolarvatus	2.9	2.5-3.3	0.17	5.8	17	—
			Duration			
canicapillus	19.1	15.1-22.6	1.67	8.7	16	—
minor	68.3	52.8-86.8	9.32	13.6	46	—
macei	20.1	11.3-16.4	3.29	16.4	31	—
dorae	32.9	20.4-45.0	7.34	22.3	23	—
darjellensis	—	—	—	—	—	—
leucotos[b]	23.0	20.4-28.6	3.41	14.8	8	—
medius	32.5	27.9-37.7	2.78	8.6	55	—
syriacus	20.2	11.3-32.7	4.26	21.0	33	—
scalaris	46.4	30.2-67.9	8.54	18.4	54	—
nuttallii	22.7	15.1-26.4	1.55	6.8	72	—
pubescens	34.9	15.1-56.6	10.56	30.2	74	—
borealis	46.4	34.0-60.4	6.25	13.5	20	—
stricklandi	61.9	52.8-75.5	6.73	10.9	69	—
villosus	31.1	22.6-37.7	3.07	9.9	93	—
albolarvatus	31.0	22.6-37.7	4.00	12.9	18	—
			Internote Interval			
canicapillus	58.1	52.8-67.9	3.98	6.9	15	(1)
minor	183.3	135.8-256.6	20.79	11.3	43	3
macei	74.9	64.2-105.7	9.84	13.1	25	3
dorae	135.7	114.5-159.4	2.22	13.4	21	2
darjellensis	84.4	79.2-90.6	3.50	4.1	11	(1)
leucotos[b]	56.1	53.1-61.3	3.09	5.5	7	(1)
medius	148.8	113.2-222.6	24.12	16.2	70	3
syriacus	53.2	32.7-114.5	12.88	24.2	68	5
scalaris	101.2	83.0-135.8	11.34	11.2	52	3
nuttallii	49.7	37.7-83.0	6.01	12.1	70	2
pubescens	82.1	52.8-109.4	15.03	18.3	71	5
borealis	100.1	94.3-120.8	6.70	6.7	19	(1)
stricklandi	109.8	98.1-120.8	5.98	5.4	65	4
villosus	65.8	52.8-79.2	4.05	6.2	90	5
albolarvatus	68.6	64.2-75.5	3.05	4.5	17	(1)

[a]*Symbols*: S.D., Standard Deviation; C.V., Coefficient of Variability; N, sample size; M, number of Rattles analyzed. Pitch is in kilohertz, duration and internote time are in milliseconds.

[b]Without the introductory and the following note, which often are atypical. See text.

TABLE 6
Analysis of Introductory Call Note of Pied Woodpecker Rattle[a]

Species	Mean	Range	S.D.	C.V.	N
		Pitch			
canicapillus	2.3	—	—	—	1
minor	2.5	2.4-2.6	0.13	5.0	3
darjellensis	2.1	—	—	—	1
leucotos	1.5	—	—	—	1
medius	—	2.1-2.2	—	—	2
syriacus	3.0	2.9-3.2	0.15	5.0	3
nuttallii	—	4.0-4.3	—	—	2
pubescens	3.5	3.4-3.6	0.08	2.3	5
borealis	2.9	—	—	—	1
stricklandi	2.9	2.5-3.2	0.36	12.6	4
villosus	5.6	5.3-5.8	0.27	4.9	3
		Duration			
canicapillus	22.6	—	—	—	1
minor	54.1	45.3-67.9	12.13	22.4	3
darjellensis	—	—	—	—	0
leucotos	33.0	—	—	—	1
medius	—	30.2-34.0	—	—	2
syriacus	41.2	37.7-45.0	3.47	8.4	3
nuttallii	—	22.6-26.4	—	—	2
pubescens	40.8	37.7-45.3	3.16	7.7	5
borealis	75.5	—	—	—	1
stricklandi	61.3	52.8-67.9	7.78	12.7	4
villosus	51.6	49.1-52.8	2.18	4.2	3
		Post-note Interval			
canicapillus	60.4	—	—	—	1
minor	173.6	158.5-188.7	15.10	8.7	3
darjellensis	67.9	—	—	—	1
leucotos	65.4	—	—	—	1
medius	181.1	—	—	—	2
syriacus	107.3	106.0-110.0	1.80	1.7	3
nuttallii	30.2	—	—	—	1
pubescens	90.6	67.9-120.8	22.85	25.2	4
borealis	143.4	—	—	—	1
stricklandi	107.5	98.1-120.8	11.32	10.5	4
villosus	84.3	67.9-105.7	19.46	23.0	3

[a]*Symbols*: S.D., Standard Deviation; C.V., Coefficient of Variability; N, sample size. Pitch is in kilohertz, duration and post-note interval in milliseconds.

by Call Notes. The presumed Rattles of the young overlap in some cases. Five fledgling Rattles have fundamental tones between 2.2 and 2.6 kHz. (mean, 2.4; Standard Deviation, 0.12, Coefficient of Variability, 5.0, sample size, 47); the notes have a duration varying from 15.1 to 37.7 msec. (mean 21.8, Standard Deviation 4.25, Coefficient of Variability 19.5, sample size 47) and internote intervals are from 49.1 to 79.2 msec. (mean 59.8, Standard Deviation 7.25, Coefficient of Variability 12.1, sample size 40). They have somewhat longer notes than the adult Rattle, which has a fundamental pitch within the range of the variable young Rattle.

Situation: A1; C 1a, 1b, 1c, 1d, 3a, 4c, 5a, 5b, 5c, 5e, 6a; E5; G1, 2
Seasonal occurrence: (2-5)

minor. The Rattle is the most prominent and most frequently heard call of this woodpecker. Its most interesting feature is the great length of the notes, which have a soft squeaking sound (figs. 6E, 7; tables 5, 6). In the European literature it is usually compared with the call of the Kestrel (*Falco tinnunculus*). Sometimes it is referred to as a courtship call (but see "function," p. 87). Playbacks elicit Rattles, searching flights, and approach and Drumming (March, April, May). Drumming is frequently combined with the Rattle (cf. Blume 1968, p. 90); for instance, a bird can Rattle before moving to a Drumming site. Drumming, played back, may also be answered by Rattles. Fledglings utter Rattles frequently and more likely when they are hungry (observations on hand-raised young where the human caretaker represents the "parent") and the parent is not in immediate proximity. The fledgling Rattle is more variable in overall duration and probably pitch (no recordings analyzed). The adult Rattles we had for analysis had 19, 15, 15, and 14 elements. Hurme (1973) observed 9.89 notes per Rattle (N=56) for males and 12.1 notes per Rattle (N=29) for females. The former also call more often than females. Seasonal peaks in Finland were during April and May, and in August. In spring the call may be repeated up to 21 times in 40 minutes (Pynnönen, 1939). Before calling, the bird commonly assumes a more upright posture, the bill slightly directed upward.

Situations: A1 (1), 2c, 3; B1 (1), B2; C9a, 9b
Seasonal occurrence: 1-12

macei. Described in detail by Short (1973).

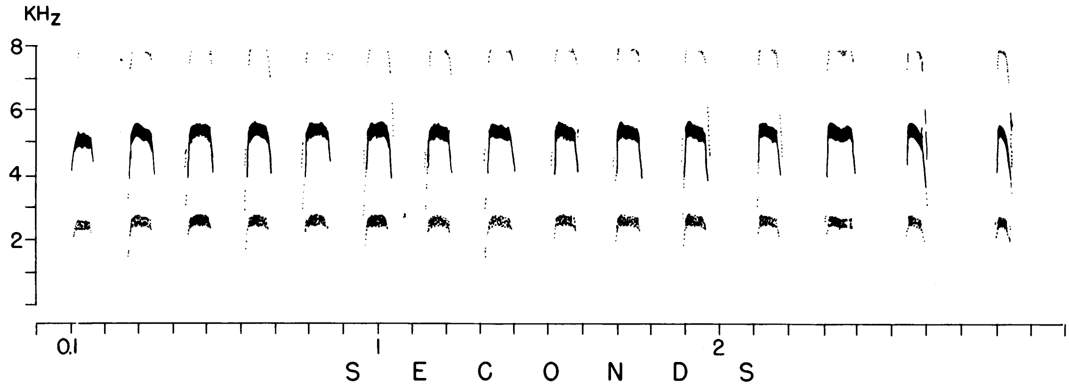


FIG. 7. Wide-band sonagram of Rattle Call of a male *P. minor*; Austria.

The notes are like the Call Notes which also precede and follow the Rattle. Short found three double notes in four analyzed Rattles. Rattles were given not only during encounters but also by birds that were feeding and greatly disturbed by the observer.

Situations: A1; C 4a, 4b, 5a, 5c, 5d, 7a
Seasonal occurrence: (4, 5)

atratus. ". . . . the shrill, descending whinny characteristic of the small dryobatines" described by Deignan (1945, p. 244) undoubtedly refers to the Rattle of this species.

Situation: Unknown
Seasonal occurrence: Unknown

auriceps. Quoting Scully, Ali and Ripley (1970) mentioned for the subspecies *auriceps* a shrill, long cry resembling the call of the kingfisher *Halcyon smyrnensis* (see also Magrath, 1909).

Situation: Unknown
Seasonal occurrence: Unknown

mahrattensis. The call described by Smythies (1953), and by Ali and Ripley (1970) as clickr-r-r-r either refers to the Rattle (most likely) or the Short Rattle. Note that the introductory note seems to be of different quality than the rest of the notes of the Rattle and to sound like the Call Note.

Situations: E4 (Ali and Ripley, 1970)
Seasonal occurrence: Nesting season

dorae. The Rattle of this species is not highly differentiated, and consists of a string of notes like inverted Vs (table 5).

Situation: A Seasonal occurrence: (April)

hyperythrus. A long, but not loud Rattle, running down at the end was noted by Magrath (1909) and compared by him with the running down of a clockwork with a broken spring or the sound made by a large fishing reel.

cathpharius. No positive records. Short (1973), considering the short Call Note and the fast Short Rattle, estimated that the Rattle will prove to have a rate of delivery of 20 to 25 notes per second.

darjellensis. The notes differ substantially from the Call Note. The fundamental tones are about 2.2 kHz. and are weaker than the first harmonics (4.4 to 4.5 kHz.). The elements are about 25 msec. in duration and delivered at a rate between 12.0 and 12.7 notes per second. The lengths of two calls were 1.06 and 1.18 seconds (Short, 1973). One of these Rattles consisted of 15 notes. Rattles may sound like a trill (Diesselhorst, 1968) and inferring from the notes of this author, they are more common than Call Notes; however Short's field experience indicates otherwise.

Situations: C4, 7 Seasonal occurrence: (4, 5)

leucotos. The Rattle (fig. 16) consists of an introductory note, similar to the Call Note although the fundamental tone is weaker than the first harmonic. The second note is intergradient between a Call Note and elements of a Rattle. In these the slightly indicated key tone of the introductory element seems to have vanished. The one recording (W. Scherzinger) was obtained near the nest after playback of Drumming as the female flew over the experimenter. The Rattle was combined with Short Rattles (fig. 16), and Call Notes were given before and after.

Situations: A2a; B2, 4
Seasonal occurrence: (4, 5)

medius. The Rattle of this species is its most common vocalization. Blume (1968) designated this call as a species-call (Artruf), following Feindt (1956) or as a call-series (Rufreihe), and a similar name (Streitrufreihe) also was used by Feindt (1956). Ferry (1962) called it *le cri d'appel*. It sounds like "kik kekekek—," and is variable in length and rhythm. Blume (1968) also wrote that during strong excitement this call becomes clearer at the end. The sound also might be variable, as mentioned by Feindt, who separated the Artruf from the Streitrufreihe. Such a distinction is questionable without a thorough spectrographic analysis. The notes have a detectable introductory element and are lower pitched than the first note (tables 5, 6). The Rattle speeds up toward the middle and slows down at the end (fig. 8). The length (up to 5.5 sec.) of the call seems more variable than in the other species. The calling bird either poses in a more upright position (horizontal surface) or turns the bill away from the trunk (vertical climbing surface). On small branches the bird may sit crosswise. The peculiar Kweek Call can progress to a Rattle. Playback of this call in early spring caused Middle Spotted Woodpeckers to approach the recorder up to a distance of about 1 m. Blume (1968) stated that Middle Spotted Woodpeckers like to give this call before entering the roosting hole, either at the last intermediate station before it or at the roosting tree itself.

Situations: A2c; B8; G; H
Seasonal occurrence: 1-12

assimilis. Stuart Baker (1927, p. 36) described a "tr-r-r-r" call, from observations of Bell, to whom he ascribed no citation.

syriacus. Winkler (1972) named the Rattle of the Syrian Woodpecker the Kürr-Ruf. The call usually commences with two Call Notes (with an interval of 0.5-0.8 second), omitted when several Rattles follow close upon each other; the first note of the call also is like a Call Note (fig. 6F). The other elements of the Rattle have a marked first harmonic with a single peak, and can appear in groups of three (seldom two) in which the central note is higher pitched than its neighbors. Twelve to 25 such elements were present in a sample of five Rattles. Besides Rattles of medium length, long, slightly falling, and rising Rattles occur. The Rattle Call is less common than the Call Note, and is regularly uttered during high, long-distance flights, after landing, and during encounters, especially during flying pursuits. Its seasonal occurrence was shown by Winkler (1972, fig. 23). Preferably the birds signal from high trees, overlooking their territory, in an upright posture. Rattles are sometimes elicited by Drumming (playback).

Situations: A1, 2b, 2c, 3; B1, 2, 4; C6, 8; D1, 5 Seasonal occurrence: 1-11 (Central Europe)

major. Blume (1968) mentioned long kreck-series that probably are Rattles. The field notes of the senior author also describe such calls, commencing in one or two Call Notes. The notes of the Rattle are of short duration and the internote intervals also are short. Notes probably are double-peaked like notes of the Short Rattle. Blume noted that these calls are heard in the fall when the birds fight for roosting holes. They also are given during pursuits on the wing. Richards (1957) wrote that a Great Spotted Woodpecker once reacted to an imitated drumming with a tchic-churr, after which it left. We also found that a Great Spotted Woodpecker reacted in the same way to the playback of a *syriacus* Drumming.

Situations: A1, 2b, 2c; B1, 4, 5; C6; D4, 5
Seasonal occurrence: 3-6

mixtus. Wetmore (1926) mentioned a low Rattle for this species. Short (1970, p. 7) described it as "ti-ti-ti-ti-ti-ti-ti-ti-ti" and noted its similarity to the Rattle of *scalaris* and *pubescens*. The posture of a female giving this

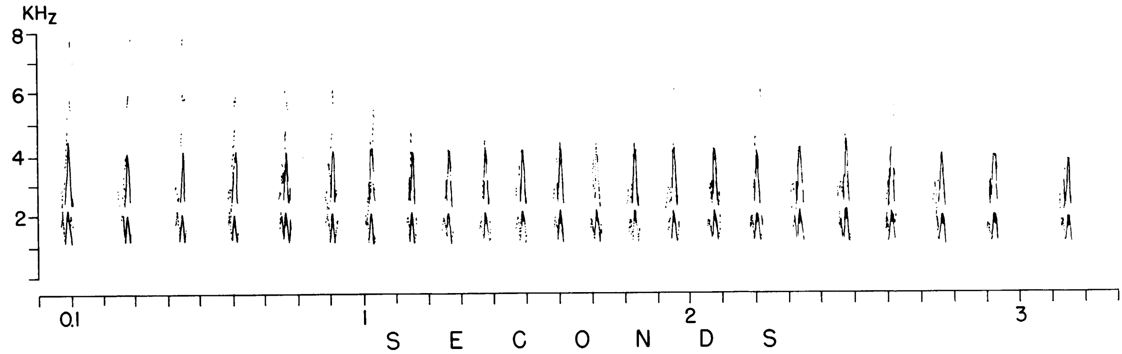


FIG. 8. Wide-band sonagram of Rattle Call of *P. medius*; Austria.

call was with slightly raised wings and sitting crosswise on a branch.

Situations: A1, 2a, 2c; C 4a, 4b, 4c, 5a, 7a; D6 Seasonal occurrence: (9, 10) (Argentina)

lignarius. The Rattle was described by Short (1970) as long and like that of *mixtus* and *scalaris*, but lower and less harsh.

Situations: A1, 2c; C4 Seasonal occurrence (11) (Argentina)

scalaris. As described by Short (1971a), the Rattle consists of Call Note-like notes. We lack a recording of a complete Rattle, so we know nothing about the first note of the Rattle (fig. 9A). A distinctive character of the Ladder-backed Woodpecker's Rattle is the clustering, descending, and shortening of the harsh-sounding last elements which may be heard in the field, too (cf. fig. 19 C to F). The other notes apparently have the tendency to be longer than the Call Note (cf. table 2 and table 5). The Rattle seems to be a distinct vocalization, even clearly separated from the Short Rattle. Rattles often are associated with Drumming and Kweek Calls and sometimes are given after an encounter when the opponent is leaving (Short, 1971a). Rattles of other individuals at a safe distance also are answered with a Rattle.

Situations: A1, 2c; B1; C1a, 1c, 2a, 3a, 3c, 4a, 5a, 5b, 5c, 5e, 5f, 6a, 7a; D2, 6; E4, 5; H Seasonal occurrence: 1-12

nuttallii. The Rattle of the Nuttall's Woodpecker is much faster than the Rattle of *scalaris* (fig. 9B, C; see also Short, 1971a). It can be introduced by Call Notes or Double Call Notes. The end of the call is not so clearly separate a part of the call as in *scalaris*, which can be used as a further field character. There is more variation in the length of the call and the separation from the Short Rattle is less clear-cut than in *scalaris*. The situations in which this call occurs are essentially the same as in the Ladder-backed Woodpecker (Short, 1971a). Playback of this call to a single male (Irvine, California) elicited Drumming, a Rattle, and approach. The Rattle was in this case also the answer to playbacks of Double Call Notes and Drumming.

Situations: A1, 2c; B1, 5; C1a, 2a, 3a, 4a, 5a, 5b, 5c, 5e, 5f, 6a; D2, 6; E4, 5 Seasonal occurrence: (2-5, 10, 11)

scalaris × *nuttallii*. Hybrids are intermediate in their Rattle Call (fig. 9D; see Short, 1971a, pp. 100-101).

pubescens. Kilham (1962, p. 126) denoted the Rattle of the Downy Woodpecker as the "Sputter," and characterized the sound of the call as "chick, chick, chick, chick, chrr-rr-rr." The notes of the Rattle closely resemble the Call Notes, though slightly longer; they become shorter and lower pitched at the end of the Rattle. The last part of the call also lacks the shrill piping quality of the previous notes and is easily audible even to the human ear (figs. 10, 11). The first note usually is pitched higher than the following ones (tables 5, 6). The call con-

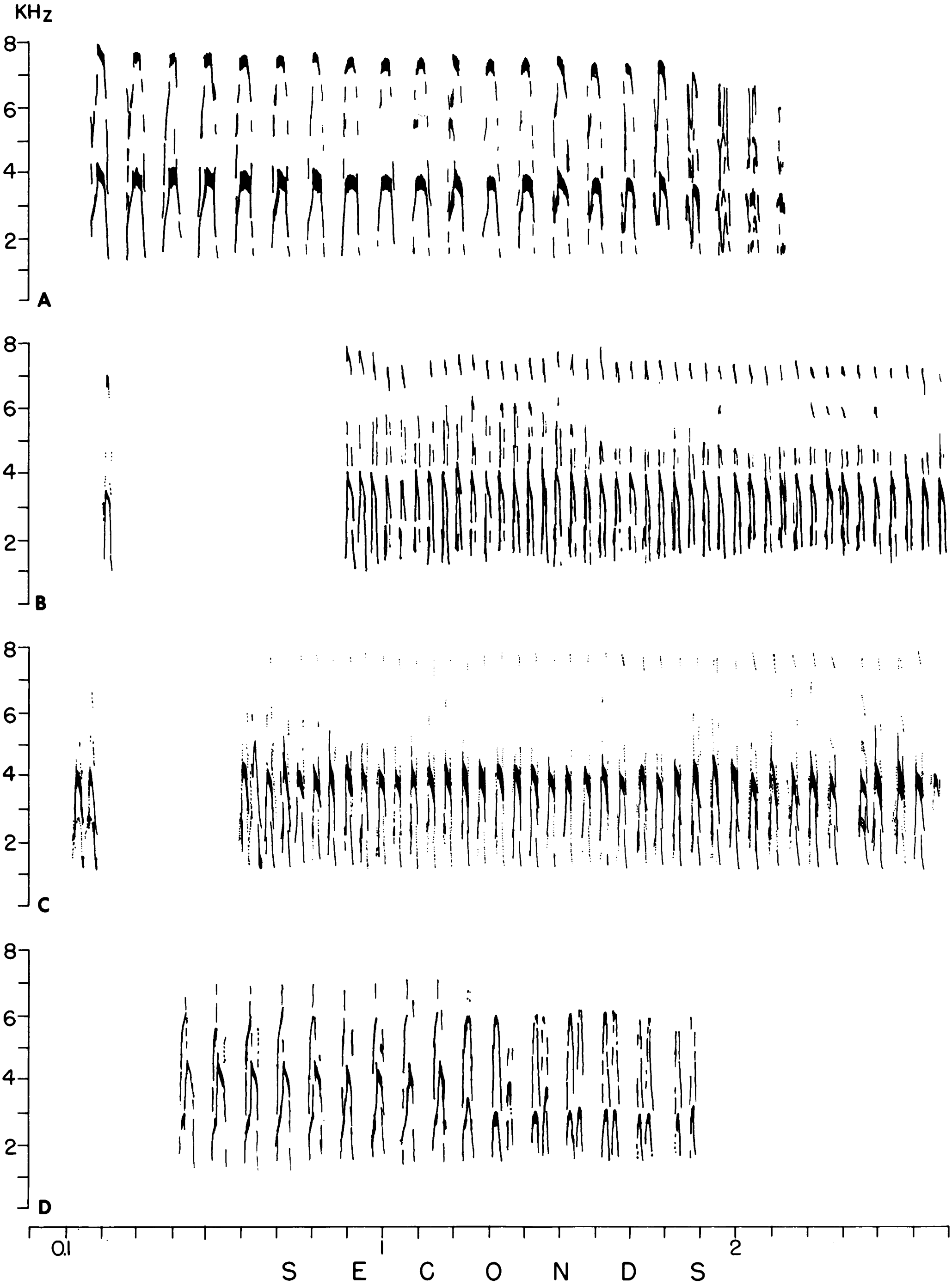


FIG. 9. Sonagrams of Rattle Call of pied woodpeckers. A. *P. scalaris*; incomplete call, the first element(s) are missing; Baja California. B. *P. nuttallii*, preceding Call Note and Rattle; Baja California. C. *P. nuttallii*, male, preceding Double Call and Rattle; California. D. Hybrid *P. nuttallii* × *scalaris*, female, incomplete call, leading part is missing; Baja California. All are wide-band.

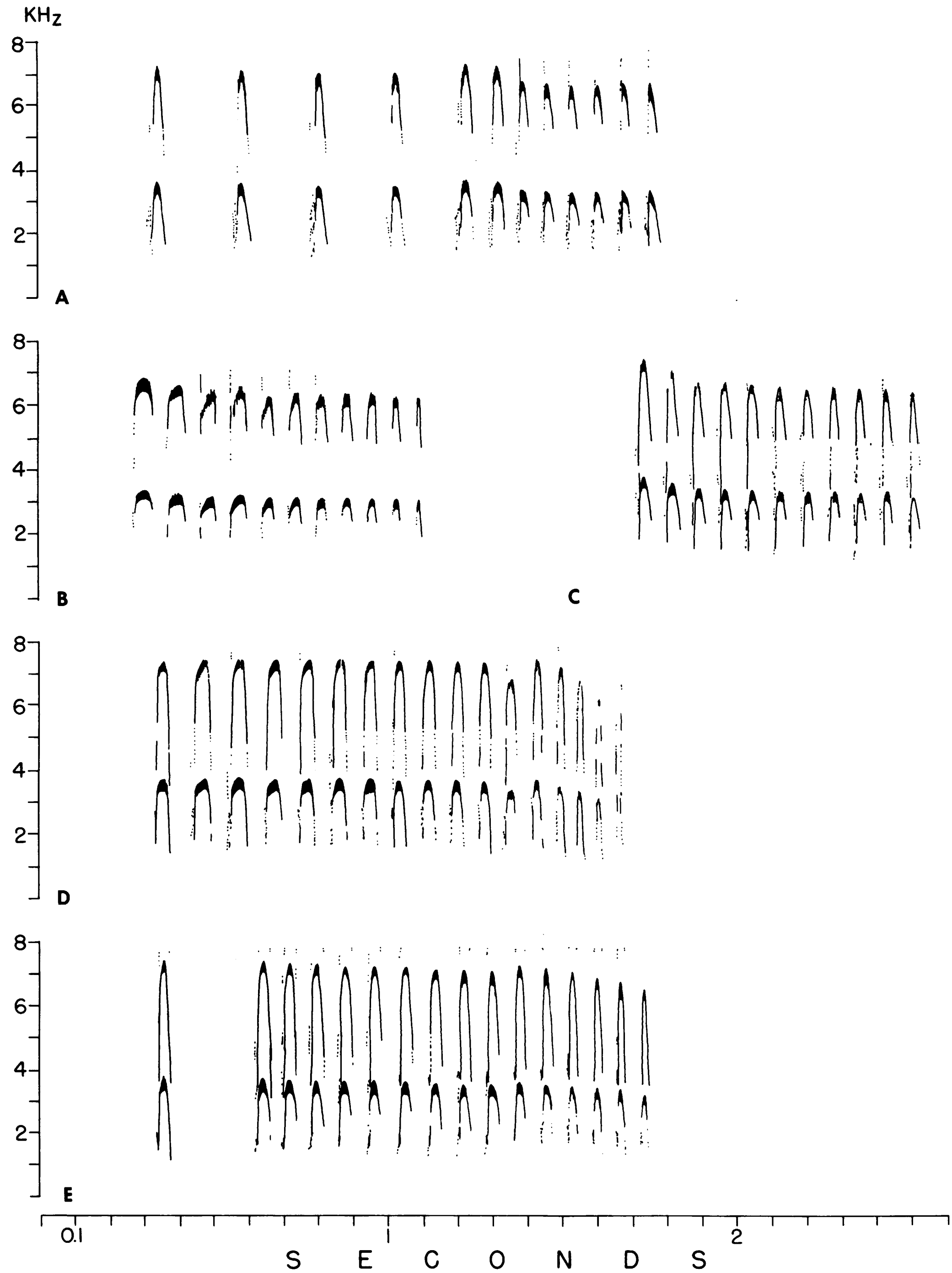


FIG. 10. Sonagrams of Rattle Call of pied woodpeckers. A. *P. pubescens*, nestling, nestling call switching to Rattle; Long Island (June 1972). B, C. *P. pubescens*, fledglings; Long Island (1971). D. *P. pubescens*, adult; New Jersey. E. *P. pubescens*, adult, Call Note plus Rattle; St. Catherines Island, Georgia. All are wide-band.

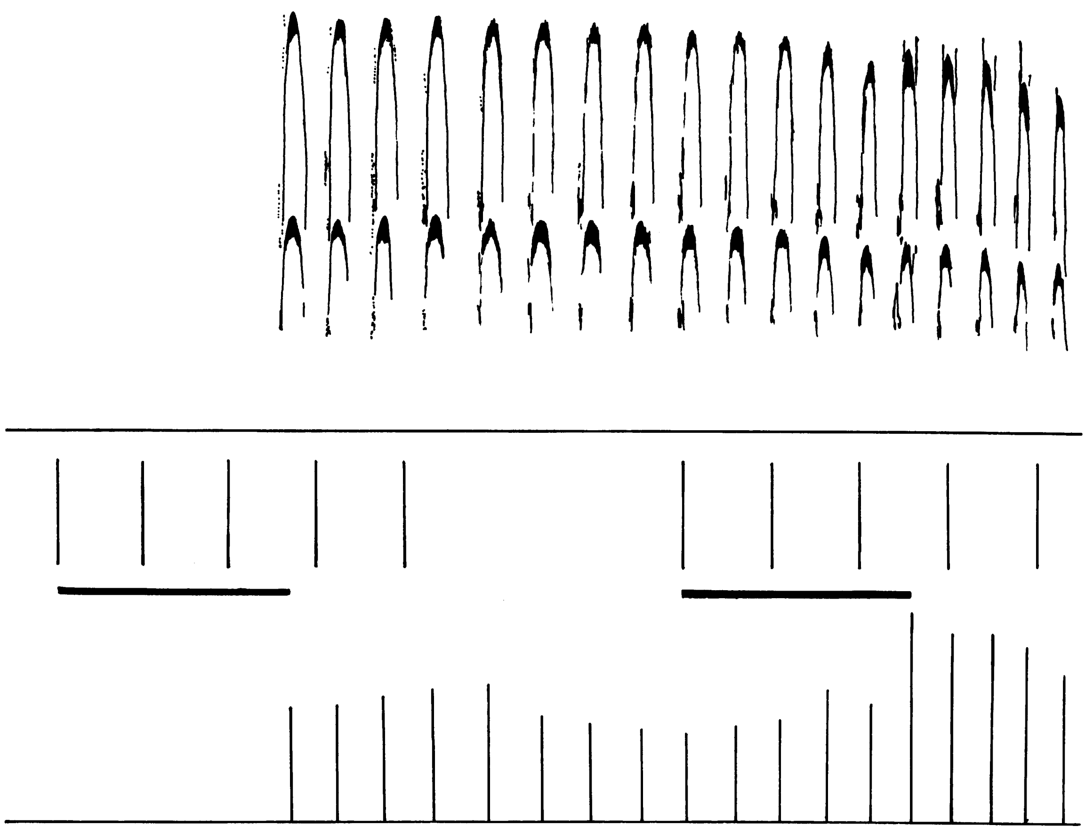


FIG. 11. Analysis of a Rattle Call of a *P. pubescens* male in relation to the Tapping of *Melanerpes carolinensis*. Top row shows wide-band sonagram, notes, pitch, and relation between fundamental tone and first harmonic tone. Middle row marks occurrence of taps; horizontal bars indicate time lag between first tap of a burst and first Rattle note, and first note of the unusually loud terminal section of this Rattle, respectively. The bottom row gives amplitudes of Rattle notes on a logarithmic scale. Recorded on St. Catherines Island, Georgia.

sists of 11-25 notes (N=11), and frequently is introduced by Call Notes. Newly fledged young and fledglings also give Rattle Calls which often are variable in length, pitch, and number of notes (fig. 10 A, B, C). In five calls the pitch was 3.2 kHz. (2.9 to 3.6, Standard Deviation 0.13, Coefficient of Variability 4.1, N=56), the duration was 40.6 msec. (25.4 to 67.9, Standard Deviation 9.16, Coefficient of Variability 22.5, N=55), and the interval between notes was 88.4 msec. (75.5 to 113.2, Standard Deviation 9.77, Coefficient of Variability 11.1, N=50). Playback of Rattles, if there is a reaction at all, is answered by approach, Rattles, Drumming, and searching for the sound source. Rattles of the male often are answered immediately (within 5 seconds). This call was also given after a Downy approached the experimenter, who played a Scolding Call as the playback was stopped for awhile. A recording obtained on St. Catherines Island (Short, personal observ.) indicates a possible reaction of a Downy male to the Tapping of a *Melanerpes carolinensis* (fig. 11). The reaction appeared not only by starting the Rattle but also by reinforcing it during the Rattle after a second Tapping burst of the Red-bellied Woodpecker. Two pairs of Downy Woodpeckers delivered Rattles frequently as they chased each other in early March (Johnston, 1944). Kilham (1962) observed that only the dominant male of his two caged male Downy Woodpeckers uttered the Rattle (reaching a peak in October and November), and this more than when that male was caged only with a female. The signaler prefers exposed branches both in captivity (Kilham, 1962) and in the wild.

Situations: A1, 2a, 2b, 2c; B1; C1, 2, 4a, 4b, 5a, 5b, 5e, 6a, 8b, 9a; D3; E5; F1; G1
Seasonal occurrence: 1-12

borealis. The Rattle of the Red-cockaded Woodpecker resembles that of the Hairy Woodpecker. It is a long call (like the rattle of a kingfisher, Ligon, 1970), descending at the end, the notes lacking any peeping quality (fig. 12). The first note is like a Call Note and somewhat higher pitched than the following notes, which also are shorter but still show the frequency modulation found in the Call Note. The juvenile Rattle Call has a different pitch (2.7 kHz., Standard Deviation 0.203, N=8) and also is variable in length of the call and duration of the notes (54.7 msec., Standard Deviation 5.33, N=8) (fig. 13A, B), which are modulated at a frequency of about 66 Hz. A seeming switch from the Chirp to the Rattle is demonstrated in figure 13A.

Situations: A1, 2a, 2c; D1; F1; G1, 2
Seasonal occurrence: (5, 7)

stricklandi. The Rattle of the Strickland's Woodpecker (figs. 13 C, D; 14) is a long, loud, harsh call (Davis, 1965). The call remains quite constant through its course; the slight increase in amplitude (frequency) modulation (see p. 82) of the last elements is barely audible (figs. 19L, M; 20A). Eighteen calls had seven to 30 (median 15.5) notes additional to the introductory note.

A male that uttered this call often gave shorter Rattles than usual. The first note is a Call Note (fig. 13D) or is transitional between a Call Note and a Rattle note. The notes of the Rattle are long and show a remarkable frequency modulation of about 70 Hz. The most common combination is a Call Note followed by the Rattle. Mated members of a pair give this call regularly, being often answered within 3 seconds by a Rattle or (female) by a Kweek Call. Playbacks elicit Rattles, approach followed by further Rattles with or without frequent Call Notes (female), and Drumming. Or two or more individuals coming to an encounter may commence Rattling. Other than Rattles, Drumming (playbacks), Call Notes, and Kweek Calls may elicit a Rattle. Frequently a bird climbs to an exposed branch or a treetop to deliver this call in upright posture.

Situations: A1, 2c, 3, 4; B1, 2, 4, 5; C1, 8a; D5
Seasonal occurrence: (3, 4, 5)

villosus. The Rattle (Sputter of Kilham, 1960, 1966a) of the Hairy Woodpecker consists of an initial note like a Call Note, and then a fast, shrill trill of lower-pitched, short notes

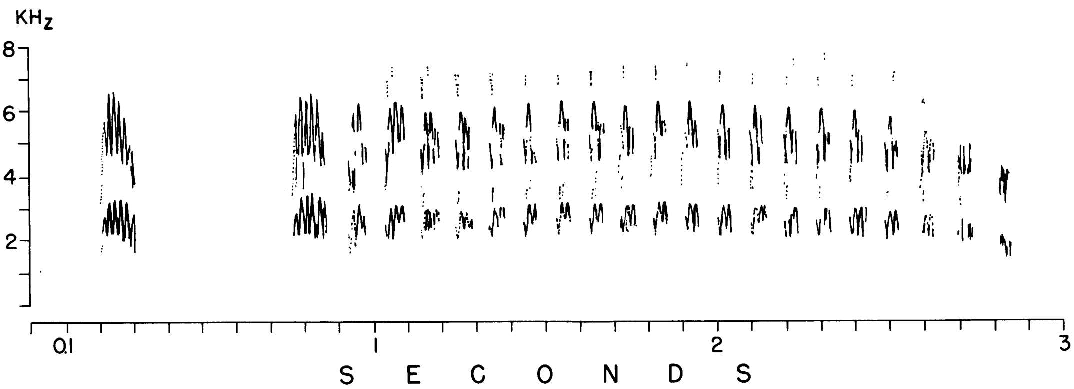


FIG. 12. Wide-band sonagram of Rattle Call of *P. borealis*; North Carolina.

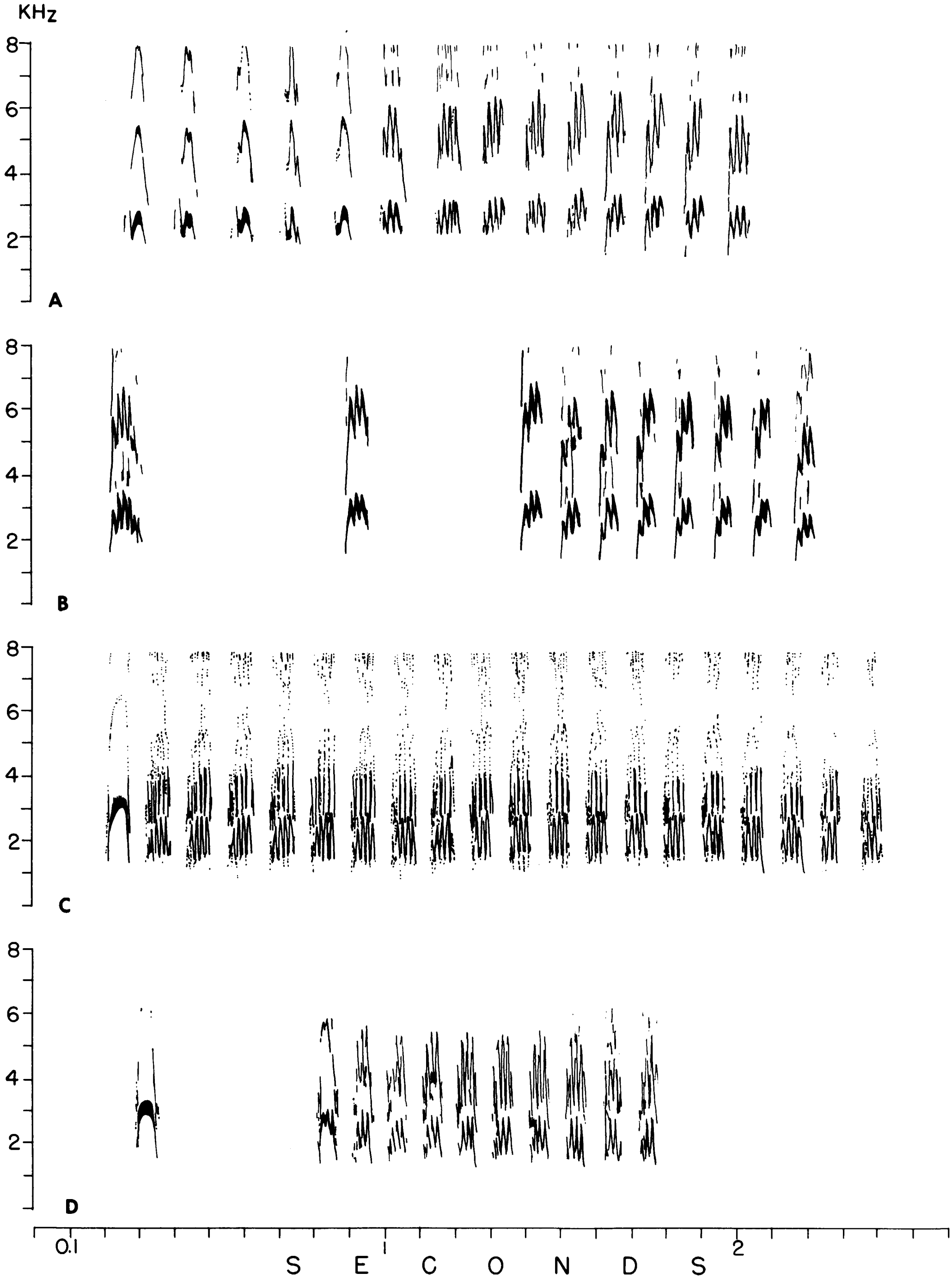


FIG. 13. Sonagrams of the Rattle Call of pied woodpeckers. A. *P. borealis*, nestling after being fed without adult, combination of nestling notes and Rattle; North Carolina. B. *P. borealis*, fledgling at the day of fledging; North Carolina. C. *P. stricklandi*, adult; Arizona. D. *P. stricklandi*, Call Note plus Rattle (form of the first rattle-note discussed in text); Arizona. All are wide-band.

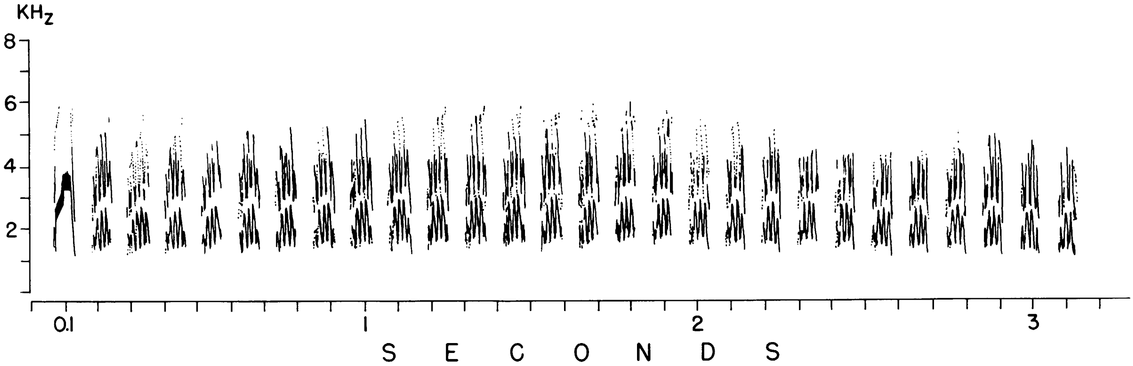


FIG. 14. Wide-band sonagram of Rattle Call of male *P. stricklandi*; Arizona.

(fig. 15A; tables 5, 6), which often diminish in pitch through the trill. Besides the introductory note the call consists of 20 to 38 (N=5) notes. The Rattle is commonly preceded by one or two Call Notes. Playback of the Rattle is answered by Rattles.

Situations: A1, 2a, 2c; B4; C 1a, 1b, 3a, 4a, 4c, 5a, 5d, 5e, 6a, 7a; D3, 6; E1; G1b
Seasonal occurrence: 1-12

albolarvatus. A male leaving an encounter with another male gave a Rattle followed by single and double notes (see p. 23), which were recorded incompletely (fig. 15B). The notes strongly resemble those of *villosus*, some of them showing doubled peaks. The Rattle's separation from the Short Rattle might prove less clear than it seems now, and should be investigated.

Situation: A2 Seasonal occurrence: (4)

tridactylus. A recording of the Three-toed Woodpecker contains a series of notes which might be the Rattle Call (see also Short, 1974a, fig. 5B) of this species (fig. 15C). The evidence, however, is not fully convincing and further data are needed. The structure of the Short Rattle Call (see p. 42) suggests that the Rattle notes are of similar quality.

arcticus. Short (1974a) gave a detailed description of this vocalization, probably the most complex call within the whole genus. In full form it consists of three parts (Short, 1974a): scream, rattle, and snarl (fig. 15D, E; table 7). These may be given either in a snarl by itself, as a rattle-snarl, as a rattle, as a scream-rattle, or in a full scream-rattle-snarl. The different sections are distinct and can be distinguished in the field, although the notes grade into one another where the sections meet. The harsh quality of the call renders it unlike any other pied woodpecker vocalization. In full form the scream-rattle-snarl is associated with a distinctive Hunched-Head Swinging Display used agonistically during encounters. Variation involves the relative lengths of the three parts, exclusion of one (scream) or two (scream and rattle or scream and snarl) parts, and hence the overall length of the complex call. It is employed interspecifically as well as against conspecific individuals.

Situations: B4; C1a, 1c, 1d, 3a, 4a, 4c, 5a, 5b, 5c, 5e, 6a, 7a; D2, 3, 6; E2, 4
Seasonal occurrence: (4-6)

Summary. (Tables 5, 6.) Within the genus the Rattle Call is the most diverse call-type, although intraspecifically it is usually constant and distinctive. Generally, it is preceded by one or two Call Notes (see p. 9). The Rattle itself is comprised of more or less uniform notes which usually form a fast series. In all cases the first note shows a close resemblance to the Call Note, even in those species in which the Call Note and the notes of the Rattle are very different (tables 2, 6). The terminal

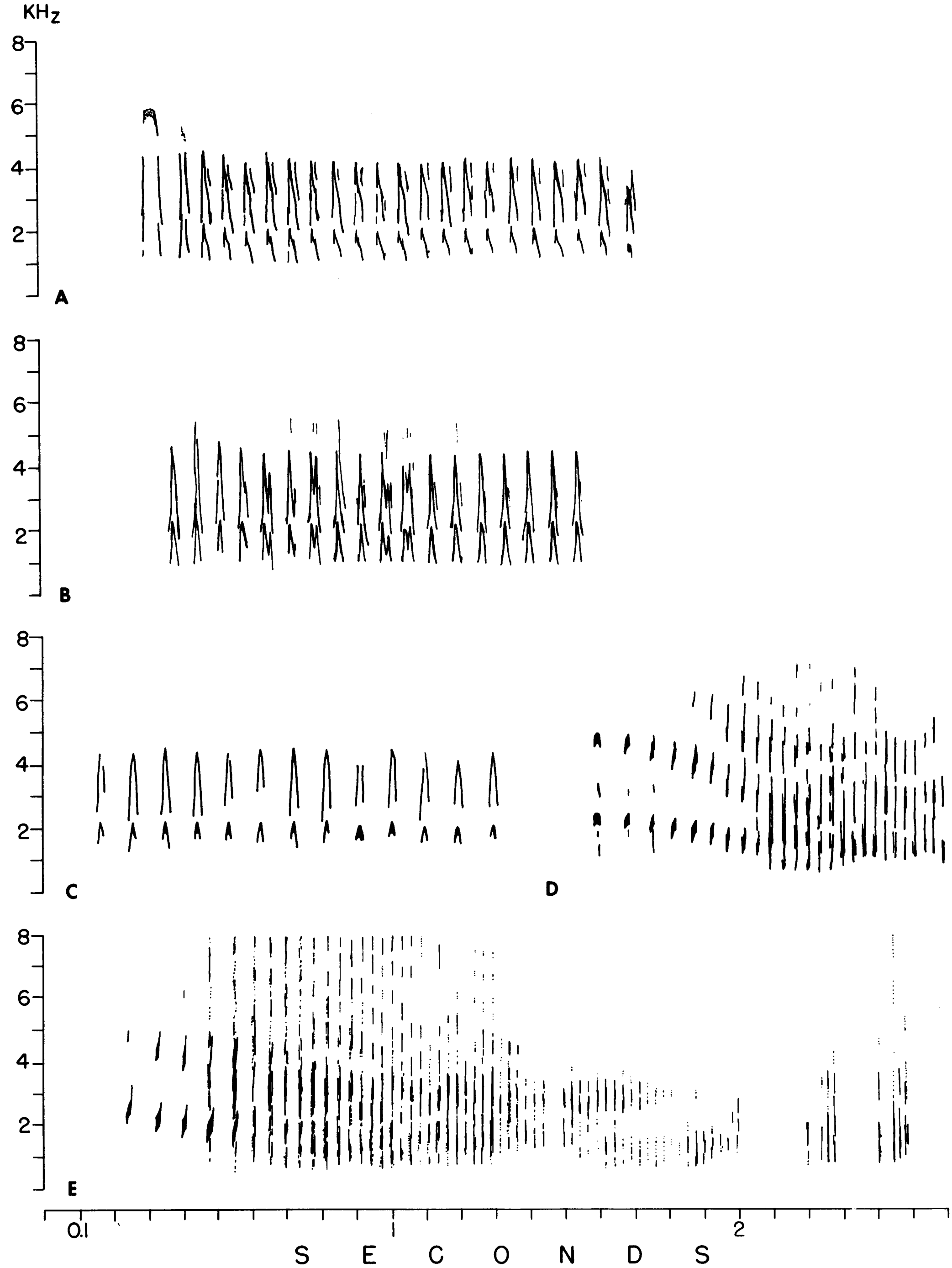


FIG. 15. Sonagrams of Rattle Call of pied woodpeckers. A. *P. villosus*, adult female; Long Island (1971). B. *P. albolarvatus*, adult male, incomplete Rattle (first notes are missing); California. C. *P. tridactylus*, series of notes that might represent a Rattle (see text); New York. D. *P. arcticus*, first part of the Rattle: scream-rattle without snarl (omitted); New York. E. *P. arcticus*, adult male, full Rattle with long snarl part (note the raklike snarls at the end of the call); New York. All are wide-band.

TABLE 7
Analysis of 12 Rattle Calls of *Picoides arcticus*[a]

	Pitch			Duration		Internote Interval					Notes per Call	
Note type	Mean	Range	N	Range	N	Mean	Range	S.D.	C.V.	N	Mean	Range
Begin Scream	2.3	2.0-2.5	12	—	—	83.6	79.2-94.3	4.50	5.4	12	—	—
Scream	—	—	—	3.8-26.4	50	—	—	—	—	—	6.0	4-10
End Scream	1.8	1.5-2.2	12	—	—	58.3	39.2-75.5	12.29	21.1	12	—	—
Rattle	—	—	—	3.8-15.1	150	30.0	18.9-52.8	6.20	20.7	166	20.6	10-33
Snarl	—	—	—	3.8-11.3	100	23.0	18.9-26.4	1.95	8.6	109	—	to 40

[a]*Symbols*: N, sample size; S.D., Standard Deviation; C.V., Coefficient of Variability. Pitch is in kilohertz, duration and internote interval in milliseconds.

part of the call generally is lower, harsher (frequency and amplitude-modulation, see fig. 19 and p. 82), and often is separated by a longer interval from the other notes. The most complex inner structure is to be found in the Rattle of *arcticus*, which has three distinguishable parts. The Rattle notes have the tendency to become shorter than the Call Note in large species (*syriacus*, *borealis*, *stricklandi*, *villosus*) and longer in small ones (*minor*, *pubescens*), though there are exceptions like *canicapillus* and *nuttallii*. The fundamental tone is stressed in *syriacus*, *scalaris*, *nuttallii*, some *pubescens*, *borealis*, and *stricklandi*, whereas the first harmonic tone is stressed in *canicapillus*, *medius*, some *pubescens*, and *villosus*. Both components are stressed almost equally in *macei* and *minor*, showing a slight tendency to emphasize the first harmonic. American *albolarvatus* has only a trifle more emphasis on the fundamental tone. The situations in which the *Picoides* woodpeckers utter a Rattle are almost as diverse as those associated with the Call Note. The distinctness of the Rattles renders them very useful field characters.

SHORT RATTLE CALL

obsoletus. Short Rattles of this species are series of notes, consisting of one to three elements, needle-like on the sonagram, and accompanied by noise; central elements are often double peaked. The gaps between such groups range from 25 to 65 msec. Elements have a duration of 12-29 msec.; marginal elements are shorter than central ones.

Situation: C2 Seasonal occurrence: (10)

cathpharius. As described by Short (1973) a recording contained a call with four notes (fig. 17A); others, not fully suitable for spectrographical analysis, were recorded when the birds apparently were involved in agonistic encounters. These latter examples (numbering about eight) consisted of three notes. The form of the notes is a sharp, tight, inverted V. The call can be rendered at a rate of four calls per second. The notes of the call shown in the figure were given at a rate of 34 notes per second.

Situations: C4, 5, probably 7
Seasonal occurrence: (4, 5)

leucotos. The calls essentially are an abbreviated version of the Rattle with which they were combined in the only recording (courtesy of W. Scherzinger) we had available (fig. 16). The one example shown in figure 17B may give an idea of the nature of the juvenile Short Rattle. It is hardly possible to attribute one of the descriptions of the calls of the White-backed Woodpecker by Franz (1937) and by Voigt (1961) to this category.

Situations: A2a; B4; F 1
Seasonal occurrence: (4-6)

medius. Short Rattles are commonly heard, commencing with a higher pitched note that is

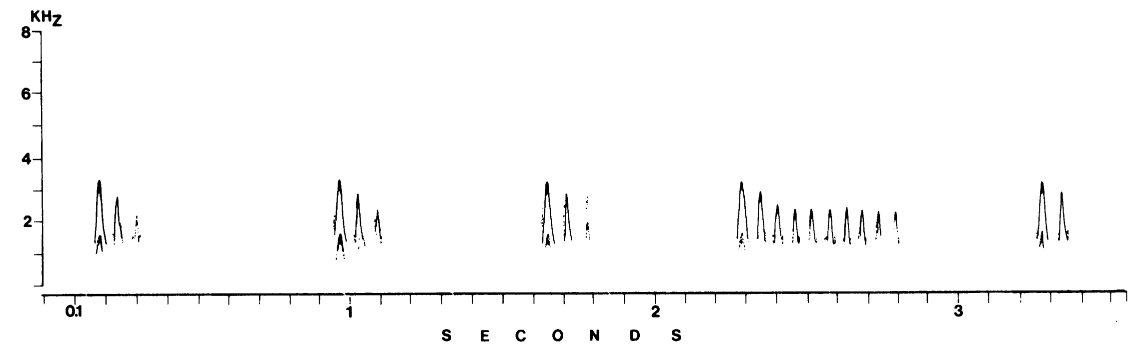


FIG. 16. Wide-band sonagram of a Short Rattle and Rattle combination of *P. leucotos*; Germany.

followed by several others (fig. 17C, D). It is probably impossible to define an acceptable boundary between Short Rattles and Rattles, although the former seems to us as if emphasizing a short e sound, and Rattles seem rather to emphasize a sound like German ü (see also Steinfatt, 1940). Short Rattles generally are as common as Rattles, although less loud and hence more likely to go undetected; they are uttered throughout the year. Feindt (1956) discussed this call in detail, especially its phonetical appearance, naming it the Artruf ("species" call). We also confirm his findings concerning the variable number of notes and the variable speed, which led him not to distinguish it from the Rattle (cf. p. 28). Many recordings are needed to provide us with information about the full range of variation included in the Short Rattle and Rattle.

Situations: A1, 2c Seasonal occurrence: 1-12

syriacus. This call was discussed briefly by Winkler (1972) as the Kreck-Ruf. It consists of a leading Call Note and one to several short, and on the sonagram, needle-shaped, notes in a series with a high rate of delivery (fig. 17E). The notes more closely resemble those of the terminal rather than of the initial part of the Rattle Call (fig. 19 H, I, J).

Situations: A2b; B2; C1d, 5, 6a; E3, 5; G2, 3
Seasonal occurrence: 2-10

major. Pynnönen (1939) described this call as ki-reck, and Blume (1968) referred to it as a loud kreck. Probably those authors did not fully distinguish the Short Rattle from the Rattle (p. 28). The call commences with a Call Note which is followed by a series of notes that form two complete "needles" on a sonagram about 30 msec. apart, the duration of the notes being about 120 msec. The fundamental tone is in the range of 1.8 kHz.

Situations: A2b; C1b, 2b, 2c, 4c; D5; E1
Seasonal occurrence: 1-5, 11

major × *syriacus*. These Short Rattles (fig. 17 I) show clear resemblance to those of *syriacus* sonagraphically, and they sound similar to those of both the parent species.

Situation: G2 Seasonal occurrence: (6)

scalaris. The Short Rattle of this species is a distinct vocalization (Short, 1971a). The notes after the leading Call Note are delivered at a higher rate than in the Rattle, namely at 12.9 to 15.2 per second. They resemble in structure the terminal notes of the Rattle Call more than the leading ones (fig. 17J). This especially is demonstrated by an analysis of the amplitude (fig. 19 E, F, G).

Situations: C5, 7, 9f
Seasonal occurrence: (3-5)

nuttallii. Rattles shorter than the usual full Rattles occur, but seem not to be distinct in their physical structure other than in their shorter duration (Short, 1971a). No data are available about the context of this call.

pubescens. A candidate for this category is the "high-intensity alarm" call, "a scolding

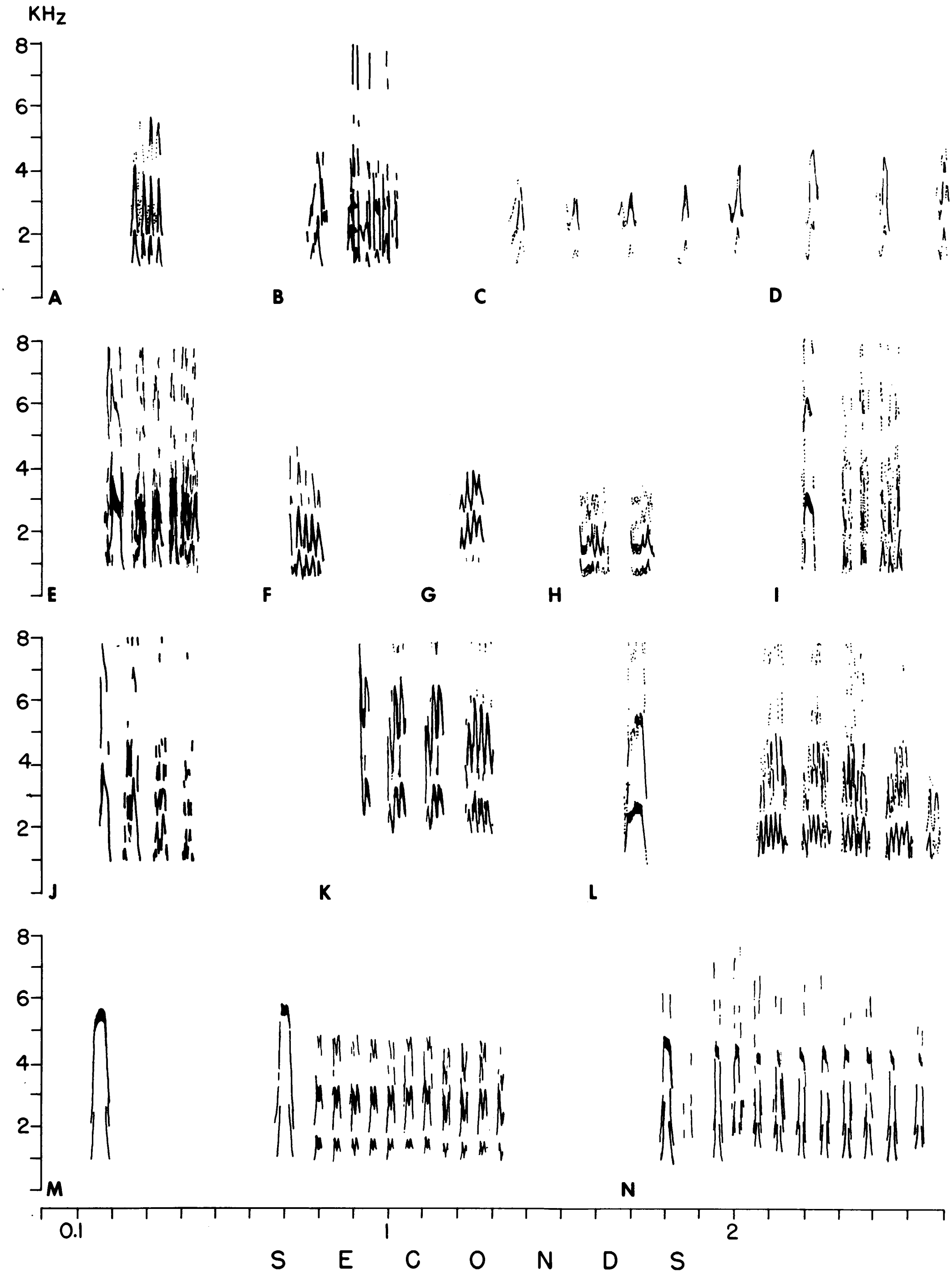


FIG. 17. Sonagrams of Short Rattle Calls and Mutter Calls of pied woodpeckers. A. *P. cathpharius*, Short Rattle; India. B. *P. leucotos*, nestling two days before fledging, Short Rattles; Austria. C, D. *P. medius*, Short Rattle; Austria. E. *P. syriacus*, Short Rattle; Greece. F. *P. syriacus*, Mutter; Austria. G. *P. major*, Mutter; Austria. H. *P. major*, Mutter-Wad Call transition, male during encounter with female; Austria. I. *P. major* × *syriacus*, immature, Short Rattle; Austria. J. *P. scalaris*, Short Rattle; Baja California. K. *P. borealis*, nestling one day before fledging; North Carolina. L. *P. stricklandi*, during encounter, Short Rattle; Arizona. M. *P. villosus*, fledgling near adult female, Short Rattle; New York. N. *P. albolarvatus*, male during encounter, Short Rattle; California. All are wide-band.

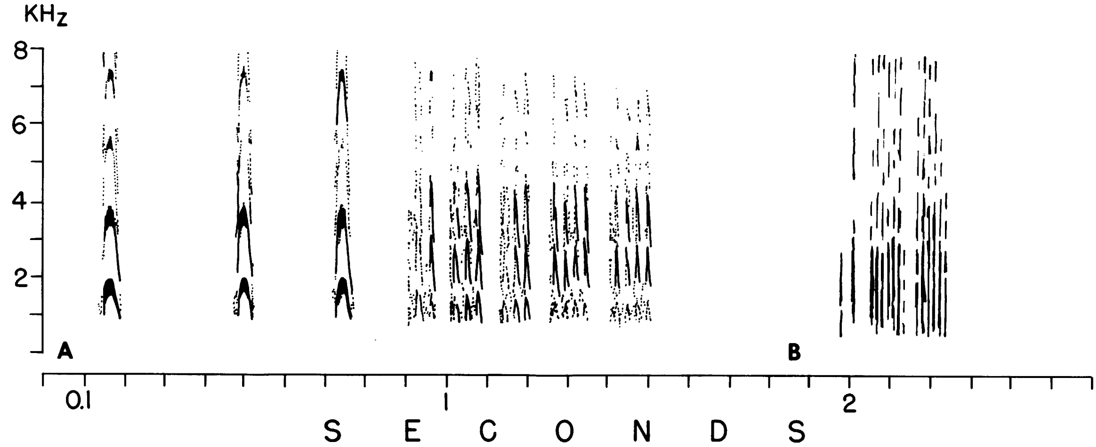


FIG. 18. Sonagrams of Short Rattle Calls of some pied woodpeckers. A. *P. tridactylus*, fledgling; Austria. B. *P. arcticus*, female leaving encounter with *tridactylus*; New York. Both are wide-band.

rather loud and penetrating *tickirrrrrr*" (Lawrence, 1967, p. 23).

borealis. Young birds near fledging delivered Short Rattles quite often. Besides such calls as the one in figure 17K, the birds gave combinations of the Call Note together with Chirps and a Loud Chirp-Short Rattle note combined with one or two Short Rattle notes. The notes of the Short Rattle have a form similar to that of the Call Note, and especially of the Rattle. They usually have two marked peaks and may even have leading or closing peaks. During a disturbance near the nest, an adult bird gave a Call Note followed by two Short Rattle notes with internote-intervals of 407 and 619 msec.

Situations: E5, F1 Seasonal occurrence: (5, 6)

stricklandi. Short Rattles are essentially brief versions of the Rattle (fig. 17L). Remarkable is the long gap (377.4 msec.) between the introductory Call Note and the first Rattle note (cf. table 6). They were noted only occasionally when the woodpeckers were participating in encounters.

Situation: C5 Seasonal occurrence: (4)

villosus. Short Rattles often are given by fledglings (fig. 17M). The alarm calls described by Kilham (1960, 1969) and Lawrence (1967) also may be Short Rattles. The Short Rattle consists of an introductory Call Note (separated from the first rattle note by a gap even greater than in the Rattle, namely 135 msec., ranging from 109 to 151 msec. in five such calls), followed by five to 14 (mean 11, N=5) short notes. The latter resemble Rattle notes but are distinctly double—or even triple—peaked, and so exhibit a tendency toward more frequency (amplitude) modulation as we find in other species. Also, the pitch drops at the end of the call. The Short Rattle frequently is uttered in combination with Call Notes.

Situations: E5, G2 Seasonal occurrence: (6)

albolarvatus. A male unceasingly uttered Short Rattles (fig. 17N) with its mate nearby throughout a long quarrel with another pair. The calling bird was not involved as directly as were the other three birds, rather it tended to stay apart from them. The calls are introduced by a note that probably is simply the Call Note (see p. 23). Compared with the Rattle the notes of the Short Rattle have a tendency toward more frequency modulation. The last notes of the Short Rattle may be lower in pitch. Besides the introductory note four to 11 notes were found, showing in this respect intermediacy between the Double Call and the Rattle.

Situations: C5f Seasonal occurrence: (4)

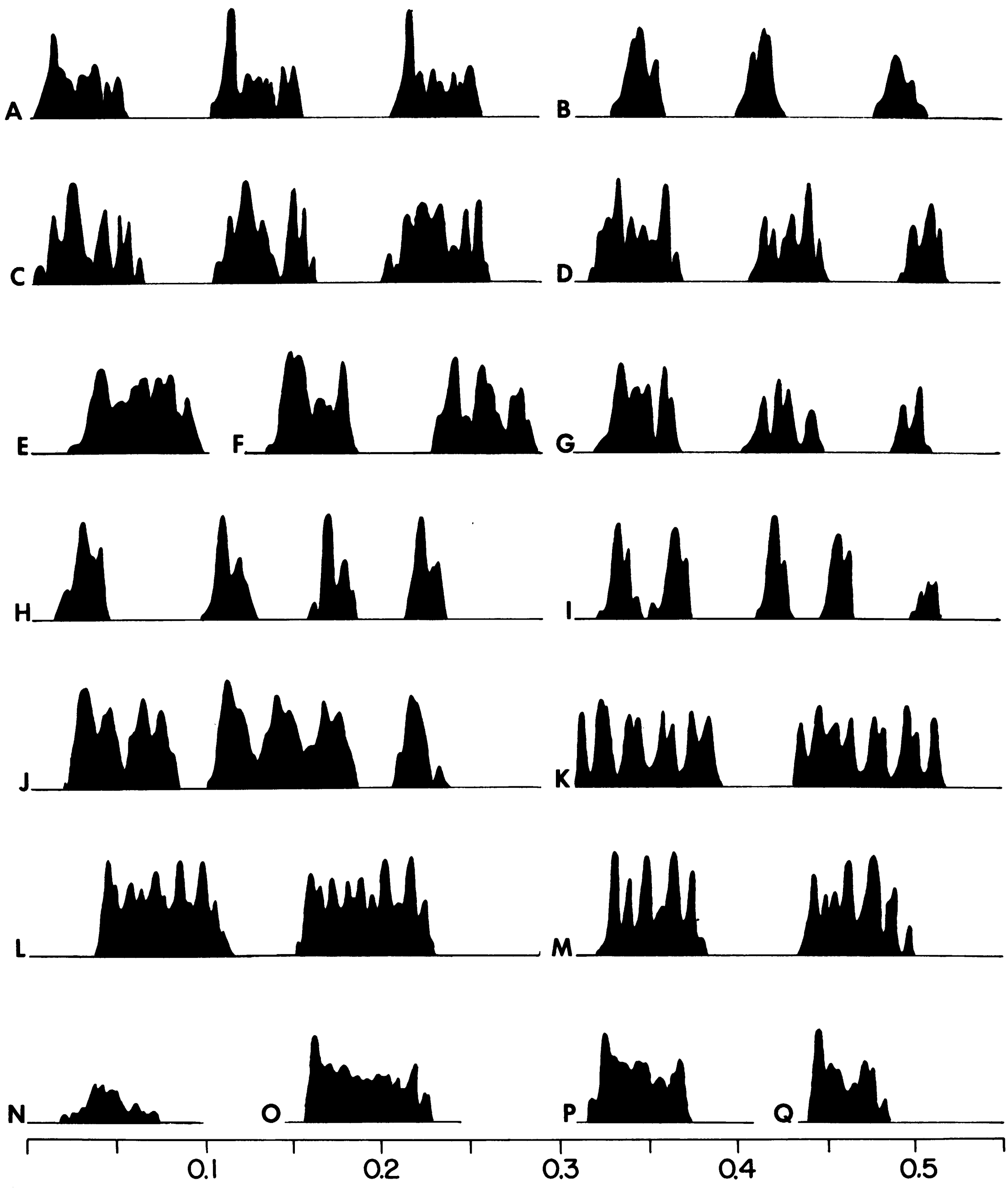


FIG. 19. Amplitude characteristics of pied woodpecker Rattle Calls, Short Rattle Calls, and Mutter Calls. A. *P. pubescens*, the first three notes of a Rattle Call, and B, the last three notes. C. *P. scalaris*, three notes from the first part of a Rattle Call, and D, the last three notes. E, F. *P. scalaris*, a note from the first part, and the last two notes before the end of a Rattle. G. *P. scalaris*, Short Rattle. H, I. *P. syriacus*, first and last notes of a Rattle. J. *P. syriacus*, Short Rattle. K. *P. syriacus*, Mutter. L, M. *P. stricklandi*, the first two, and then the last two notes of a 19-note Rattle. N, O, P, and Q. *P. minor*, the first, the third, the penultimate, and the last note of a Rattle.

tridactylus. Two recordings were available for analysis (fig. 18A). They are taken from juvenile birds close to the time of fledging. They commence with a Call Note and consist of needle-like notes that are approximately 30 msec. apart and 2 kHz. in pitch. In juveniles the Short Rattles may be combined with Chirps.

Situation: G Seasonal occurrence: (6)

arcticus. The group of calls described by Short (1974a) in great detail as the Kyik-ek Call resembles physically the Short Rattles of the previous species, and thus is so categorized. The call usually consists of an introductory Call Note, or at least a note like a Call Note, plus one to four groups of elements that form thin vertical needles on the sonagram. At its extreme this call becomes a grating sound (fig. 18B). Short (1974a) heard this call far more often from the female of a pair.

Situations: C5g, 7b, D4, 5
Seasonal occurrence: (4-6)

MISTLE THRUSH CALL

major. This species utters a call that resembles the wooden rattle call of the Mistle Thrush (*Turdus viscivorus*) (e.g., Tooby, 1943; Witherby et al. 1938; see fig. 21). Apparently the same call (see the description in Feindt, 1956, p. 111) was designated as "vocal drumming" (e.g., Pynnönen, 1939; Feindt, 1956). It was uttered mainly by quarreling woodpeckers, especially when flying, and as reaction to Drumming (a male called 30 times in 25 minutes; Pynnönen, 1939). This sound is said by them to be made by rapid movements of the tongue (fast probing with the tongue in fact may produce a sound, but, judging from the sonagrams, sound reproduction in the manner described by those authors seems to be mere speculation). We heard this call only very rarely. Pynnönen mentioned that it sometimes sounds like a rough "kerret" (compare with his denotation of the Short Rattle). Sonagrams reveal a striking similarity to the "Rattle" portion of the *arcticus* Rattle, a similarity also recognized with the unaided ear. The calls consist of seven to 20 elements following in a very regular rhythm, the mean interval being 35.5 msec. (N=56). Each element has principally the same structure as a "Rattle" element of *P. arcticus*.

Situation: C7a Seasonal occurrence: (6)

medius. Observations of such a call were cited by Feindt (1956).

Situations: B1; C5, 6
Seasonal occurrence: 3-6

MUTTER CALL

syriacus. This call has as its most characteristic feature a strong frequency modulation at about 60 Hz. (figs. 17F; 19K). The frequency peaks correspond with forked peaks of amplitude (fig. 20B). The Mutter is softer than the harsh Short Rattle and is uttered only when two woodpeckers are at close distance. It is associated with head swinging movements and displays, and may appear in series.

Situations: 1d; C 2a, 5 (2), 5a, 7a, 8; G
Seasonal occurrence: 2-9

major. Blume (1968) established a category of calls that he named Rä Calls. To this probably belong two of our categories. A large part of Blume's class includes the Wad Call, and presumably he also includes the Mutter (fig. 17G). This call is lower in amplitude than the Short Rattle, and shows the same frequency modulation as the Mutter of the Syrian Woodpecker. It is uttered at close distance to other individuals, sometimes in a loose series. The Mutter is strongly associated with Headswinging Displays and a more or less erected crown. These occur when a bird is near an opponent, and they usually precede the aggressive approach of the signaler. Transitions to the Wad Call were registered during a heterosexual encounter (fig. 17H).

Situations: C5 (2), 5a Seasonal occurrence: 1-9

KWEEK CALL

kizuki. A call sounding like the Rattle of *minor*, but rougher, and given mainly in spring (together with Drumming and frequent Rattles), was described by Jahn (1942).

canicapillus. The vocalization, described by Short (1973), consists of an introductory element and a well-marked squeaking, main com-

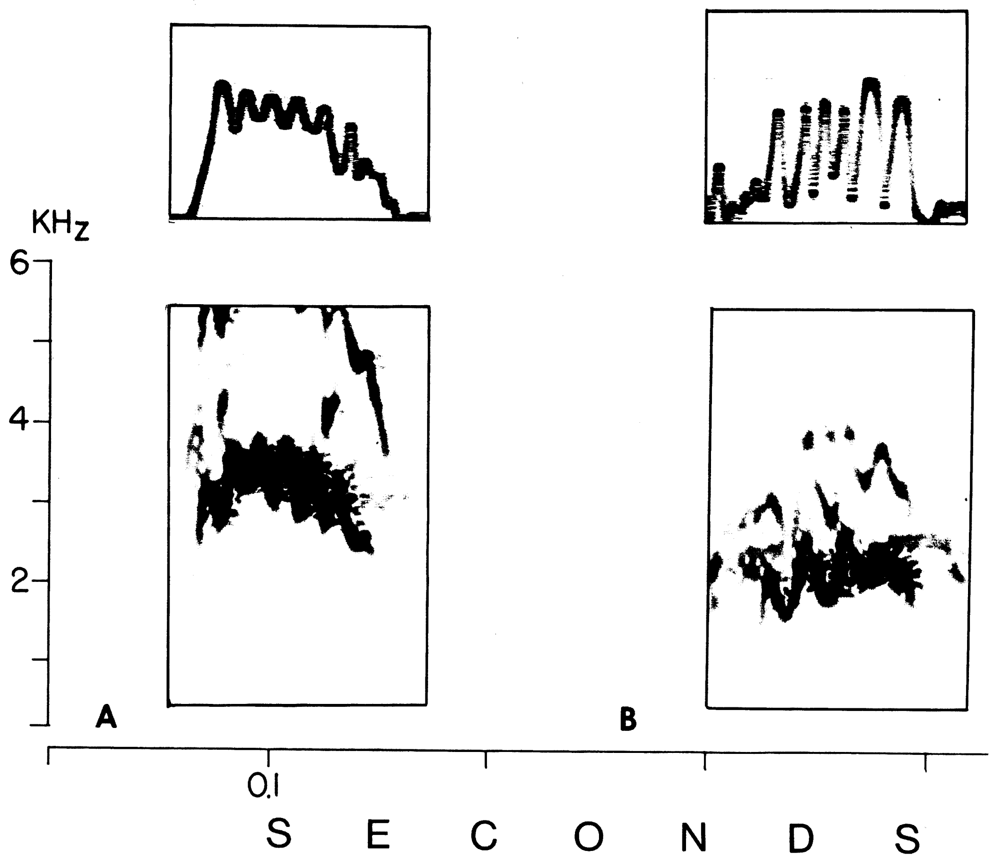


FIG. 20. Examples of frequency-modulated notes. A. Rattle note of *P. stricklandi*. B. Mutter note of *P. syriacus*. The upper figures picture the amplitudes on a logarithmic scale, the lower figures show the sonagrams. Note the different correlation between amplitude and frequency modulation in these two examples.

ponent (fig. 22A). The latter is emphasized strongly at the fundamental tone which ranges from 2.2 to 2.8 kHz. Variation affects both the length (55 to 120 msec., N=12) and the course of the pitch. The most noteworthy combination of this call is one with the Rattle (fig. 6C; see p. 23; also Short, 1973). The information and available recordings only treat the calls of adults feeding fledged young. But perhaps the curious squeaking noise of a male chasing a female, and later of the female alone, reported by Stuart Baker (1927), is also an example of this call.

Situations: C2, 4a, 5a, 5b, 5d, 6, 7a; D2, 6
Seasonal occurrence: (4, 5) (India)

obsoletus. The Kweek notes are long and squeaking and rich with strong harmonics. They occur in series of which we could analyze one (fig. 23A) obtained by C. Chappuis. The notes begin with a narrow peak followed by a wider and higher peak in the middle, which leads to a falling of the pitch in an irregular manner, closed by an abrupt descent of the pitch. The mean pitch (middle peak measured) was 1.4 kHz. (range 1.1 to 1.6 kHz., Standard Deviation 0.20 kHz., N=5) and the internote intervals were 344 msec. (range 327-364 msec., Standard Deviation 15.4 msec., N=4). Within the one series analyzed the pitch of the five notes fell constantly from the beginning to the end, and the internote interval increased.

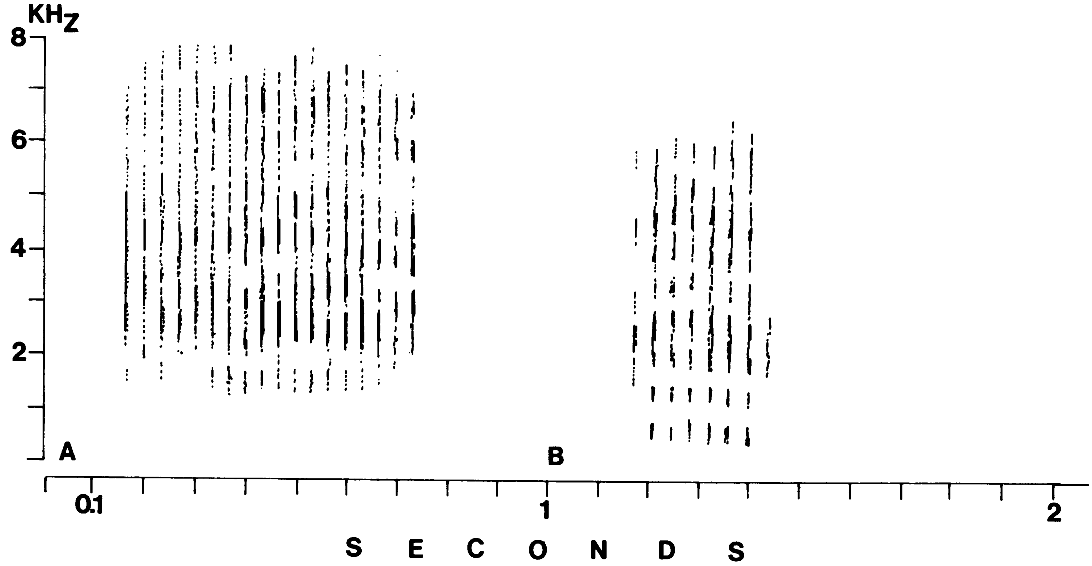


FIG. 21. Wide-band sonagrams (150 Hz. filter) of the Mistle Thrush Call of *P. major*; Germany (A) and Austria (B). No geographical difference is implied.

Situation: A2 Seasonal occurrence: (7)

minor. Soft chwuit calls given by a female that approached a tape recorder partially in aerial display after a playback of Drumming may represent the Kweek of this species.

Situation: B2 (2) Seasonal occurrence: (3)

macei. Short (1973) found that the calls occur mostly in series that are longer and louder than those of *canicapillus*. Occasionally they were associated with Rattles but not in the same intimate relationship as in *canicapillus*. They appeared during extended encounters, especially male-male encounters when a female was present.

mahrattensis. Smythies (1953) reported a shrill note, quite unlike calls of most woodpeckers; this might be a reference to a Kweek.

leucotos. The record of Blume, Ruge and Tilgner (1975) contains Kweeks of a type which we later characterize as Type II Kweeks (p. 47). They were recorded during dummy experiments at the nest. The 170 msec. (range 140-200 msec., Standard Deviation 22.3 msec., N=11) long calls consist of a short element, followed by a hoarse, squeaking element (fig. 23B). The former element is needle-like on a sonagram, and the falling leg is by far the most pronounced part (it is less steep than the practically vertical initial element). The squeaking element is of considerable length and low pitch (0.53 to 0.65 kHz.), and is best characterized by its strong, irregular frequency modulation, especially at the beginning. The squeaking tone, becoming less modulated, then rises to the closing element, which has an irregular, inverted U-shape with the peak at 1.79 kHz. (range 1.5 to 2.2 kHz., Standard Deviation 0.26 kHz., N=11) and lasts 34 msec. (range 15 to 75 msec., Standard Deviation 17.2 msec., N=11). The call comes in series with intervals of 235 msec. (range 225 to 250 msec., Standard Deviation 10.2 msec., N=8), and may grade into Wickas and at the end of such a mixed series to Twitters.

Situation: E Seasonal occurrence: Unknown

medius. The nasal, curious Kweek call of *medius* is one of the best known bird vocalizations among European ornithologists. Blume (1968) called it Quäken, Ferry (1962) designated it as *le chant vocal*. According to our data, Kweeks may occur as single notes but mainly (92 percent of cases) are in series of

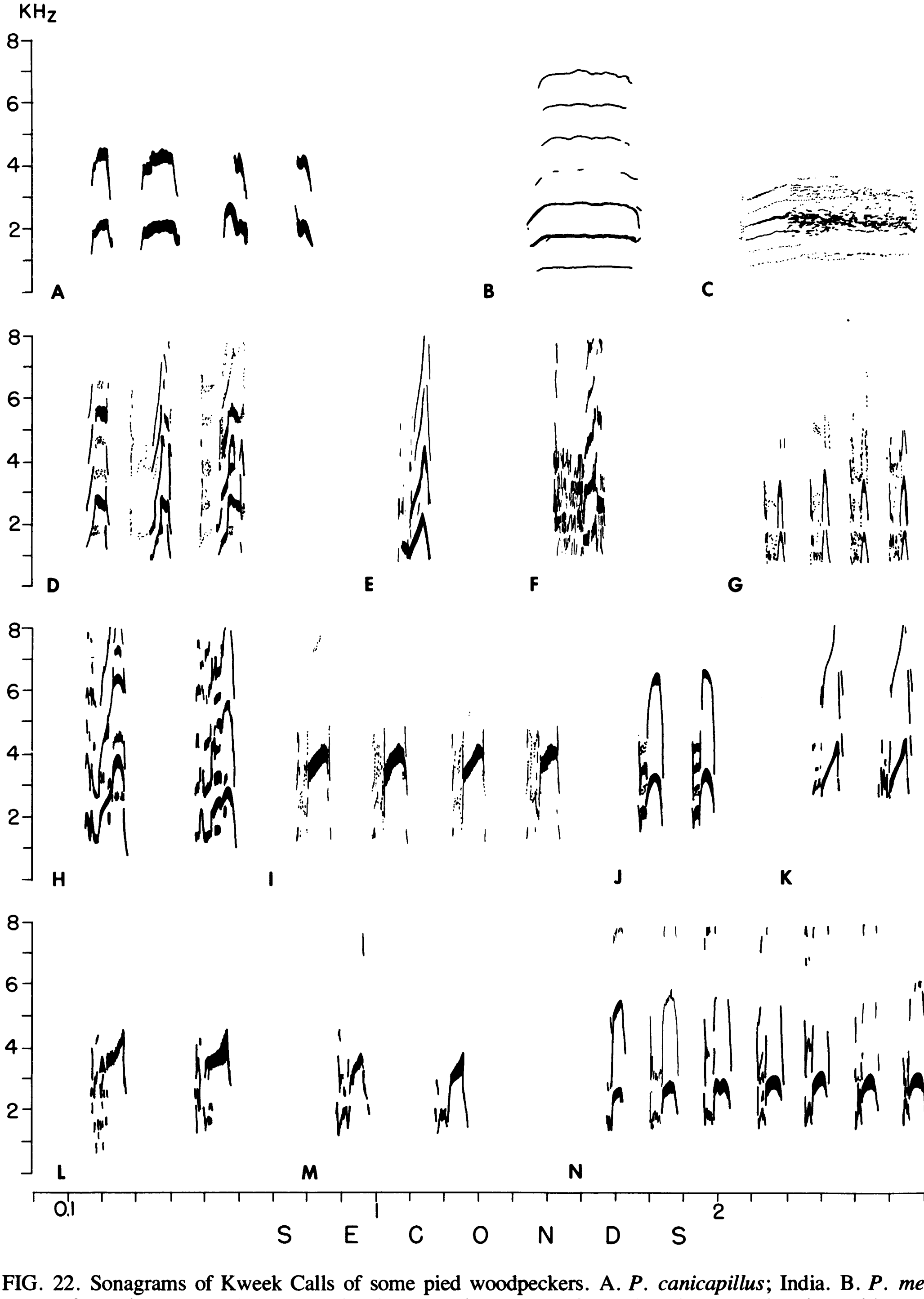


FIG. 22. Sonagrams of Kweek Calls of some pied woodpeckers. A. *P. canicapillus*; India. B. *P. medius*, one note of a series, narrow-band; Austria. C. *P. medius*, note (of an otherwise normal series) with croaking sound at the end, narrow-band; Germany. D. *P. syriacus*, female, Type I Kweek, part of a series; Austria. E. *P. syriacus*, Type II Kweek, part of a series; Austria. F. *P. syriacus*, Type II Kweek, part of a series; Greece. G. *P. major*, presumably of Type II Kweek, part of a series; Sweden. H. *P. scalaris*, Type I Kweek; Baja California. I. *P. nuttallii*, Type I Kweek, part of a series; California. J. *P. nuttallii*, Type I Kweek, part of a series; Baja California. K. *P. nuttallii*, Type II Kweek, part of a series; Baja California. L, M. *P. scalaris* × *nuttallii*, Kweeks, parts of series; Baja California, N. *P. pubescens*, Type I Kweek, female; New York. All are wide-band except B and C, which are narrow-band.

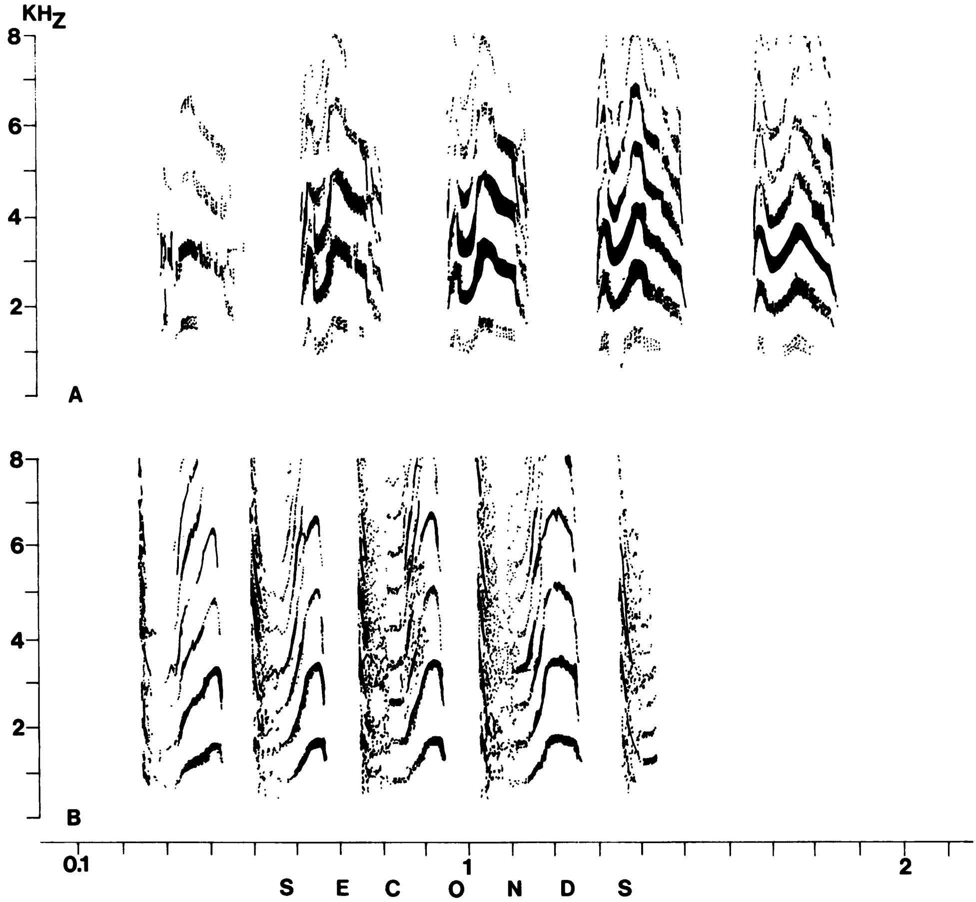


FIG. 23. Wide-band sonagrams of Kweek Calls of two pied woodpeckers. A. *P. obsoletus*; West Africa. B. *P. leucotos*; Austria. Analyzed with 300 Hz. filter (A) and 150 Hz. filter (B).

two to 14, mostly four to six (average 6.0, N=48). Feindt (1956) cited an observation of Reblin who heard a series of 31 notes. Series show internote-intervals (within series) of 750 msec. (range 570 to 981 msec., Standard Deviation 134.7 msec., N=7). The notes are rather long, averaging 332 msec. (range 166 to 528 msec., Standard Deviation 87.7 msec., N=10), loud, rich in overtones, and have an irregular frequency modulation (figs. 22B, C; 24) that can be very extreme, even reaching a croaking sound (fig. 22C). The pitch is 1.6 kHz. (range 0.8 to 2.3 kHz., Standard Deviation 0.69 kHz., N=10). This great variation (Coefficient of Variability of 44) reflects the variance between series rather than that within series, which is low (Coefficient of Variability 2 to 3.5). This call is given mostly by the male (Ferry, 1962; Conrads, personal commun.; personal observ. of the authors), but Blume (1968) mentioned a form of duetting by members of a pair. Occurrence of this call peaks in the spring (figured in Ferry, 1962). Crown and nape feathers frequently are erected during this call, which is uttered in the treetops, and, most importantly, often is given during display flights (Feindt, 1956). The Kweek may be combined with a closely following Rattle.

Situations: A1, 2b(2), 2c, 4; D2, 3; H
Seasonal occurrence: 1-6

assimilis. Ali and Ripley (1970, p. 215) cited Whistler, who noted a rapidly repeated "toi-whit, toi-whit, toi-whit," that may refer to a Kweek Call or a Wicka Call, or both (see p. 54).

syriacus. The Kweek of the Syrian Woodpecker was described by Franke (1953) as Kjuig, Quuig was used by Winkler (1971a, 1972), and Ruge termed it the Güg-Reihe (Ruge, 1970). Two types of this call, recognizable even to the ear, can be separated. Type I has a U-shaped introductory part, and an inverse, U-shaped main part with several harmonics (fig. 22D). The call mainly is a reaction (of the female, in many cases) to Drumming and the presence of other (male) woodpeckers. Often this call (also Type II) is used when a bird follows another one on the wing. Playback (see Winkler, 1971a) elicited approach, frequent Call Notes, searching flights, Kweeks, Drumming (female), approach to a hole (male), and, once, Rattles and Wickas from an incoming male. A Rattle Call was heard to follow one group of five Kweek notes. Adults near a fledgling also may give this call. The Type II Kweek is a loud ascending, peaked note (figs. 22E, F; 28B) with a duration of 111 msec. (range 83 to 121 msec., Standard Deviation 17.4 msec., N=12). It reaches a pitch of 2.3 kHz. (range 1.8 to 3.0 kHz., Standard Deviation 0.37, N=12). As in the previous type, this Kweek mainly is given in series of about six notes (Franke, 1953), with an internote-interval of 291 msec. (range 177 to 460 msec., Standard Deviation 133.3, N=8). Type II Kweeks show transitions and combinations with Wickas. Often Kweeks are interspersed in Drumming bursts. It remains to be mentioned that Type I Kweeks do not elicit reactions from *P. major* (Winkler, 1971a).

Situations: A2b, 2c, 3; B1, 2, 4; C1c, 2, 5, 5g, 6a, 8b; D1, 3; H Seasonal occurrence: 2-5, 7

major. Sonagrams from recordings made by us, by G. Thielcke, by Blume, Ruge and Tilgner (1975) and by the Swedish Radio (fig. 22G) show calls similar to the Type II Kweek of the Syrian Woodpecker. There is some geographical variation. Calls of birds belonging to the subspecies *numidus* last 67 msec. (range 52 to 76 msec., Standard Deviation 7.5 msec., N=20), and thus they better demonstrate the general structure of this call than do the shorter calls of the European subspecies. The vocalization begins with a short, inverted V-element; the ascending leg almost always is unclear or lacking on a sonagram and only the falling leg shows a marked track. The latter descends until a flat or convex element connects at a frequency of 0.96 kHz. (range 0.86 to 1.03 kHz. in 18 examples) to an inverted V-element which reaches a pitch of 1.9 kHz. (range 1.4 to 2.2 kHz. in 21 examples) and has a duration of 36 msec. (range 30 to 45 msec., Standard Deviation 4.8 msec., N=20). This last element often does not drop back to the pitch of the connect-

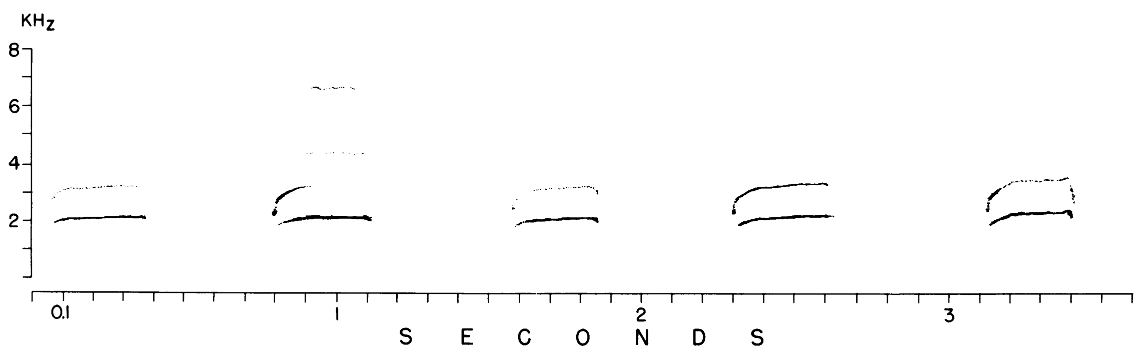


FIG. 24. Narrow-band sonagram of Kweek Call series of *P. medius*; Austria.

ing portion. As previously mentioned, the European subspecies utter shorter calls of the same, more "compressed" structure. Type II Kweeks of the race *pinetorum* have a duration of 40 msec. (range 30 to 49 msec., Standard Deviation 3.88 msec., N=21), and the connection is as low as 0.90 kHz. (range 0.78 to 1.03 in 11 examples), whereas the 22 msec. (range 15 to 30 msec., Standard Deviation 3.9 msec., N=20) last element attains 1.9 kHz. (range 1.5 to 2.3 kHz., Standard Deviation 0.18 kHz., N=15). Because these calls are so short it is reasonable to conclude that the call-series described by various authors (e.g., Pynnönen, 1939; Blume, 1968) for this species also are of this type. This conclusion is further supported by the fact that Kweeks of Type II always are uttered in series. The internote intervals within such series are for these races as follows: *numidus*, 118 msec. (range 98 to 136 msec., Standard Deviation 10.5 msec., N=17); *pinetorum*, 88 msec. (range 68 to 106 msec., Standard Deviation 7.5 msec., N=19); and *major*, 113 msec. (range 105 to 132 msec., Standard Deviation 7.1 msec., N=15). The notes themselves have a duration of 54 msec. All the recordings we have analyzed seem to have occurred during aggressive encounters. These Kweeks sound sharp and Wicka-like (and thus perhaps may better be put there). Kweeks of this type may be combined subsequently with Rattles. On the other hand Kweeks uttered, for instance, by a male flying toward a female sound a bit more hoarse, and sometimes "squeakier." Stechow (1937) mentioned courting calls (considered by Pynnönen, 1939, as a variation of the "call series"). Werner (1961) noted a long series of gigigi calls as a male, apparently after Drumming, approached a female and gave a display-flight. All this likely involves a Kweek which probably can be related to the Type I Kweek of *syriacus* (and of other species). Also such Kweeks may be given alternately with Drumming. One recording from a female calling during a pair-to-pair encounter exhibits four Type I Kweek notes (pitch 2.3 kHz., fig. 25), with a short introductory element (15.5 msec.), an inverted U-element (70.5 msec.), and long internote intervals (229 msec.).

Situations: C 2c (2), 4c, 6b; D3; H
Seasonal occurrence: 1-5, 9

scalaris. Short treated the Kweek, then designated by him as the Queek Call, in detail (Short, 1971a). This call is rendered as a single note, a double note, or in series. Its frequency and duration vary considerably. The general structure of a Kweek note (fig. 22H) has a short inverted U-shaped introductory element, the falling part more pronounced, and the main part that is of about the same form but broader and higher pitched (the rising, concave part is pronounced). Thus this Kweek must be regarded as representing Type I. Harmonics are well marked and tend to be stronger in long Kweeks than in short ones (Short, 1971a). Kweeks are associated with Overt Attacks, Fluttering Displays, Bill Directing postures, and other actions during intraspecific and interspecific encounters.

Situations: Clc, 1d, 4c, 5a, 5c, 5e, 6a, 7a; E5
Seasonal occurrence: (2-5)

nuttallii. Short (1971a) recognized two types of long Kweek Calls, Type A calls (= Type II here) and Type B calls (= Type I here). Type I calls, as in Type II calls given in series, have their main part more regularly inverted U-shaped than the other, which has a pointed peak (fig. 22 I, J, K). The two types show transitions to one another. Short also noted short Kweeks. The situations during which the calls are uttered are as in *scalaris*. Miller and Bock (1972) found that the females react to Drumming with *yipe* notes (possibly Kweeks). Both *nuttallii* and *scalaris* also deliver Kweeks during interspecific encounters with each other, and *nuttallii* with *villosus*, and they seem to react to such calls of the other species (Short, 1971a).

Situations: B1; Clc, 1d, 4c, 5a, 5c, 5e, 6a, 7a, 9b; E5
Seasonal occurrence: (2-5)

scalaris × *nuttallii*. Short (1971a) discussed the variation of hybrid Kweeks in detail. Generally they are similar to the calls of the parental species and show more or less intermediacy (fig. 22 L, M).

pubescens. Kilham (1962, p. 126) described

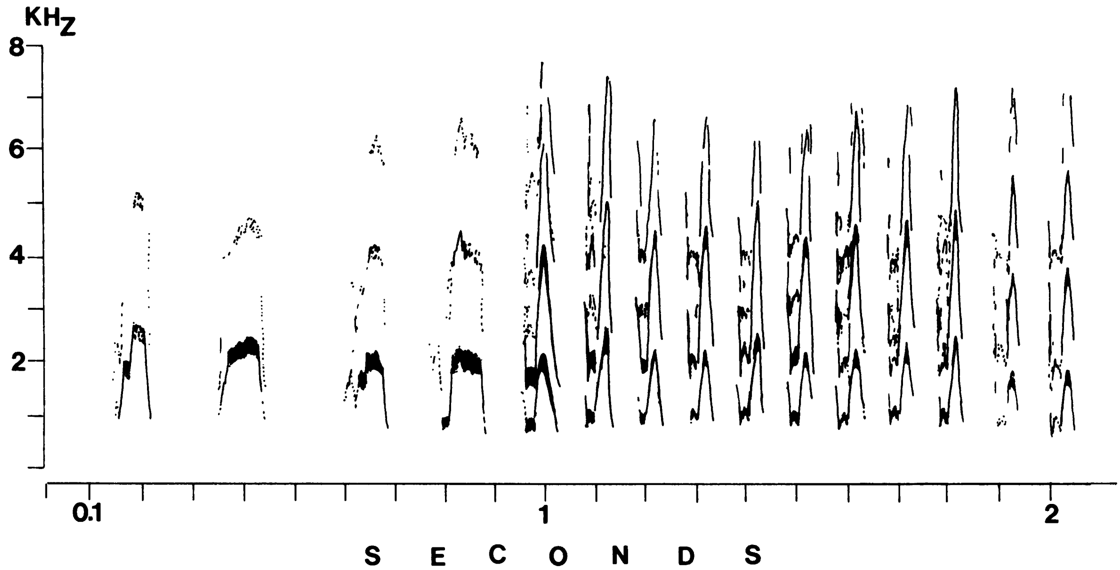


FIG. 25. Wide-band sonagram of Kweek Call of *P. major*, female; Austria. The call combines Type I (left) with Type II (right) features.

calls of the Downy Woodpecker that sound like "*check, check, check, check*" and, at higher intensities, like "queek, queek . . . ." We heard similar calls of Downy Woodpeckers when the birds were involved in Flutter Displays, as did Kilham. The calls in figure 22N were given by a female near her fledged young. The notes are similar in shape to those of the previous species (Type I Kweeks), and also are given in series.

Situations: A2b; B1; C2 (2), 5; H
Seasonal occurrence: (2-5)

borealis. The vociferous Red-cockaded Woodpecker regularly utters single or loosely strung, shrill Kweek notes. These are broad and inverted U-shaped; an introductory part is not developed (fig. 26; fig. 27 A to D). The pitch is 3.3 kHz. (range 2.1 to 4.1 kHz., Standard Deviation 0.47 kHz., N=21) and the duration, 64 msec. (range 45 to 72 msec., Standard Deviation 10.3 msec., N=21). Internote intervals within series are about 682 msec. (range 354 to 921 msec., Standard Deviation 181.5 msec., N=13). Transitions to the Call Note occur (fig. 27D). A situation in which this call was uttered regularly was when an adult had fed a young bird or remained near it after feeding. This call is heard year round (Carter, personal commun.).

Situations: A1, 2b, 2c; C5f; D3, 5; E1; H
Seasonal occurrence: 1-12

stricklandi. The Strickland's Woodpecker Kweek is a loud call, mainly delivered in series; but single notes also occur. On a sonagram the 105 msec. (range 71 to 136 msec., Standard Deviation 17.8 msec., N=23) note has an introductory element shaped like an arrowpoint; the leg approaching the following, main element is significantly stronger than the rising first part. The main part is long, namely 75 msec. (range 45 to 106 msec., Standard Deviation 14.0 msec., N=23), and of an inverted U-shape, the peak mostly lying asymmetrically near the end of the note at a frequency of 2.5 kHz. (range 2.2 to 3.1 kHz, Standard Deviation 0.23 kHz., N=24). Between these two parts an element may occur that looks somewhat blurred, having a more noisy character (fig. 27E, F, G). Kweeks may lead to a Rattle. This was noted from females

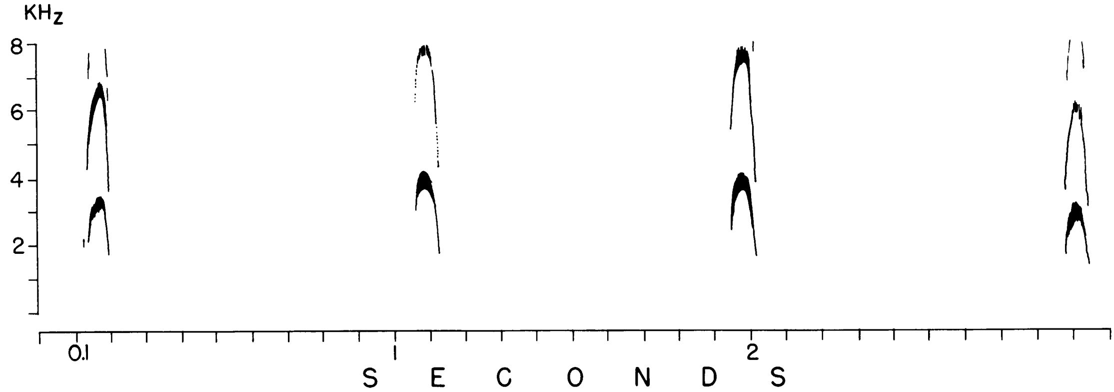


FIG. 26. Wide-band sonagram of Kweek Call (complete series) of *P. borealis*; North Carolina.

just before the nesting period. The call is not always clearly separable from Wickas (see p. 55), when several birds are involved in an interaction. Probably all sorts of transitions occur between these calls. Kweeks are mostly given by females especially in answer to Drumming or Rattles. Some days before incubation the male may utter Kweek Calls near the hole. The kweek also was heard from a woodpecker (sex unknown) that approached the tape recorder from which Drumming was broadcast; the bird was flying above the tree tops coming from a great distance.

Situations: A1, 2b, 2c; B1, 2; C2a; D3, 4, 5
Seasonal occurrence: (3-5)

villosus. As in the previous species the Kweek shows a short introductory part and a loud, long main part of about an inverted U-shape (fig. 27H, I). To our knowledge the call is always rendered in series. Even to the ear considerable variation is detectable. Kilham (1966a, p. 252; 1969, p. 170) noted such calls as sounding like "*queek*, *queek*, *queek*" and "*chewi*, *chewi*, *chewi*" (respectively, Type I and Type II). Combinations with Rattles also were noted. Calls during encounters between perched birds sound different from such during the Flutter Aerial Display, a commonly accompanying display. Kweeks are used interspecifically, as against *nuttallii* (Short, 1971a).

Situations: A2b; B1, 2; C5a, 5b, 5d, 5g, 6a (2), 9a, 9b, 9d Seasonal occurrence: (2-5)

albolarvatus. The loud Kweeks sound rather similar to those of *stricklandi* and *villosus*. As in other species two types seem to be recognizable. Type I (fig. 27J) is a series of notes which resemble the Kweeks of the Strickland's and the Hairy woodpeckers. The key or fundamental tone is weak or even not detectable on the sonagram. The notes are 86 msec. long (range 75 to 91 msec., Standard Deviation 4.4 msec., N=12) and consist of three elements, as do other Kweeks of the same type. The connection between the leading element and the inverted U-shaped main element has a pitch of 0.96 kHz. (range 0.86 to 1.03 kHz., Standard Deviation 0.062 kHz., N=6). The main part is 63 msec. long (range 56 to 68 msec., Standard Deviation 4.1 msec., N=12) and goes up to 1.8 kHz. (range 1.7 to 1.85 kHz., Standard Deviation 0.06 kHz., N=5). Within series the intervals between the notes are 218 msec. (range 203-242 msec. Standard Deviation 11.34, 10 examples). In the Type II Kweek, a very loud call often delivered during encounters, the element between the introductory element and the main element is the longest part of the call, giving it its characteristic shape (fig. 27K). During the course of the series the notes go down to 0.84 kHz. (range 0.69 to 0.98 kHz., Standard Deviation 0.060 kHz., N=22) and up to 2.1 kHz. (range 2.0 to 2.3 kHz., Standard Deviation 0.08 kHz., N=9). The duration of a note is 129 msec. (range 105 to 147 msec., Standard Deviation 13.0 msec., N=14), and time between notes in a series is 202 msec.

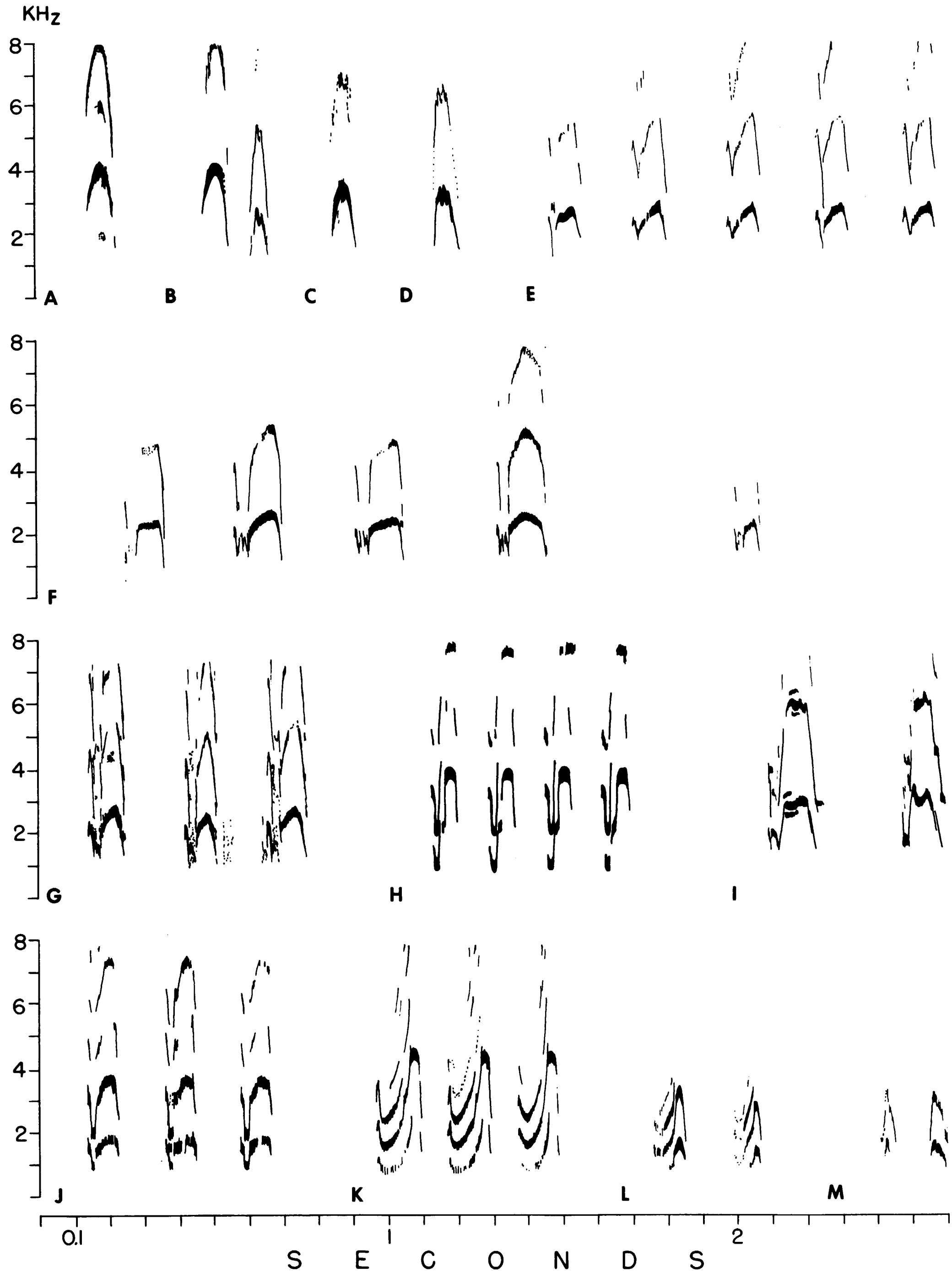


FIG. 27. Sonagrams of Kweek Calls of some pied woodpeckers. A, B, and C. *P. borealis*, various Kweek notes (from irregular series); North Carolina. D. *P. borealis*, Call Note-Kweek Call transition; North Carolina. E. *P. stricklandi*; Arizona. F. *P. stricklandi*, female, male in proximity; Arizona. G. *P. stricklandi*, Kweek Calls during encounter; Arizona. H. *P. villosus*, female approaching male before copulation, part of a series; New York. I. *P. villosus*, Kweek Calls during an encounter with *P. nuttallii*, part (lacking two elements) of a series; Baja California. J, K, L, and M. *P. albolarvatus*, Type I Kweek Call, Type II Kweek Call, then two examples (L, M) of Kweek-Twitter call transitions; California. All are wide-band.

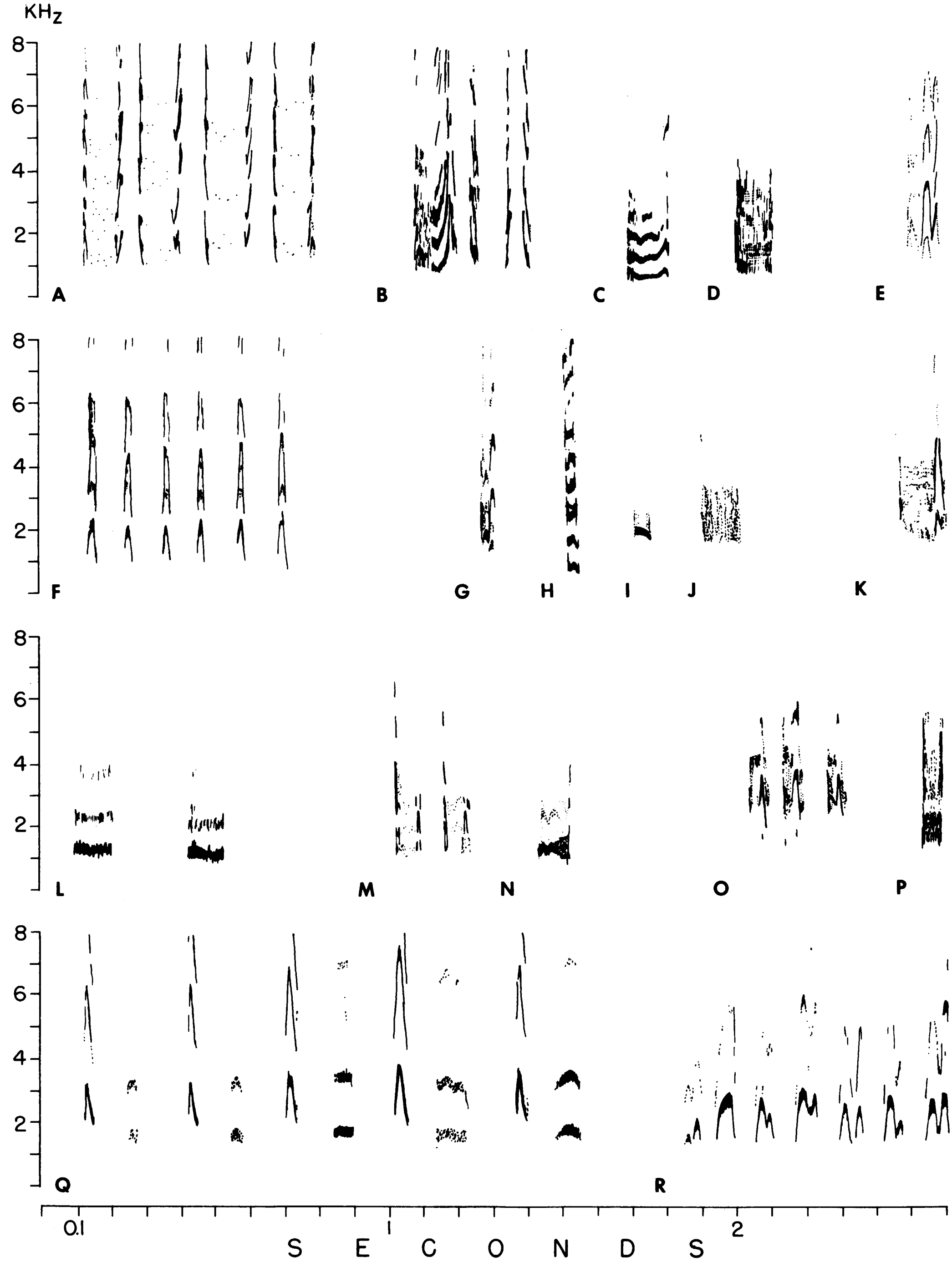


FIG. 28. Sonagrams of Wicka, Twitter, and Wad calls of some pied woodpeckers. A. *P. syriacus*, Wicka Calls; Austria. B. *P. syriacus*, transition from Type II Kweek to Wicka; Greece. C. *P. syriacus*, Wad Call; Austria (during relief at the nesting hole). D. *P. syriacus*, noisy Wad; Greece. E. *P. syriacus*, first note of a series of Kweek Calls; Austria. F. *P. syriacus*, rattling Twitter of fighting juveniles; Austria. G, H, I, and J. *P. major*, Wad Calls, male flying to female before copulation, call at relief at nesting hole, and then two notes (I, J) during copulation; Austria. K. *P. scalaris*, Wad Call; Baja California. L. *P. scalaris*, Wad Call (soft, sounding like "kwee"); Baja California. M. *P. nuttallii*, Wad Calls; Baja California. N. *P. nuttallii*, noisy Wad Call; Baja California. O. *P. pubescens*, male near fledging, Wad Calls; New York. P. *P. pubescens*, juvenile bird flying; New York. Q. *P. borealis*, Wicka Call; North Carolina. R. *P. borealis*, Twitter of adults close together; North Carolina. All are wide-band.

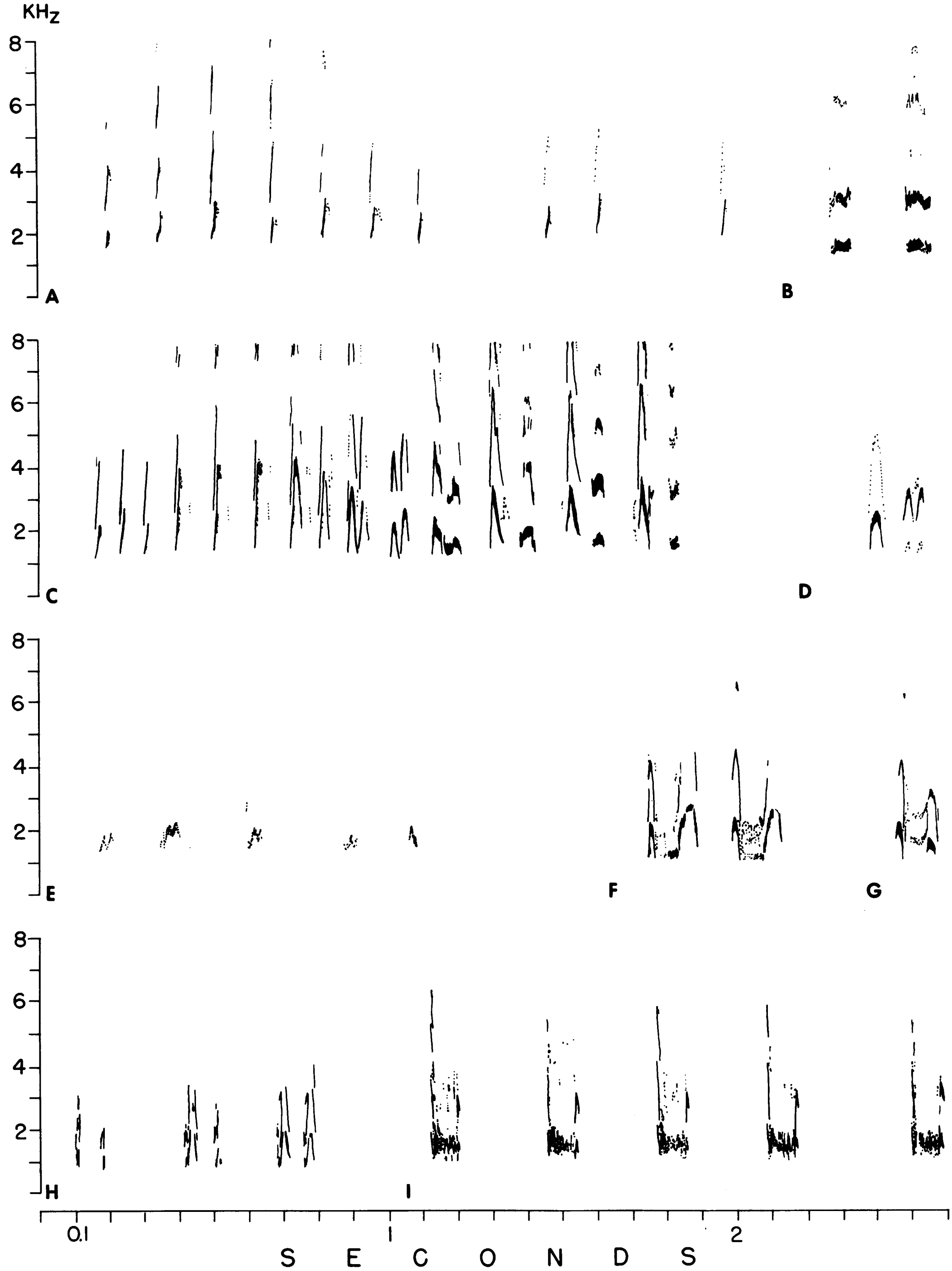


FIG. 29. Sonagrams of Wicka, Twitter, and Wad calls of some pied woodpeckers. A. *P. borealis*, Twitter, adult flying to nesting hole; North Carolina. B. *P. borealis*, adult perched near nesting hole, Wad Call; North Carolina. C. *P. borealis*, adult near other adult, transition from Twitter to Wicka; North Carolina. D. *P. borealis*, peeping-twittering notes of an adult near another adult; North Carolina. E. *P. borealis*, adult before flying towards nest; North Carolina. F, G. *P. stricklandi*, twuit-sounding Wicka during encounter; Arizona. H. *P. stricklandi*, Twitters during Swinging Display; Arizona. I. *P. stricklandi*, male, during display flight near a hole, Wad Calls; Arizona. All are wide-band.

(range 181 to 223 msec., Standard Deviation 13.4 msec., in 12 examples). Between this type and the Twitter transitions often occur (fig. 27L, M). A high correlation exists between the Flutter Aerial Display and the Type II Kweek. Those flights, and so the calls, are performed during brawls between pairs, and by birds approaching a nesting hole in display, coming from a great distance.

Situations: A1, 2b; C5g (2); D1; H
Seasonal occurrence: (4)

tridactylus. Short (1974a) heard a Kweek call sounding like such calls of *villosus* and *scalaris*. This call also was rendered in a series. Lanz (1950) heard hoarse, soft gyff gyff notes in spring. In Voigt (1961) a "song" is described, namely a series of sounds (vocal "u"), the first note lower. Inferring from the Wicka of this species one can predict that this call will prove similar to those of the species just treated.

Situations: C, including 5c
Seasonal occurrence: (4, 5)

Summary. This call is recognized by its squeaking sound, loudness, and long duration. Usually it is given in series. In some species two types are found, of which the second is related to the very similar Wicka Call. The "typical" Kweek is represented by the first type, in which calls consist of mainly three elements: a short introductory element (inverted V-shaped); a noisy, frequency modulated, connective part; and the main part that usually is inverted U-shaped. With respect to their situations and time of occurrence it is noteworthy that these calls (especially Type I) typically are heard during the premating and mating season. Common are combinations with Rattles. If one hears Drumming one is also likely to hear Kweeks either as reaction to this signal or as an accompanying one. Two species have peculiar Kweeks. *Picoides medius* has a very long Kweek, the main element being the only one. This also holds for *borealis*, which seems to use the Kweek regularly throughout the year in a context probably more generalized than in the other species.

WICKA CALL

obsoletus. The notes are given in rapid series. Two-thirds of the notes form a noisy segment. At the end of the note a V-shaped structure follows in the sonagraphic representation. The sound is similar to the corresponding notes of *minor*. The duration of the notes was 92 msec. (range 57 to 131 msec., Standard Deviation 23.0 msec., N=14) with internote intervals of 160 msec. (range 135 to 196 msec., Standard Deviation 18.8 msec., N=12) duration.

Situation: C2 Seasonal occurrence: (10)

minor. During experiments with dummy birds at the nest hole, attacking Lesser Spotted Woodpeckers produce sounds which may be described as "shwicka. . ." and which were designated as Kreck Calls by Blume, Ruge, and Tilgner (1975). However, the use of the term "kreck" seems a very loose one (e.g., compare Rattle and Short Rattle). On the sonagram this call reveals its very noisy character. Within the noise two marked elements are detectable, namely a leading, short, fast-falling one, and also short, trailing element forming the call's typical sound. The calls, about 172 msec. (N=2) in duration, appear in fast series (internote interval 280 msec.).

assimilis. As mentioned in the previous section a description of a call in Ali and Ripley (1970) may refer to a Wicka.

leucotos. The Wicka Calls are similar to the Kweeks but lack or have an indistinct middle part. The falling leg of the first element is the most marked structure of the call; the closing element is lower in amplitude and reduced to a short, peaked element with a distinct rising leg. Wickas occur together with Kweeks and Twitters.

Situation: E Seasonal occurrence: (4)

syriacus. This call was designated as the Zicke Call by Winkler (1972) and as the Kreck Call by Ruge (1970). It is rendered mainly in short series. The major elements are a fast-rising part (with a sound like a whip), and a fast-falling or clicking part (fig. 28A). Although the description "zicke" or "wicka" indicates that one note consists of the rising part, followed by the other, it is the combination of a falling part (relatively low in amplitude) and a rising part (loud) which forms a unit. Barely seen on the sonagram of some calls is a middle part which connects the two more stressed elements. However, this connection can be well marked and is noisy (see fig. 5 in Ruge, 1970). In figure 24B a transition or combination of a Kweek (Type II) and a Wicka is shown. Wickas usually are heard from two birds involved in a combat during an attack. A Syrian Woodpecker even may give this call without seeing an opponent, as happens in experiments where Drumming is played back to a bird.

Situations: B1; C2c, 4c, 5a, 5c
Seasonal occurrence: 1-12

major × *syriacus*. Young, fledged hybrids rendered "chuk-ka" calls when at close distance and showing aggressiveness (Winkler, unpublished data).

borealis. This sounds like "tsi-voo" ("she-u" or "wic-a"; Ligon, 1970, p. 256). The first syllable appears in the sonagram (fig. 28Q) as a sharply peaked, loud note, with distinct harmonics (also found in the second syllable), with the falling leg flatter than the rising one, and also longer and better marked. The second syllable is a low pitched, long, somewhat queeking note. Its length is quite variable, as also is its distance from the first element. The frequency does not change much, and, although generally of variable shape at the end, a hump and a dropping of the pitch are characteristic. The first part of this element usually shows a concave form. On some sonagrams there is a blurred connection between the syllables, rarely represented by a well-marked initial part of the second element. Characteristically, this call appears in clusters of calls that also may contain Twitters and Twitter-Wicka transitions (fig. 29C). Wickas were given by adults that had just fed the young, by another or other adults in the vicinity, and especially when two or three adults were close together and employing visual displays as well (see Ligon, 1970). When a bird would fly to another one this call also was rendered, sounding here more like "wicka" (Winkler, personal observ.). In one instance as an adult gave a regular series of wickas, another called and maintained the same rhythm.

Situations: A2c; B1 (2); C4; D6; H
Seasonal occurrence: (5, 7)

stricklandi. A short, inverted V-like element followed by a low part with quite constant frequency, and a final, inverted U-shaped element form this call which sounds like "twuit" (fig. 29F, G). As in the other species the call typically occurs in series. Transitions to the Twitter and Kweek are frequent. Wickas usually are given during encounters, with the opponents at close distance.

Situations: C4, 5 Seasonal occurrence: (3, 4)

villosus. During male to male conflicts "wicka-a-wicka-a-wick" calls are given which resemble those of *Colaptes auratus* (Kilham, 1966a, 1969). Similarly, Lawrence (1967, p. 22) described "aggressive-social" notes that clearly represent this call.

tridactylus. The Wicka of this species was designated by Ruge (1975) as Keckern (this name has a broader meaning for that author; see also Twitter, Wad). It is very similar to the corresponding calls of *stricklandi* (and to some extent of *borealis*). Wickas appear in series. Calls on the record of Blume, Ruge and Tilgner (1975) have a duration of 74 msec. (range 64 to 83 msec., Standard Deviation 4.9 msec., Coefficient of Variability 6.6, N=11), and an internote interval of 101 msec. (range 98 to 106 msec., Standard Deviation 2.9 msec., Coefficient of Variability 2.9, N=11). Other sonagrams by Ruge also show the presence of Wicka-Twitter transitions. The calls are typical of encounters and also are accompanied by Head Swinging Displays (Ruge, 1968).

arcticus. A low Wicka Call was heard by Short but was not recorded.

Summary. This call type has features which are very similar to those of the Type II Kweek Call. The distinguishing character is the connection between the starting and the closing element of a note. This connection is weak or almost nonexistent in the Wicka. However, the border between these calls seems arbitrary, and using it simply serves to break up an apparent continuum. Wickas seem exclusively to accompany encounters, and mark attacks. During these situations are found not only Wickas, but also Twitters, and Kweeks and all sorts of transitions between them (and combinations with them).

TWITTER CALL

canicapillus. Poliwanowa, Schibnew and Poliwanow (1974) noted low Twitters when two adults feeding young came close to each other.

leucotos. The Twitters are constructed like the Wickas but are shorter in duration and the ending element is the more marked one. Series of Twitters appear to start with a complete note and to continue with notes which consist solely of the terminal element. They occur together with Kweeks and Wickas.

Situation: E Seasonal occurrence: (4)

syriacus. Short (1973, p. 280) reported a Rattle-like call of *syriacus* which has a rate of delivery of eight to 10 notes per second. We regard it here as a series of Twitter notes (fig. 28F), which bear resemblance to some introductory notes of the Kweek (fig. 22F). They were recorded when two juvenile birds were fighting over a roosting hole.

Situation: C5 Seasonal occurrence: 7

nuttallii. The fast irregular Tewk Calls in Short (1971a, fig. 24E) resemble the Twitters of the other species and here are treated as such.

borealis. Twittering notes are uttered by this species very frequently, mainly in bursts of two to six notes or in groups of such bursts. Two types can be recognized: "tyet"-sounding notes that are fast-rising sonagraphically (fig. 29A); and more peeping notes that are double peaked (fig. 28R). The notes of the first type tend to have a little appendage. The note rises to 2.5 kHz. (range 1.6 to 3.2 kHz., Standard Deviation 0.47 kHz., Coefficient of Variability 18.5, N=53), and harmonics are marked. The note has a duration of 18 msec. (range 11 to 30 msec., Standard Deviation 4.0 msec., Coefficient of Variability 21.6, N=48). Notes low in amplitude are also low in frequency and of short duration. Some notes attain a higher frequency (3.7 to 4.3 kHz., mean 4.0, N=8). The small appendage can show a resemblance to an arrowpoint-like peak. Rarely a falling element completes the note, which then has a duration between 30 and 38 msec. (N=3). Similar notes are found when transitions to the Wicka are present (fig. 29C). Internote intervals are 154 msec. (range 120 to 272 msec., Standard Deviation 29.9 msec., Coefficient of Variability 19.4, N=42), corresponding to a rate of delivery of 6.5 notes per second. The intervals are shorter before transitions to the Wicka, namely 78 msec. (67 to 91 msec., N=3), thus covering a range of rate of delivery from 11 to 14.7 notes per second. Besides the usual situation, a parent flying to the hole to feed young, and also a single bird that had been excavating a hole gave this call when flying away from the observer. Birds approaching a fledgling also uttered Twitters of this type. Notes of the second type consist of two more or less equivalent inverted V- to U-shaped elements. The quite variable pitch of the peaks ranges from 1.5 to 3.0 kHz. (N=18). The notes have a duration of 67 msec. (60 to 91, N=9) and, in series, internote intervals from 113 to 128 msec. (N=5), which corresponds to a rate of delivery from 7.8 to 8.8 notes per second. The notes may occur together with Kweeks and transitions to the latter also may be found (fig. 29D).

Situations: A2b, 2c; B1 (2); C6, 8b (Type II); D 2, 4; H Seasonal occurrence: (5, 7)

stricklandi. The Twitter Call of this species is like that of *syriacus* and to some extent like that of *borealis* (Type II) (fig. 29 H; fig. 30A, F). The notes occur in slow series, in the rhythm of the accompanying Head Swinging movements, or almost in the fashion of a speeded up Rattle Call. The general structure of the notes resembles that of the Kweek. A blurred, noiselike introductory element leads to a rounded peak. Usually well marked, the middle part of the peak sometimes is hardly recognizable on a sonagram, or only its harmonics may show clearly. Occasionally the note may be reduced to the introductory element. Especially

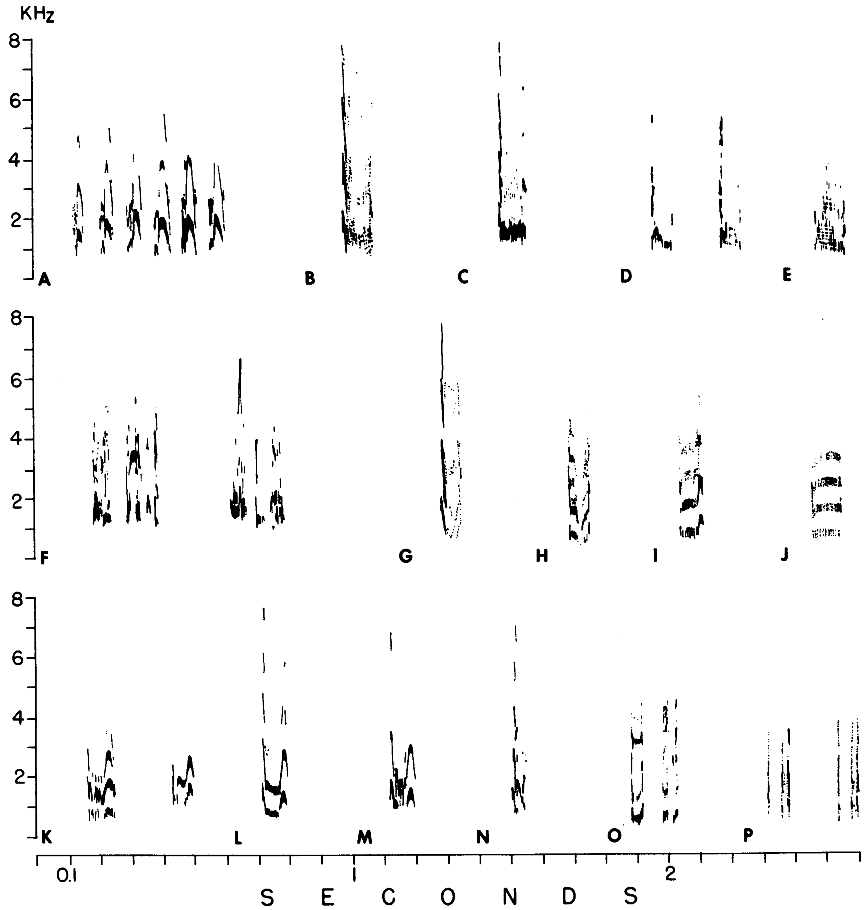


FIG. 30. Sonagrams of Wicka, Twitter, and Wad calls of some pied woodpeckers. A. *P. stricklandi*, rattling Twitter during encounter; Arizona. B, C, and D. *P. stricklandi*, Wad Calls of a male relieving at breeding hole, of a female leaving male at an initial hole, and of male flying to female; Arizona. E. *P. stricklandi*, noisy Wad; Arizona. F. *P. stricklandi*, Wad-Twitter combinations or transitions during relief at nest; Arizona. G. *P. villosus*, Wad Call, at rest before copulation; New York. H, I, and J. *P. villosus*, Wad Calls during copulation; New York. K, L, M, and N. *P. albolarvatus*, Wad Calls, during an encounter, by a male demonstratively flying to hole, by a male at hole, and by male leaving female; California. O. *P. tridactylus*, Wad Calls, adult near fledgling; Austria. P. *P. arcticus*, Wad Calls, male and female together; New York. All are wide-band.

during Head Swinging movements, the notes sometimes show a tendency toward pairing. The pitch of the main part averages 1.85 kHz. (range 1.4 to 2.2 kHz., Standard Deviation 0.22 kHz., Coefficient of Variability 11.6, N=74), and complete notes have a duration from 19 to 91 msec. (mean 42 msec., Standard Deviation 13.9 msec., Coefficient of Variability 32.9, N=80). The intervals between notes in series are 123 msec. (range 60 to 377 msec., Standard Deviation 88.5 msec., Coefficient of Variability 71.9, N=83). This high variation reflects that between series rather than within them. Series with short notes also have short intervals, and vice versa. Most intervals in such short-note series are about 83 msec. long.

Twitters may show transitions to and combinations with Wads (see fig. 30F). They also occur together with Wickas.

Situations: C5 (2), 8b

Seasonal occurrence: (3-5)

villosus. Kilham (1960, 1966a, 1969) mentioned notes given by a bird when close to another one, especially during encounters when Head Swinging Displays also are present. Similar descriptions were given by Lawrence (1967). Both match our own field notes.

Situations: C5 (2), 8b

Seasonal occurrence: (2)

albolarvatus. Figure 27L and M and figure 30K depict several forms of the Twitter. Its general structure is that described for *stricklandi*.

Situations: C5 (2)

Seasonal occurrence: (4)

tridactylus. A male involved in Swinging movements near a female gave chattering, twittering calls, according to Scherzinger (1972). Sonagrams published by Ruge (1975) show calls that much resemble the Twitters of the previous species. That author included them in his "Keckern" category.

Situations: C2a (2)

Seasonal occurrence: Unknown

Summary. In many cases Twitters resemble miniature Kweeks and Wickas. These also are the calls to which Twitter Calls form transitions. Twitters basically are double-peaked notes. Between the peaks a connection is present that can show more or less frequency modulation. The notes may be reduced essentially to one peak or even to its rising leg. They usually are strung into series or are paired, especially when Head Swinging movements accompany the vocalizations, as very commonly is the case.

WAD CALL

minor. At nest relief, Lesser Spotted Woodpeckers utter calls that resemble Wad Calls of *major*, but are softer (Blume, Ruge and Tilgner, 1975). Wads also are given during copulation, with a duration of about 50 msec. A falling leg, a noisy middle part, and a rising leg are visible faintly on the analyzable sonagrams (two notes).

Situations: C9e; D7

Seasonal occurrence: (4)

leucotos. Tet, tet calls and similar vocalizations were mentioned by Schubert (1969).

medius. Feindt (1956, p. 105) gave a good account of the various "intimate single-calls" which represent Wads of our terminology. He named them "Ablöseruf" (relieving-call), "Begattungsruf" (copulation call, see also Steinfatt, 1940) and "Variante des Balzrufes" (variant of the courting-call = Kweek). Smacking Wad Calls (table 8) are given during "hopping-flights" of the male dismounting and flying off from the female. Szemere (1929) heard a presumed Wad Call from a Middle Spotted Woodpecker during a Wing Spreading Display. The call sounds very like the same call of *major*. This is confirmed with sonagrams made from recordings published by Blume, Ruge and Tilgner (1975). The notes have the same structure as in the Great Spotted Woodpecker (table 8). However, these recordings also contain Wads of a second type, the noisy Wad Call (table 8), distinguished by its long duration and noise, which seems to form most of the note (however, some frequency bands do seem to be well-marked).

Situations: C2b, 9; D7

Seasonal occurrence: (1, 5)

syriacus. The typical call uttered by relieving birds at the nest is shown in figure 28C. A similar call is given when two usually mated birds are near each other (fig. 28D). The call seems to consist of a leading, clicking element, the characteristic lower, main element, and a closing, clicking element. The pitch of the main element is indicated in table 8.

Situations: C2, 8b; D7

Seasonal occurrence: 5, 6, 7

major. The call was named Wäd or Rä by Blume (1968). Wad Calls exhibit some variation of the same basic call (table 8, fig. 28G to J). The typical call starts with a short clicking element, continues with a variable main part,

TABLE 8
Wad Calls of Pied Woodpeckers[a]

Species	Pitch					Duration					Shortest Interval (N)[b]
	Mean	Range	S.D.	C.V.	N	Mean	Range	S.D.	C.V.	N	
medius G	0.83	0.65-0.98	.010	1.7	23	45.0	32.0-49.0	0.81	1.8	29	—
medius K2	0.92	0.69-1.10	.049	5.3	8	105.3	40.0-205.0	21.21	20.0	8	—
syriacus	0.59	0.53-0.66	.063	10.7	3	111.1	101.9-128.3	8.67	7.8	9	475.5 (3)
major W	1.85	1.81-1.89	.041	2.2	5	33.4	30.2-41.5	5.52	16.5	7	535.8 (5)
major K	1.07	0.98-1.15	.058	5.4	5	170.6	166.0-173.6	4.14	2.4	5	166.0 (4)
major R	1.75	1.64-1.85	.069	4.0	8	38.2	33.9-45.3	4.70	12.3	8	143.4 (6)
major V	0.70	0.66-0.78	.050	7.1	7	28.6	26.4-34.0	2.97	10.4	7	339.6 (4)
scalaris S	—	—	—	—	—	126.8	120.8-135.8	8.27	6.5	5	256.6 (4)
scalaris E	1.18	1.11-1.23	.048	4.1	11	105.0	98.1-128.3	9.22	8.8	11	301.9 (7)
nuttallii	1.19	1.07-1.31	.070	5.9	10	79.6	67.9-86.8	6.33	8.0	12	135.8 (9)
borealis	1.39	—	—	—	2	—	60.4-67.9	—	—	2	218.9 (1)
stricklandi	1.27	0.98-1.48	.166	13.1	23	77.2	60.4-105.7	14.15	18.3	22	211.3 (10)
villosus G	0.69	0.57-0.82	.059	8.6	37	65.5	52.8-90.6	6.45	9.8	36	173.6 (33)
villosus D	0.65	0.53-0.74	.057	8.8	15	63.9	56.6-67.9	4.01	6.3	16	150.9 (6)
albolarvatus	0.78	0.65-1.07	.122	15.6	9	80.3	71.7-98.1	7.01	8.7	14	264.2 (11)
tridactylus	0.67	0.62-0.74	.067	9.4	3	28.3	15.1-49.1	16.45	58.1	4	37.7 (2)
arcticus	—	—	—	—	—	65.8	60.4-71.7	4.28	6.5	7	188.7 (6)

[a]*Symbols*: S.D., Standard Deviation; C.V., Coefficient of Variability; N, sample size; W, before copulation; K, noiselike, during copulation; K2, noisy type; R, mournful; V, relief at nest hole; S, smacking of tewk type; E, kwah type; G, smacking; D, mournful, during copulation. Pitch is in kilohertz, duration, and shortest interval in milliseconds.

[b]For those Wad Calls given in series (the number of such is indicated by N in parentheses), the shortest interval between notes is given to suggest the rate of utterance.

and ends up with a further clicking element. Of the first clicking element, all that usually can be seen on a sonagram is a fast-falling leg. The second clicking element is more accented than the first, the more conspicuous rising leg ending in a little peak. This clicking element gives the call its typical smacking sound (fig. 28G, H), as described by Blume (1968). The longer main part, with negligible clicking elements, characterizes the plaintive Wads given during copulation by one of the sexes—the opposite sex utters long, noisy calls (fig. 28I, J). Long plaintive calls (pitch 0.39 kHz, duration 97 msec., N=11) also were given by a male at the hole (excavation prior to breeding) when a female passed by in flight. There are combinations and transitions to the Mutter (see p. 42).

Situations: C2b, 7b, 8b, 9c, 9e; D7; H

Seasonal occurrence: 2, 4-7

scalaris. The low Tewk Call, the Wicka, and the Kwah Call of Short (1971a, p. 89) represent the Wad of this account (fig. 30K, L). The Tewks correspond to the smacking Wad of the previous species, and the Kwahs to the plaintive and noisy Wads of copulating *major*. In fact, the physical structure and situation of these notes are quite similar. The structure of the call is very much the same as in the other species (e.g., *major*). In the Kwah type of the Wad the main part is more pronounced and forms a flat U (the pitch was measured at the lowest point; see table 8 and fig. 28L). In the Tewk and Wicka type the central part hardly can be seen on the sonagram, and thus the clicking-smacking elements are significant (table 8, fig. 28K). The second clicking element is almost like a Call Note and has a duration of about 23 msec. (range 22 to 26 msec., Standard Deviation 1.7 msec., Coefficient of Variability 7.2, N=5). The call is used both intra- and inter-specifically (Short, 1971a), and may occur interspersed with Kweeks.

Situations: C5a, 5b, 5e, 7, 8b

Seasonal occurrence: (2-5)

nuttallii. Because of their physical resemblance to Wad Calls the Wicka Calls of Short (1971a) are seen here as Wad Calls. On the other hand it seems more reasonable, before more information is available, to categorize faint Tewks (Short, 1971a) under the Twitter (see p. 56). Two extremes of Wads are found: a more smacking one, and one with a more pronounced central part (fig. 28M, N). Because pitch and length are identical these types were lumped in table 8. The Wad is probably identical with the sucking notes reported by Miller and Bock (1972).

Situations: C5a, 5b, 5e, 7, 8b
Seasonal occurrence: (2-5)

pubescens. As shown in figure 28 O, Downy Woodpeckers have a Wad call similar in structure to calls of related species. This very soft call is presumably the one called Chirp or Chirr by Kilham (1962, 1974a) and "*tut-tit-wi-tut-it*" by Lawrence (1967, p. 23). The harsher Chrrr noted by Kilham (1962), used in encounters (to the senior author this call sounded like someone grating over a comb, but very softly), as the other notes, cannot be categorized until studied sonagraphically (see also the "*khrae-khrae*" call in Lawrence, 1967, p. 23).The call in figure 28 O was given by a male approaching a fledgling to feed it.

Situations: C5, 8b; H
Seasonal occurrence: fall, spring (Kilham, 1962)

borealis. In figure 29B a call is shown which resembles the Kwah-type Wad of *scalaris*. The sole recording does not yield sufficient information for discussing variation and the circumstances of delivery (table 8).

Situation: D6 Seasonal occurrence: (7)

stricklandi. The variable Wad (fig. 29 I, fig. 30B to F: table 8) shows the same general structure as in the other species. Its sound can be described as "tyet" or, in some cases when noisy, as "tshd" (see fig. 30E). It starts with a clicking-smacking element, fast-falling, then the main part, which is more or less noisy (irregularly frequency modulated), with harmonics barely present, and it ends with a sharp (needle-shaped on the sonagram) element. The notes occur frequently in evenly spaced series. Most calls are given when the calling bird is involved in some activity belonging to pair formation and pair maintenance. A noteworthy circumstance is the occurrence of this call as vocal accompaniment of the gliding Display-Flight which is employed in nest-demonstrating ceremonies. Wads may occur in close combination with, and in transitions to, Twitter Calls. Wad Calls also occur in contexts when Drumming and Tapping are common.

Situations: C2b, 2c, 7b; D2 (2), 3, 5, 7
Seasonal occurrence: (3-5)

villosus. Wads of this species are known as "jeek," "teuk," "tewk," intimate notes, "eejew-jew-jew," etc. (Kilham, 1960, 1966a, p. 252, 1969, p. 170; Lawrence, 1967, p. 22; Short, 1971a). On the sonagram (fig. 30G to J), two types again are recognizable. The first or smacking type is best told by the pronounced falling leg of the first clicking element; the main part and second clicking element are hardly detectable (fig. 30G, table 8). Another Wad Call with a significant central part occurs, especially during copulation (perhaps mostly by the female, see Lawrence, 1967). Both types are given in more or less regular series (e.g., for one series of eight, the intervals had a Coefficient of Variability of 11.2). They may occur in contexts when Tapping is present, and even as reaction to this signal (Kilham, 1966a). Both seemingly are important in nest-demonstrating behavior. Noteworthy also is the combination of Wad Calls with aerial displays.

Situations: C2g, 2c, 7b, 9b, 9e; D2 (2), 3, 7
Seasonal occurrence: (2-6)

albolarvatus. The Wad Calls are of similar structure to those of the previous species. The dropping leg of the first element is more emphasized than the rising one; the central part and the relatively long (26 msec., N=12) second clicking element are well marked (fig. 30 L to N). The sound quality may be described as "tyet." The calls appear in series and are frequent in nest-demonstrating behavior. They may be heard in combination with Kweeks during aerial displays (for instance, in a female flying from one tree to another with other individuals nearby), and in loose connection with Tapping.

Situations: C7b; D2, 3; H
Seasonal occurrence: (4)

tridactylus. Some of the calls described by Scherzinger (1972) very likely refer to Wad Calls. An adult near a fledgling bird uttered a call with about the structure of a Wad Call (see *pubescens*, p. 50). Ruge (1975) believed that intimate calls are absent in this species. However Wadlike calls were depicted by him, but as "Keckern" (see p. 58).

arcticus. In the repertoire of this species is a call consisting of three clicking elements. In their characteristic sequence they are very like the Wad Calls of other species; only the central part is missing (fig. 30P; table 8). They belong to the Yeh Call complex of Short (1974a). The elements, vertical on the sonagram, go as low as 0.69 kHz. (range 0.57 to 0.74 kHz., Standard Deviation 0.067 kHz., Coefficient of Variability 9.8, N=5). The interval between the second and the third (last) element averages 23 msec. (range 18 to 30 msec., Standard Deviation 3 msec., Coefficient of Variability 13.6, N=8). Thus the ratio of note-duration to interval of the last elements is about 0.35 (0.32 for *albolarvatus*, see p. 60). This together with the low pitch justifies putting this call in the Wad category (this was suggested by Short, 1974a). The notes are given in series (for instance one series of eight had internote intervals of 281 msec. with a Coefficient of Variability of 30.7).

Situations: C4a, 5a, 5b, 5e, 7a, 8b; D7
Seasonal occurrence: (4-6)

Summary. This call is low in pitch and amplitude. Usually it has a smacking sound, corresponding to a short leading, and a longer closing element. Characteristically (e.g., in comparison to some Twitters) the falling leg of the first clicking element is the most emphasized portion. Between these elements a vocal component (more or less frequency modulated up to the level of a noise) can be detected. This component is the most significant one in some types of the Wad Call, especially those given during copulation. The recurrent situation is the close meeting of the (prospective or real) members of a pair.

SOFT NOTES

minor. Nestling Lesser Spotted Woodpeckers uttered soft musical notes after they had been removed from their nest and put into an artificial nest. Even in the fledgling period such notes were heard occasionally.

Situation: F5 Seasonal occurrence: (6)

syriacus. When six-day-old birds were brought back to normal temperature from overheating or overcooling, as well as following struggles among the siblings, Soft Notes were emitted (fig. 31F). This call was not detected in well-feathered nestlings.

Situation: F5 Seasonal occurrence: (5)

major. Nestlings in the field and in captivity were heard to give this call, but no tape recordings were made (Winkler, personal observ.).

Situation: F Seasonal occurrence: (5)

pubescens. Kilham (1962) noticed that nestlings in captivity returning from feeding to their dark cabinet and settling down gave a variety of soft musical notes.

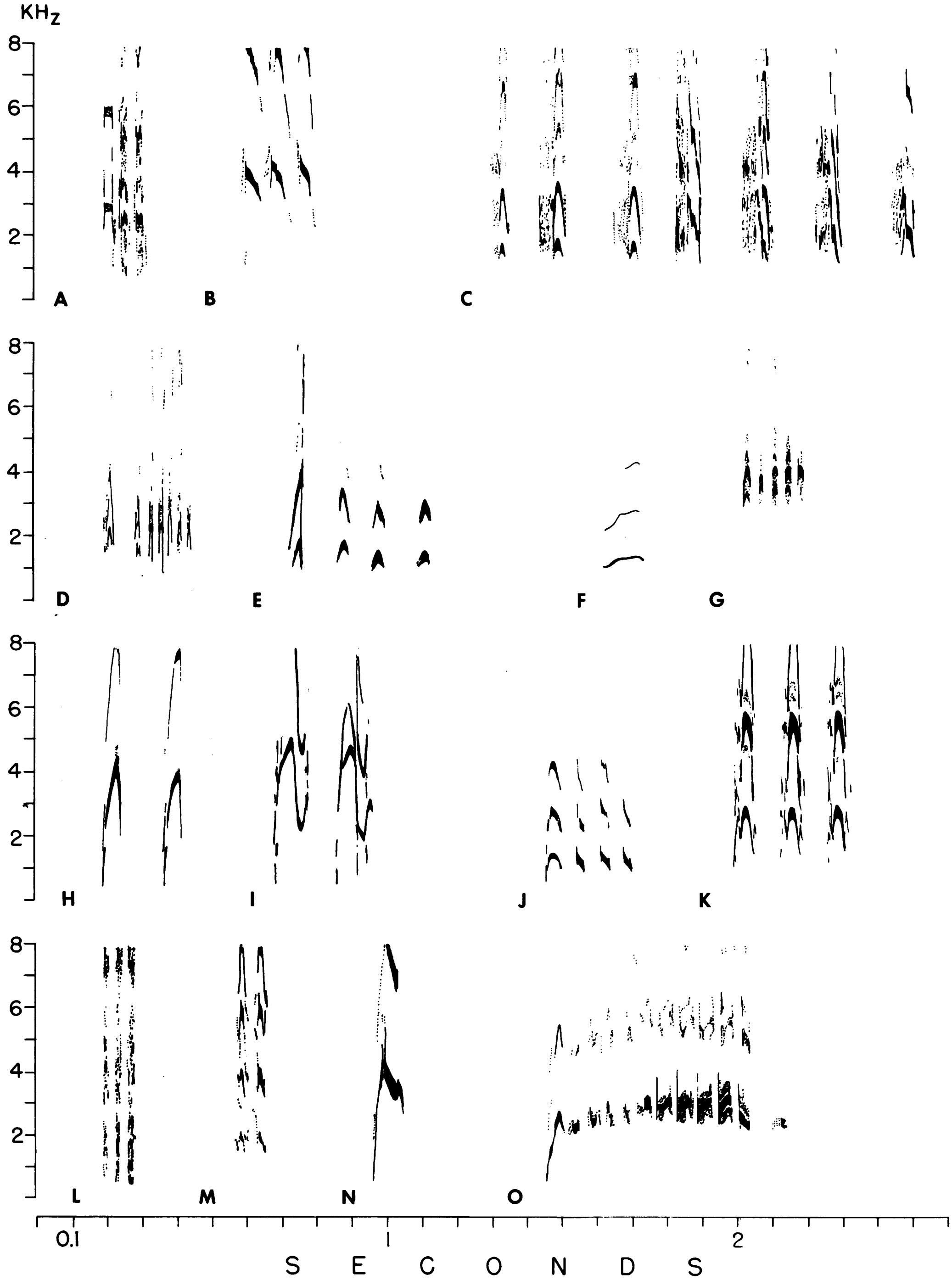
Situation: F5 Seasonal occurrence: (5)

borealis. In May 1977, we recorded Soft Notes similar to those of *pubescens* from two nestling birds about six days of age as they were being banded in Mississippi.

Summary. Clearly musical, moderately long notes of nestling pied woodpeckers were heard only rarely. The situation in which they occur (F5, see table 1) seems quite typical, and should be easily induced experimentally. Because of its weakness this vocalization cannot be heard at a distance; recording requires very close proximity, or, even better, removing the birds from the nest. Without doubt this call also will be found in the other species of the genus.

DISTRESS TRILL

This is a vocalization of nestling woodpeckers. It was heard from *syriacus* (fig. 31G)


KHz
8
6
4
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A
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1
2
S E C O N D S

and *leucotos* (fig. 31D). The musical Distress Trill of *syriacus* was given by a six-day-old nestling disturbed by its siblings, or by the human experimenter (Winkler, personal observ.). A similar trill was recorded as a nestling White-backed Woodpecker sat in the nest entrance, then suddenly rushed back into the hole, probably attacked by its sibling.

CHIRP CALL

canicapillus. The nestlings call only when the parents are close to, or at the hole. As a rule the nestlings are quiet when their parents are absent, rarely calling very softly (Poliwanowa, Schibnew and Poliwanow, 1974).

Situations: F2, 3 Seasonal occurrence: (5-6)

minor. Nestlings utter rattling calls which sound rather harsh in their early stages, and become more musical as the birds become older. These early calls appear on the sonagram, roughly as short, vertical columns (about 25 msec. in duration). The columns cover a wide frequency range mostly with the quality of a noise; only a central part shows the structure of the sound, starting and ending with clicking elements. Later in nestling life the notes lengthen to about 60 msec. duration. It is the central part of the note that then becomes more pronounced, thus giving the note a more musical sound. Notes of long duration may show some frequency modulation. There occur transitions to the Loud Chirp. According to Poulsen (1949), Chirps are elicited mainly by the sound of adults' toes and claws scratching on the bark rather than by the birds darkening the entrance of the nest hole.

Situation: F1 Seasonal occurrence: 5-6

darjellensis. Chirps seem to be very low, and rare, judging from the observations of Diesselhorst (1968).

leucotos. The Chirp of rather old nestlings (fig. 31C) consists of notes that commence with a variable noisy or even a peaked element. This is followed by an inverted V-shaped, or in other cases U-shaped, part that has regular harmonics and is especially significant in combinations with Call Notes (fig. 31E). Commonly the call shifts to the Loud Chirp Call.

Situation: F1 Seasonal occurrence: (6)

medius. Chirp notes of 17-day-old nestlings are long (86 msec.) and consist of three parts. The first is a noiselike element, but also containing formed structures with harmonics. The second, the longest and the most pronounced element, is peaked. The note terminates in a short, noisy element.

Situation: F1 Seasonal occurrence: 5-6

himalayensis. The calls of the nestlings heard in the background of a recording by Thielcke sound very similar to those of other comparably sized members of the genus.

syriacus. The Chirps are of low amplitude, and are barely heard from a distance. Most of the time when the parents are absent from the hole the young are silent. The most effective way to elicit Chirps proved to be by artificially darkening the entry into the nest.

Situation: F1 Seasonal occurrence: 4-6

major. Contrary to the situation in *syriacus*, nestlings of *major* call unremittingly in the

FIG. 31. Sonagrams of nesting vocalizations of pied woodpeckers. A. *P. minor*, harsh Loud Chirp, three- to seven-day-old nestlings; Germany. B. *P. minor*, musical Loud Chirp, 11- to 13-day-old nestlings; Germany. C. *P. leucotos*, Chirp and Loud Chirp (after third note) during a feeding scene, nestling one day before fledging; Austria. D. *P. leucotos*, Distress Trill, nestling one day before fledging; Austria. E. *P. leucotos*, Call Note-Chirp combination, nestling one day before fledging; Austria. F. *P. syriacus*, Soft Note, nestling about 10 days old; Austria. G. *P. syriacus*, Distress Trill, nestling about 10 days old; Austria. H, I. *P. syriacus*, Loud Chirp ("begging"), nestling about two weeks old; Austria. J. *P. major*, Chirp, nestling about three weeks old; Austria. K. *P. major*, Loud Chirp, nestling about two weeks old; Austria. L. *P. major* × *syriacus*, Loud Chirp, nestling 10 days old; Austria. M. *P. major* × *syriacus*, Loud Chirp, nestling 10 days old; Austria. N. *P. major* × *syriacus*, Loud Chirp, nestling 15 days old; Austria. O. *P. major* × *syriacus*, Chirp, nestling 15 days old; Austria. All are wide-band.

hole. As the young grow the call becomes louder, and thus nests can be detected at a great distance. Figure 31J gives an idea of the structure of the notes, which changes with age. The notes sound harsher when the nestlings are only a few days old. Chirps become more intense when one scratches the bark (Poulsen, 1949), or more so if one darkens the entrance to the nest (Winkler, personal observ.).

Situation: F1 Seasonal occurrence: 4-6

major × *syriacus*. The hybrids behave rather like nestlings of *major*, calling even when the parents are not present. Chirps are harsh and of a structure similar to that of the species mentioned above (fig. 31 0).

Situation: F1 Seasonal occurrence: 5-6

pubescens. Chirps, especially of nestlings only a few days old, are harsh and do not differ to our ears from Chirps of other pied woodpeckers.

Situations: F1, 2 Seasonal occurrence: (6)

borealis. Figure 32B shows the Chirp Call of an advanced nestling. The structure resembles that of the other species. Again the first part of the note is quite long, consisting mainly of two clicking elements, the second of which leads to the arrow-shaped main part of the call. Besides transitions to the Loud Chirp Call, combinations with Call Notes occur (see fig. 32D).

Situation: F1 Seasonal occurrence: 5-7

stricklandi. The Chirps of nestlings a few days old are harsh and practically undistinguishable from the Chirps of other pied woodpeckers.

Situation: F1 Seasonal occurrence: (5)

villosus. The notes are short and, as in the other species, three parts are recognizable (fig. 32G).

Situations: F1, 2 Seasonal occurrence: 3-5

tridactylus. At least in late nestling stages the Chirps consist mainly of the inverted V-shaped central part. However, there are indications of a clicking first element (fig. 32 I) that may be more prominent in younger birds. The sound is of a quality similar to those of other congeners.

Situation: F1 Seasonal occurrence: (6)

arcticus. The notes are inverted V-shaped, and short, commencing with a clicking element (fig. 32K). The call is uttered almost continuously, perhaps more so than in any other pied woodpecker (Short, 1974a).

Situation: F1 Seasonal occurrence: 5, 6

Summary. All nestlings give series of notes which range from a very soft chatter to a fairly loud, musical "rattle." To the human ear these sound similar, and are characteristic for the genus. The notes generally consist of three parts, which vary ontogenetically in their form. Some species are very quiet when no parents are in the immediate vicinity of the nest. Others seem never to cease their calling activity. If the presence of one of the parents is detected by a nestling, all the nestlings then give the call, which is their most common vocalization. The Chirp Call shows similarities to the Loud Chirp into which it often grades. Nestlings near fledging frequently utter Call Note-Chirp combinations.

LOUD CHIRP CALL

canicapillus. Descriptions (Poliwanowa, Schibnew and Poliwanow, 1974) are insufficiently detailed to allow us to define and describe a Loud Chirp Call clearly, as separated from the Chirp Call.

minor. Loud Chirps (fig. 31A, B) have a structure similar to the Chirp Call and show a similar ontogeny. One difference between these two call-types is the loudness of the Loud Chirp. The structural element that carries the distinct characters of the call is its central part. The call also tends to lengthen and to show some irregular frequency modulatoon. The call is uttered by a young bird being fed; the other nestlings mainly keep calling with Chirp Calls. The Chirp-Loud Chirp transition is fast and almost discrete.

Situation: F3 Seasonal occurrence: 5, 6

leucotos. The structural change that separates the Loud Chirp Call from the Chirp Call is demonstrated in figure 31C. Most changes

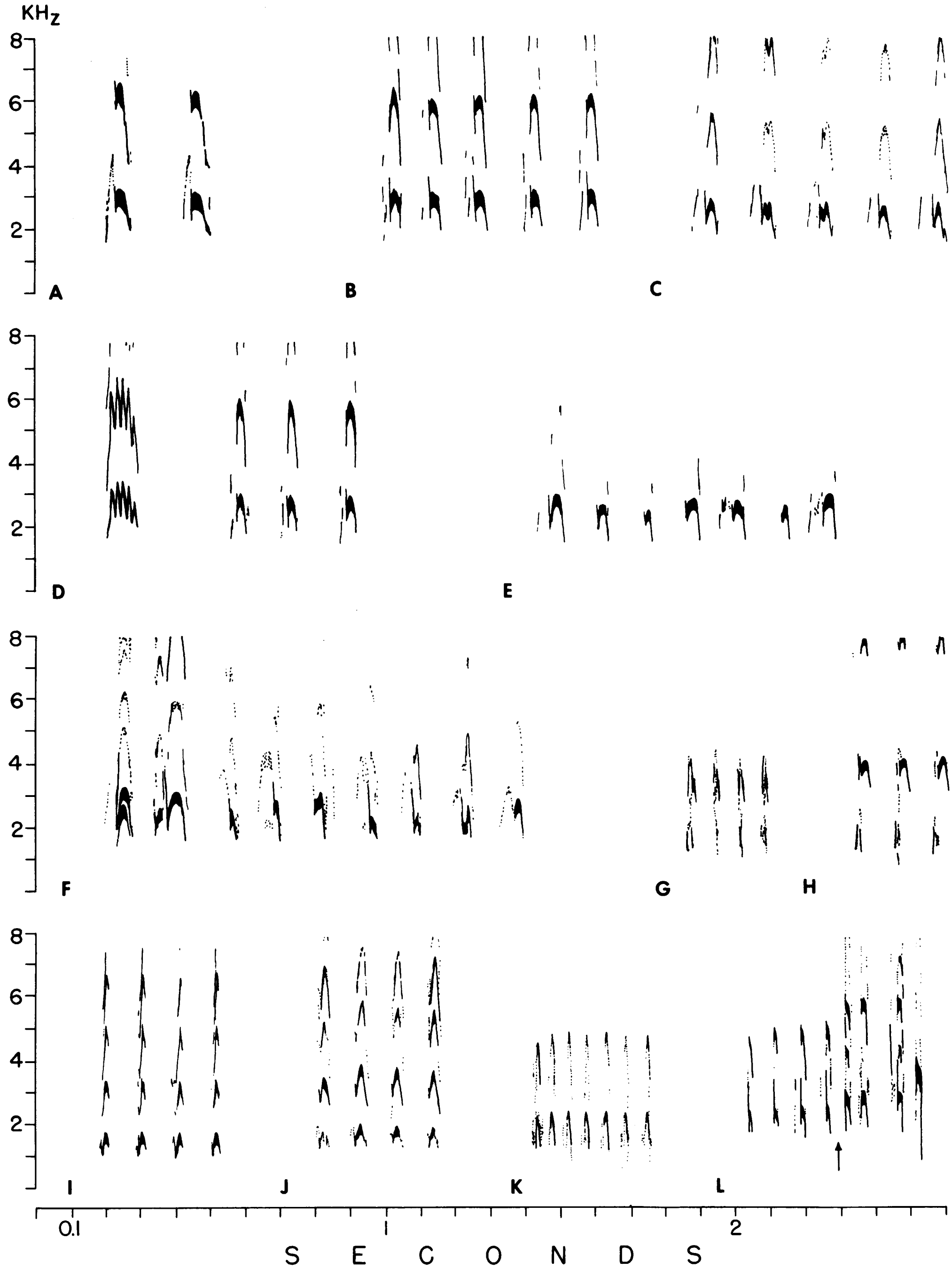

FIG. 32. Sonagrams of some juvenile calls of pied woodpeckers. A. *P. pubescens*, Loud Chirp, nestling; New York. B. *P. borealis*, Chirp (no adult at nest), two days before fledging; North Carolina. C. *P. borealis*, Loud Chirp (adult at nest entrance), two days before fledging; North Carolina. D. *P. borealis*, Call Note-Chirp combination, nestling two days before fledging; North Carolina. E. *P. borealis*, loud feeding calls, fledgling; North Carolina. F. *P. borealis*, loud feeding calls, fledgling; North Carolina. G. *P. villosus*, Chirp; New York. H. *P. villosus*, Loud Chirp; New York. I. *P. tridactylus*, Chirp, nestling just before fledging; Austria. J. *P. tridactylus*, Loud Chirp, nestling just before fledging; Austria. K. *P. arcticus*, Chirp; New York. L. *P. arcticus*, switch from Chirp to loud Chirp (marker) during feeding; New York. All are wide-band.

are in the central part, which becomes louder and irregular in its frequency.

Situation: F3 Seasonal occurrence: (6)

medius. Especially in late nestling stages Loud Chirps become similar to Squeaks (fig. 33E; see p. 68). They also show strong similarities to the Chirp.

Situation: F3 Seasonal occurrence: 5, 6

syriacus. Loud Chirps consist usually of regularly formed notes (fig. 31H, I) that are elicited by the parent's approach to the hole. Darkening of the entrance by hand or a microphone inevitably elicits this signal.

Situations: F2, 3 Seasonal occurrence: 4-6

major. Loud Chirps (fig. 1, fig. 31K) almost show the structure of Call Notes. Nonetheless, they have a separate ontogeny and form no transitions. Hence, this call is not an ontogenetical forerunner of the Call Note, as one could infer from Blume (1968, p. 47). Loud Chirp Calls are elicited by the approach of the parents and by darkening the hole-entrance (see also Blume, 1968).

Situations: F2, 3 Seasonal occurrence: 4-6

major × *syriacus*. As in the last species the Loud Chirp undergoes ontogenetical development (fig. 31L to N). The notes change from a rather harsh quality in younger birds to a more musical rendition. As in their parental species the young react to artificial shading of the nest entrance by uttering these calls.

Situations: F2, 3 Seasonal occurrence: 5,6

pubescens. The notes of the Loud Chirp Call have a needle-shaped introductory part, a predominant central part, and a faintly outlined closing element (fig. 32A).

Situations: F2, 3 Seasonal occurrence: (6)

borealis. The Loud Chirps of this species are very similar to the calls of the aforementioned species (fig. 32C). Interestingly, the Loud Chirp differs from the Chirp by having a broadened introductory element, whereas the central one is less regularly formed.

Situations: F2, 3 Seasonal occurrence: 5-7

villosus. Comparing figure 32G with figure 32H, one readily appreciates the main differences between the Chirp and Loud Chirp calls. It is the main part of the note that is most pronounced in the Loud Chirp, which is somewhat higher pitched and longer than the Chirp Call.

Situation: F3 Seasonal occurrence: 4-6

tridactylus. The structure is like that of the Chirp Call. The central part is longer, higher pitched, and louder, as in the previous call-type (fig. 32J).

Situations: F2, 3 Seasonal occurrence: (6)

arcticus. Loud Chirps (fig. 32L) are not only louder, and contain a longer central part, but also are less regular (especially when given during feeding) than are Chirp Calls.

Situations: F2, 3 Seasonal occurrence: 5, 6

Summary. The Loud Chirp Call is a louder, exaggerated sibling of the Chirp Call. Structural differences between them involve chiefly the central part of the notes. This portion becomes louder, higher pitched, longer, and sometimes irregularly frequency-modulated (one exception seems to be *borealis*). Irregularities especially occur during the action of being fed by the parent, the common situation in which this call is given. Structural similarities to the Squeak also exist.

SQUEAK CALL

This is a loud squeaking call of longer duration than the Call Note, given by fledged or nearly fledged young.

minor. The squeak Call of *minor* was noted in hand-raised fledglings fed by the senior author (Winkler, 1971b). In the presence of the human "parent," hungry Lesser Spotted Woodpeckers also frequently uttered squeaking notes (fig. 33C). Squeaking notes occur as well in the late nestling stages (fig. 33A, B).

Situations: F3; G2, 5 Seasonal occurrence: (6) (Central Europe)

leucotos. Young one day before fledging gave loud squeaking notes (fig. 33D) when a parent fed them.

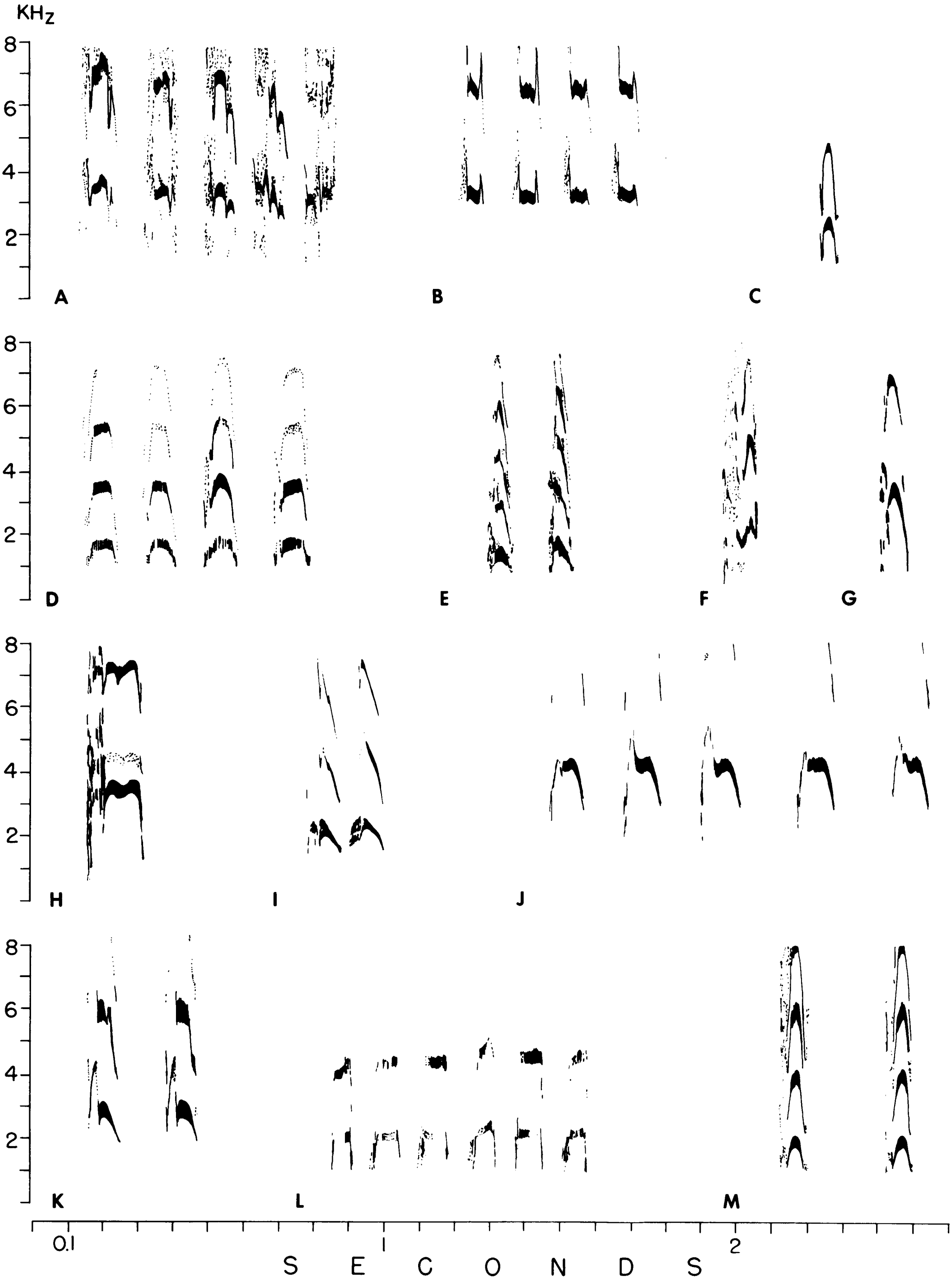

FIG. 33. Sonagrams of Squeak Calls of some pied woodpeckers. A. *P. minor*, nestlings 11 to 13 days old; Germany. B. *P. minor*, nestlings 13 to 15 days old, Loud Chirp-Squeak; Germany. C. *P. minor*, fledgling, intermediate Squeak Call-Call Note from bird in close proximity to human provider; Austria. D. *P. leucotos*, juvenile; Sweden. E. *P. medius*, nestling, 17 days old, Loud Chirp-Squeak; Germany. F, G, H. *P. syriacus*, fledgling; Austria. I. *P. major*, nestling, 12 days old, Loud Chirp-Squeak; Germany. J, K. *P. pubescens*, nestling; New York. L. *P. villosus*, nestling; New York. M. *P. tridactylus*; fledgling; Austria. All are wide-band.

Situation: F3 Seasonal occurrence: (6) (Central Europe)

medius. Fledglings of this woodpecker uttered loud, squeaking notes as they were fed by adult birds. The Squeak sounded similar to the squeaking of larger members of the genus (e.g., *major*). Squeaking notes of 17-day-old birds are shown in fig. 33E.

Situations: F3, G5
Seasonal occurrence: (6) (Central Europe)

syriacus. First heard from nestlings a few days before fledging, this loud call commonly is heard from fledglings, and shows transitions to the Call Note (fig. 33 F-H). Variation correlates roughly with the distance between the young and the parent or human provider, being loudest at a direct, close approach by either the young or the parent. The frequent calls of fledglings when parents are far away often are transitional between the Squeak and the Call Note.

Situations: F3; G2, 3, 5 Seasonal occurrence: (5-7) (Austria, Europe)

major. This call was frequently heard from fledglings both in captivity and in the field. It is a high-pitched, loud call which is longer than the Call Note but shorter than the corresponding call of *syriacus*. Nestlings as young as 12 days of age show squeaking elements (fig. 33 I).

Situations: F3; G5
Seasonal occurrence: (5, 6)

pubescens. The Squeaks of Downy Woodpeckers are quite long. The introductory part of the note is somewhat peculiar compared with the other species (fig. 33J, K). Rattles of newly fledged birds sometimes have a slightly squeaking tone (fig. 10 B, C).

Situations: F3; G5 Seasonal occurrence: (6) (northeastern United States)

villosus. The only example we have is shown in figure 33L. The Call Notes of fledged young also resemble a somewhat squeaking sound when the birds are near a parent, but this does not show on the sonagram.

Situations: F3; G5 Seasonal occurrence: (6, 7) (northeastern United States)

borealis. The call was not heard from nestlings even near fledging. Fledged young give a barely squeaklike call (fig. 32F), which is more an excited begging (Loud Chirp) than a true squeak such as is found in the other species. These Loud Chirps (plus squeaklike notes) are probably what Ligon (1970, p. 257) called loud, demanding "Whew-Whew" calls.

Situation: G5 Seasonal occurrence: (6, 7)

tridactylus. The calls pictured in figure 33M were uttered by recently fledged young (W. Weber) and we consider them as "fledgling" calls.

Situation: G5
Seasonal occurrence: (7) (Austria, Europe)

arcticus. The only squeaklike notes are found in Loud Chirps (fig. 32L). A fledgling observed by Winkler was completely silent as the parent fed it.

Summary. (Table 9.) The Squeak Call apparently develops from the Loud Chirp Call, and becomes a distinct call after fledging. In its physical structure two characters are noteworthy: the high-pitched, fairly long squeaking part, and a more or less noiselike, distinct, introductory element. In general, this call sonagraphically looks like a high, lengthened Call Note with a stressed introductory part in which transitions to a Call Note are common. Other than these relations to other calls, a similarity to the Kweek Calls is noteworthy.

SCREECH CALL

syriacus. Figure 35B shows the Screech Call given during a sustained fight between two juvenile birds (see also Distress Cry). The note is noiselike and shows only faint structures that resemble strong frequency modulation. The length of this call is 166 msec., and more stressed frequencies are at 1.2, 2.5, and 3.4 kHz. The peculiar Distress Cry described below (p. 71) occurred during the same combat and is somewhat similar in regard to those measurements.

TABLE 9

Squeak Calls of Pied Woodpeckers[a]

	Pitch in kilohertz					Duration in milliseconds					Intercall interval in milliseconds				
	Mean	Range	S.D.	C.V.	N	Mean	Range	S.D.	C.V.	N	Mean	Range	S.D.	C.V.	N
minor, nestling 11-13 days old	3.4	3.2-3.5	0.12	3.5	4	87.7	83.0-98.1	7.14	8.1	4	156.6	135.8-188.7	23.6	14.9	4
minor, fledgling	2.3	2.3-2.4	0.09	3.8	5	54.3	45.3-71.7	10.87	20.0	5	431.4	41.5-1079.3	564.8	130.9	3
leucotos, nestling Austria	1.7	1.6-2.0	0.20	11.4	3	67.9	52.8-79.2	13.6	20.0	3	—	150.9-211.3	—	—	2
leucotos, nestling Sweden	1.7	1.6-1.8	0.06	3.4	11	84.7	67.9-98.1	9.30	11.0	11	183.4	150.9-211.3	18.6	9.9	10
medius, nestling 17 days old	1.6	1.5-1.7	0.07	4.7	7	77.1	67.9-83.0	5.71	7.4	7	187.4	169.8-200.0	12.78	6.8	6
syriacus, fledgling	3.3	3.1-3.6	0.25	7.5	3	125.8	75.5-158.5	44.22	35.2	3	—	—	—	—	—
major, nestling	2.3	2.2-2.5	0.06	2.8	13	89.7	83.0-98.1	4.91	5.5	13	—	—	—	—	—
pubescens, nestling 1)	4.3	4.2-4.3	0.03	0.7	8	99.5	90.6-105.7	6.03	6.1	8	249.1	203.8-279.2	28.81	11.6	8
pubescens, nestling 2)	3.6	3.4-3.7	0.11	3.0	8	—	—	—	—	—	—	—	—	—	—
pubescens, nestling 3)	2.8	2.8-2.8	0.02	0.7	5	81.5	75.5-83.0	3.38	4.1	5	189.4	162.3-218.9	23.17	12.2	5
pubescens, nestling summary	3.7	2.8-4.3	0.58	15.7	21	92.6	75.5-105.7	10.41	11.2	13	229.9	162.3-279.2	40.68	17.7	14
villosus, nestling	2.3	2.1-2.4	0.09	4.2	7	79.2	60.4-90.6	11.73	14.8	7	127.2	105.7-143.4	15.36	12.1	7
tridactylus, fledgling	1.9	1.9-2.0	0.04	2.1	7	77.6	67.9-83.0	5.27	6.8	7	337.1	288.1-418.9	45.14	13.4	6

[a] *Symbols*: S.D., Standard Deviation; C.V., Coefficient of Variability; and N, sample size. The numbers following the *pubescens* samples refer to three different nests, which gave somewhat different results.

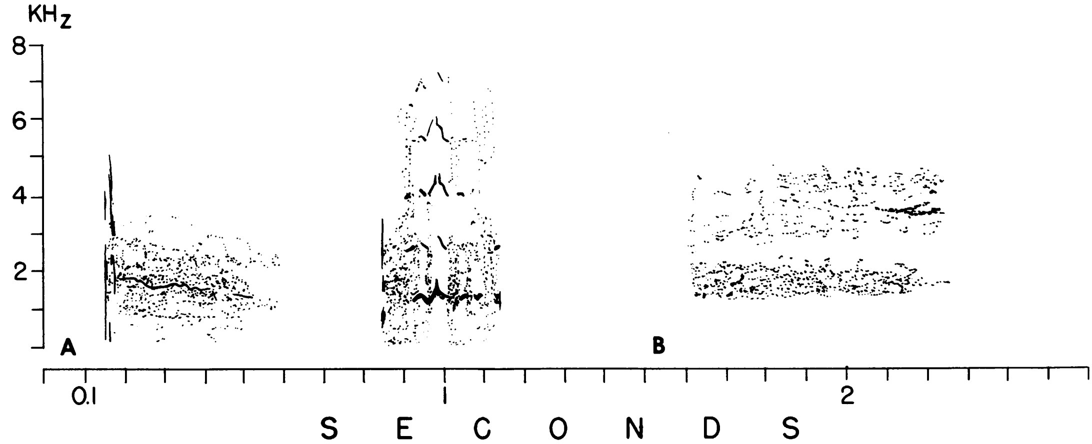

FIG. 34. Wide-band sonagrams of Screech Calls of two pied woodpeckers. A. Screech Call of nestling *P. tridactylus*; Germany. B. Screech of nestling *P. arcticus*; New York.

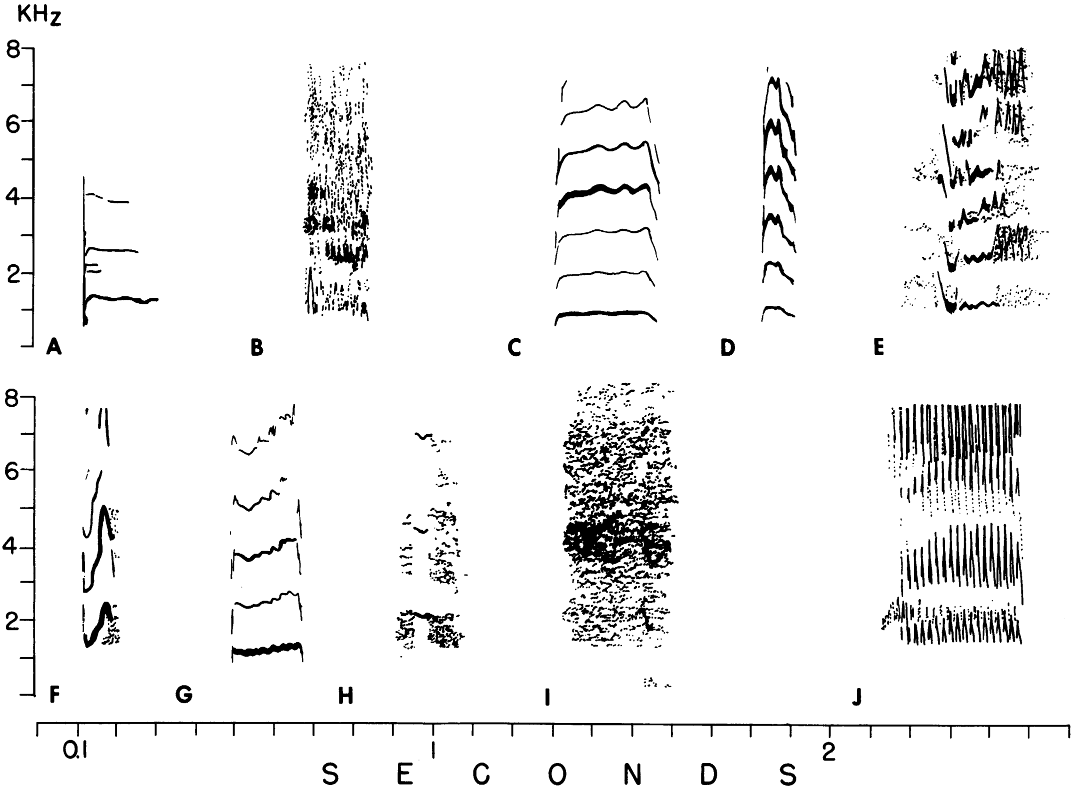

FIG. 35. Sonagrams of Distress Cries of some pied woodpeckers. A. *P. syriacus*, nestling call during fight, narrow-band (see text); Austria. B. *P. syriacus*, juvenile, noisy Distress Cry during flight; Austria. C. *P. major*, Distress Cry, long, little frequency modulation, narrow-band; Austria. D. *P. major*, Distress Cry, short, considerable frequency modulation, narrow-band; Austria. E. *P. major*, Distress Cry, long significant frequency modulation and noise; Austria. F, G, H, and I. *P. pubescens*, four types of Distress Cries (cf. C, D, E), narrow-band; New York. J. *P. borealis*, fledgling; North Carolina. Others than wide-band A, C, D, F, G, H, and I are narrow-band.

Situation: H
Seasonal occurrence: (8) (Central Europe)

major. Screechlike vocalizations appear together with Distress Cries (see that section and fig. 35E).

pubescens. Noiselike, screeching notes appear together with Distress Cries (fig. 35 I).

tridactylus. The recording we could analyze was made during severe disturbance, the darkening of the entrance by the hand of the experimenter at the breeding hole as the young (one week before fledging, W. Scherzinger, personal commun.) uttered these peculiar notes. They show parts with sounds like the Distress Cry, almost pure, noiselike sections, and transitions between the two (fig. 34A). The fundamental tone of the sections that show similarities to the Distress Cry is at a frequency between 1.1 and 1.8 kHz. The calls have a duration between 453 and 830 msec.

Situation: H
Seasonal occurrence: (6) (Central Europe)

arcticus. This call was recorded when both parents were at the nesting hole. Probably the young birds produced this noise (fig. 34B).

Situation: H Seasonal occurrence: (6)

Summary. This call is given by juvenile birds in situations of menace either by enemies or by conspecifics. Its second important character is its lack of clear soundlike structures. However, there is definitely a resemblance to the Distress Cry, which is given in situations of still greater danger.

DISTRESS CRY

This call is uttered by adults and by young birds as well at times of severe danger.

leucotos. Cries similar to those of *major* (see below) were heard during banding of a female. This is also confirmed by sonagrams made of recordings of a bird in a similar situation published by Blume, Ruge and Tilgner (1975). The notes are about 280 msec. long, the gap between two notes in a series (which is commonly the form of their appearance) is about 100 msec. The pitch is about 0.75 kHz. The ratio of Call Note pitch to Distress Cry pitch is about 5 to 2 (see table 10).

Situation: H

medius. On the record of Blume, Ruge and Tilgner (1975), Distress Cries of hand-held birds are included and composed of notes that are about 395 msec. in duration. A note commences with a long noisy part, proceeds to a part with many harmonics (starting at 1.7 kHz., with the third harmonic emphasized), and ends with a second noisy part, shorter than the first. The middle part constitutes about 40 percent of the entire note.

Situation: H

syriacus. This call (the Schirken of Winkler, 1972) was mainly from a bird caught at the roosting hole and held in the hand. Similar cries were heard from a female that was chased by a European Tree Sparrow (*Passer montanus*). The calls are loud and generally of the quality described for the other species. In the record of Blume, Ruge and Tilgner (1975), a Distress Cry is included in which the call is composed of notes that largely consist of noiselike structures (see also fig. 35B). During a struggle between two captive birds near fledging the call shown in figure 35A was recorded.

Situations: E5, H

major. This vocalization (figs. 1; 35C to E) was termed Schirken by Blume (1968: see his sketch of a sonagram, p. 62). The basic feature of this call is that it consists of a series of long, loud notes, which show irregular frequency modulations and are rich in harmonics. The length of the notes may vary considerably. Frequency modulation can be very pronounced, so peaked calls can be found, culminating in a noiselike form (fig. 35E). This call frequently is heard when a human catches and bands a bird (Blume, 1968; personal observ.). Some birds call in the nest when resisting being extracted by the bander. A hand-held bird also often elicits the Distress Cry. In nonexperimental conditions encounters with competitors for a hole are occasions for the Distress Cry. Great Spotted Woodpeckers besieged by Black Woodpeckers (*Dryocopus martius*; Blume, 1968, and personal commun.) or Starlings (*Sturnus vulgaris*) utter Distress Cries in their holes.

TABLE 10
Distress Cries of Pied Woodpeckers[a]

	Pitch of fundamental tone			Most emphasized harmonics[b]	Note duration			Note intervals[c]			Ratio of Call Note pitch to C.V. pitch
Species	Mean	Range	N		Mean	Range	N	Mean	Range	N	
major	1.1	1.0-1.3	18	1, *3*	154.1	83.0-256.6	17	93.7	75.5-135.8	18	2.46 or 5/2
pubescens	1.5	1.2-1.8	18	1, *2*, 3	223.5	128.3-301.9	18	145.7	75.5-234.0	13	2.46 or 5/2
borealis	2.0	1.8-2.3	8	1	386.9	286.8-430.2	8	129.8	98.1-196.2	5	1.39 or 3/2

[a]The samples consist of such calls or parts of calls that do not have significant frequency modulation, with the exception of *borealis*, in which the "carrier frequency" of the fundamental tone was measured.
[b]Italicized harmonic is that receiving greatest emphasis.
[c]Measured from the end of one note to the beginning of the next.

Situations: E5, H

pubescens. The Distress Cry of the Downy Woodpecker (fig. 35F to I) is of the same general form and structure as described for *major*. Rich in harmonics, of variable frequency modulation, and sometimes noiselike, this call has all the features that are described for the other species. The recordings were obtained from hand-held birds.

Situation: H

borealis. In sound and appearance on the sonagram (fig. 35J) the Distress Cry of the Red-cockaded Woodpecker is characterized by a strong, regular frequency modulation of 55 to 63 Hz. The recording was made as a newly fledged bird was caught and held in hand.

Situation: H

tridactylus. On the record of Blume, Ruge and Tilgner (1975), Distress Cries given by hand-held birds consist of series of noiselike notes (about 330 msec. long, the gap between notes about 83 msec.). Sometimes short sounds with several harmonics starting at about 0.88 kHz. are detected within single notes. In the noise a wide band of frequencies around 1.2 kHz. (and its harmonics) are more pronounced than others.

Situation: H

Summary. Distress Cries given in situations of greatest calamity to the woodpeckers are easy to obtain experimentally. They are the calls of pied woodpeckers richest in harmonics and loudest in amplitude and they last quite long. Additionally, they have (within a burst) a high rate of delivery. Their sound structure and relation to other calls such as the Call Notes (see tables 2 and 10) make them promising objects for comparisons and analyses of basic features of the vocal apparatus of these woodpeckers.

TAPPING[1]

minor. Winkler observed and recorded on tape the Tapping of a male of the subspecies *ledouci* in northern Tunisia. Prior to Tapping, the bird had Drummed and then flown to a hole where it Tapped. A female was nearby and inspected the hole after the male left. The Tapping signal was fairly loud, and the strokes were directed at the hole entrance. The intervals between single strokes were 141 msec. (range 124-155 msec., Standard Deviation 8.3 msec., Coefficient of Variability 5.9, N=18).

Situation: D3 Seasonal occurrence: (4)

medius. The Tapping of the Middle Spotted Woodpecker was heard only from a bird (per-

[1]In the present paper the term Tapping is used in the sense of Lawrence (1967, p. 15), i.e., "ritual tapping," and is not to be confused with any feeding technique. Also not considered is the "irrelevant" (displacement) pecking in agonistic situations.

haps a male) that performed it at the entrance to a hole. It resulted in a second bird (probably a female) coming to the site. This occurred regularly over several days. The signal is loud and quite slow in rhythm. It remains doubtful whether the few published data about Drumming of this species in reality refer to Tapping.

Situation: D3 Seasonal occurrence: 2, 4, 12

major. Tapping (fig. 36A) is performed as a typical part of nesthole demonstration (presumably mainly by the male) at the entrance to a hole (Blume, 1961, 1968).

Situation: D3 Seasonal occurrence: (3, 4)

stricklandi. In the few occasions when Tapping was observed, only the male performed it. It is carried out, as in the other species, at the entrance to the presumed nesting hole, and is a loud, slow instrumental signal (fig. 36B). Of 10 analyzed Tappings one consisted only of two strokes, the others of five to 11 (mean 8.1). Tapping occurs after Display Flights to the incompletely excavated hole (see Kweek, Twitter) prior to the bird initiating a period of excavation. The signal not only stimulated the female to approach, but also attracted an Acorn Woodpecker (*Melanerpes formicivorus*), which regularly supplanted the Strickland's Woodpecker!

Situation: D3 Seasonal occurrence: (4)

pubescens. In Downies either sex may perform Tapping at a potential nest site, thus attracting the opposite sex. Tapping is performed in bursts of nine to 10 taps each at a rate of four taps per second. Transitions to Drumming occur (Kilham, 1962). The Rattles of a male *pubescens*, obviously elicited by the Tapping of a Red-bellied Woodpecker (*Melanerpes carolinus*), probably represent a "misunderstanding" of this signal (fig. 11). However, this also

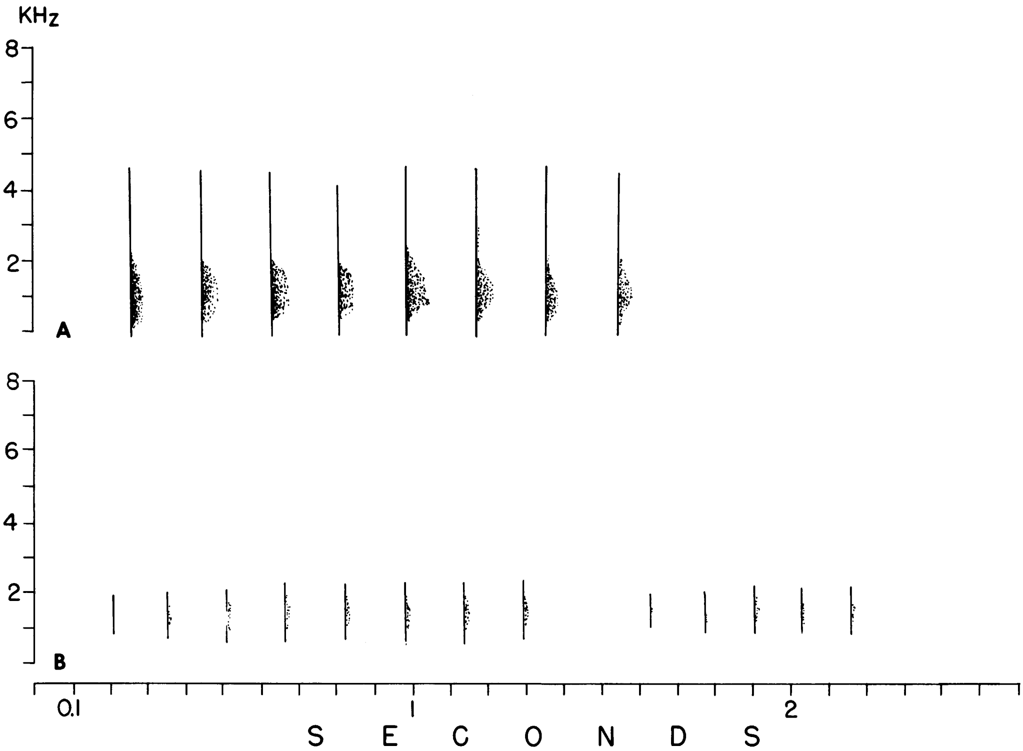

FIG. 36. Wide-band sonagrams of Tapping of German *P. major* (A), and an Arizona male *P. stricklandi* (B).

provides an indication of the "normal" intraspecific reaction.

Situation: D3 Seasonal occurrence: (5, 6)

villosus. It was noted (Kilham, 1966a) that Hairy Woodpeckers tap at a suitable nesting site, and during changeovers in the work of excavating. The Tapping rate was about two to three blows per second.

Situation: D3 Seasonal occurrence: (3, 4)

albolarvatus. A male White-headed Woodpecker was observed several times in one day tapping at the entrance of a hole after flying to it, uttering Kweeks, and near the hole, Twitters. Before and after Tapping the bird slipped into the hole for a short time. Once a female also was attracted by the sound. The Tapping is a slow, and, in the instances witnessed, not a very loud instrumental sound, performed with peculiar, stiff movements of the head, like a puppet on a string.

Situations: D3 Seasonal occurrence: (4)

Summary. This instrumental signal is very specific with respect to the situation, which invariably is the same. Also, the physical features of Tapping are very uniform even beyond the limits of the genus. This is demonstrated by the two instances of intergeneric interaction (involving in both cases the picid genus *Melanerpes*). Males mainly give this signal that apparently occurs only during a limited period of the season, namely during nest-site selection. This probably is one reason why this signal is so rarely described.

DRUMMING

moluccensis. Drumming is performed (fig. 37A) in bouts of up to five minutes in length, with six to eight rolls delivered per minute. The four recorded drums are 580 to 680 msec. long and contained 17 to 20 beats. Basic frequencies of the sound are between 1.3 and 2.0 kHz. Drumming has a diurnal peak in the morning (Short, 1973).

Situation: B
Seasonal occurrence: (4) (Malaya)

kizuki. Jahn (1942) mentioned the Drumming of this woodpecker.

canicapillus. The Drumming of the Gray-capped Woodpecker is soft but carries far, usually given from a bare tip of a twig at the top of a large tree overlooking the surroundings (Ali and Ripley, 1970; see also Caldwell and Caldwell, 1931; and Smythies, 1953).

minor. Males and females Drum (fig. 37B) in rather long rolls, up to about 1.3 seconds long, containing more than 30 beats in a Drum. These are performed high in treetops, but also on artificial, suitable sounding objects, often in the vicinity of a prospective hole. The intervals between consecutive rolls are usually short (longer in females), and thus up to 14 rolls can occur in a minute (Hurme, 1973). Basic frequencies often are at about 1.3 kHz.; harmonics can be strong, and weak signals also are detectable at lower frequencies. More than 170 rolls in a row were noted both from females and from males (Blume, 1968; Hurme, 1973; Pynnönen, 1939). Drumming often is interspersed with Rattles, and can be given in reaction to either Drumming or Rattles, as well as after encounters between pairs (Tracy, 1933). There are many accounts in the literature about Lesser Spotted Woodpeckers Drumming in winter; a report on seasonal occurrence is found in Hüe (1949-50).

Situations: A3 (1); B1 (1); C2a; D6 (1); H
Seasonal occurrence: 1 to 7, 10 to 12

macei. Drums weakly in the pair formation period in India (Proud, 1958).

auriceps. It is known that this species Drums during March and April (Ali and Ripley, 1970).

mahrattensis. The Drumming is a muffled dr-r-r-r. . . . in bursts of one to two seconds during the breeding season (Ali and Ripley, 1970).

dorae. Drumming was mentioned by Meinertzhagen (1954).

hyperythrus. Both sexes are known to Drum (Diesselhorst, 1968; Ali and Ripley, 1970).

darjellensis. Both males and females Drum fairly loudly. Three analyzed rolls (fig. 37D) were 1 to 1.18 second in duration and contained 21 to 26 beats per second (Short, 1973; see also Diesselhorst, 1968). When adults are disturbed, Drumming may be performed after they feed the nestlings (Diesselhorst, 1968).

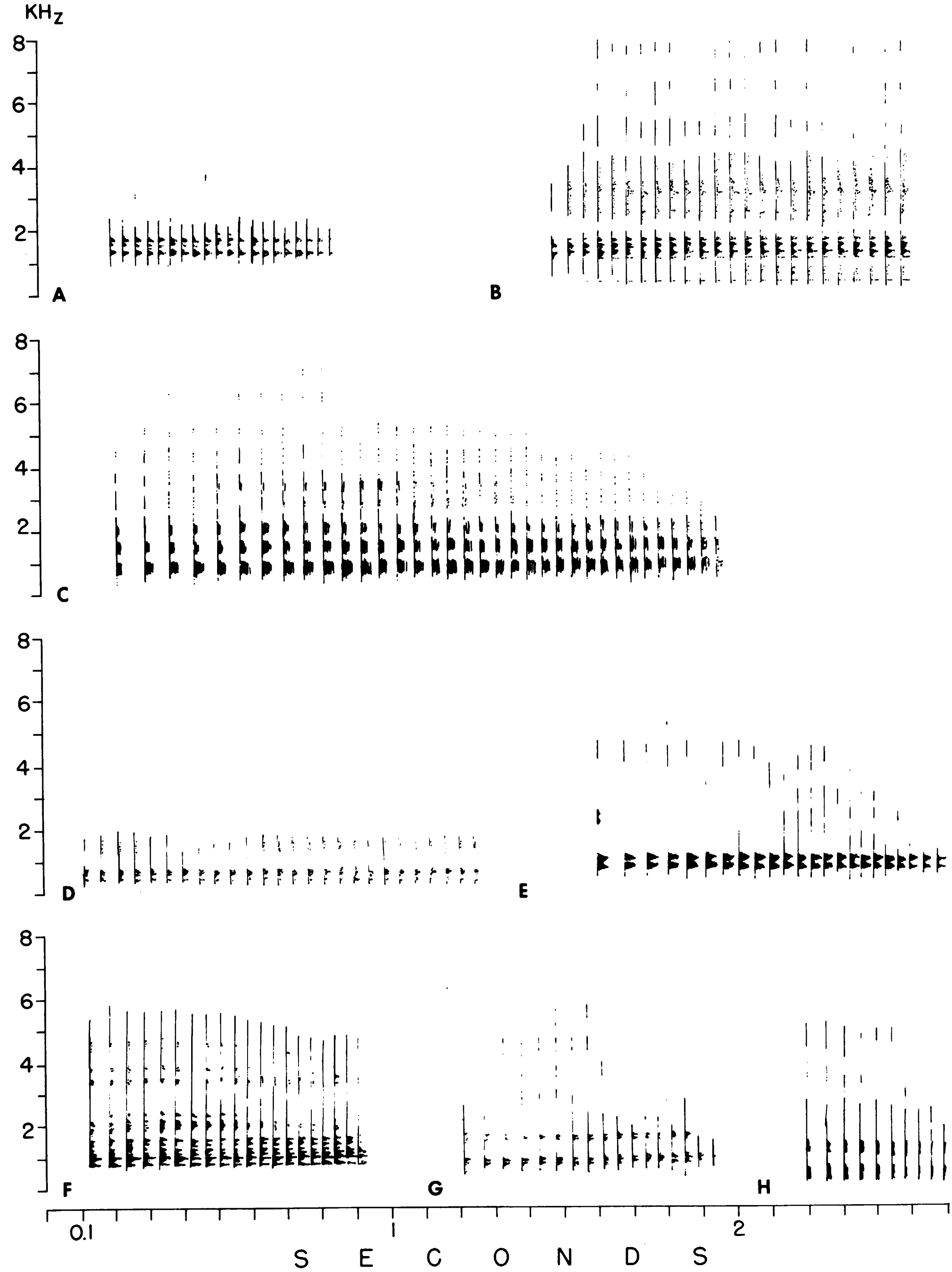

FIG. 37. Wide-band sonagrams of Drumming of some pied woodpeckers. A. *P. moluccensis*; Malaya. B. *P. minor*; Germany. C. *P. leucotos*; Sweden. D. *P. darjellensis*; India. E. *P. syriacus*; Austria. F. *P. major*; Japan. G, and H. *P. major*; Austria.

Situations: A1; C1, 2, 4, 7a, 8b; E5
Seasonal occurrence: (5)

leucotos. Thirty to 40 beats make up the average roll (Blume, Ruge and Tilgner 1975; personal observ.), which is about 1.7 seconds long. The first interval within a roll is the longest, and the intervals become shorter toward the end (fig. 37C). The frequency rises from 15 to 19 up to 22 to 25 beats per second during the roll. A main portion of the frequencies of the sound is in the region of 1 kHz. Both sexes Drum. Other observations concerning Drumming are found in Franz (1937) and Schubert (1969). Drumming of adult birds disturbed at the nest occurs after feeding the nestlings. This Drumming can consist of very short rolls (five beats, 0.26 duration for the roll) at the beginning of a bout of Drumming.

Situations: A3 (1); B; C9a, 9b; E1; H
Seasonal occurrence: (4-6)

medius. There seems to be no reliable information about the Drumming of this woodpecker (see Tapping).

himalayensis. Both sexes Drum during breeding season (Ali and Ripley, 1970).

assimilis. Both sexes Drum quite loudly at frequent intervals (Ali and Ripley, 1970).

syriacus. Both sexes Drum in rolls of 0.8 to 1.2 seconds. In a full Drumming series five to six rolls occur per minute. Commonly there are 16 to 31 beats per roll (fig. 37E). Females show a tendency to Drum less frequently and in shorter bursts than males (Ruge, 1970). Within a roll the longest intervals occur at the beginning, and the shortest near the end. On the basis of present evidence it can be shown that the acoustical characters of the sounding substrate affect both the length of the roll and the number of beats per second. If a bird uses a resonant substrate Drumming may be performed without any other obvious external stimulus. In the first half of the day Drumming occurs 1.7 times more often than in the second half. Drumming may be elicited by Drumming (also interspecifically by Drumming of *major*; see Winkler, 1971a), or even by Call Notes. After nest-relief during incubation the relieved bird often Drums.

Situations: A1 (1), 3; B1 (1); C2, 4a, 9a; D6; E1; H
Seasonal occurrence: 1-9

leucopterus. Drumming has been reported by Dement'ev and Gladkov (1966).

major. The Drumming of both male and female consists of short, loud rolls that usually are shorter in duration in females. The roll speeds up markedly from start to finish. Variation is affected by several factors. Features such as the number of beats per second, the length of the roll, the number of rolls per minute, the number of rolls in a series, the regularity of the course of the amplitude (both within and between rolls), and others, can be affected. Some of the main factors which influence these characters are stage of breeding cycle, social status (mated, unmated), character of the instrument (sounding board), and motivation. A further source of variation is geographical, which, however, will be fully appreciated only when all the other influences are accounted for (see fig. 37F to H). In a typical Drumming bout six rolls per minute are delivered, but there are also records of as many as 11 per minute (Radermacher, 1971; see also Langelott, 1957). Drumming can be ended by giving a Rattle (Blume, 1968; Winkler, personal observ.). There are many circumstances described in the literature (e.g., Pynnönen, 1939; Langelott, 1957; Blume, 1961, 1965, 1968; Steinfatt, 1937, Pulliainen, 1963; and Richards, 1957). Among them is the observation (Blume 1965; Pynnönen, 1939) that unmated or widowed males Drum much more frequently than do mated individuals. Drumming also plays a role in nest demonstration. A typical sequence is: Drum—fly to the nesting hole—enter the hole—fly back to the signal post-Drum (Blume, 1961). The nesting tree frequently is used as a signaling site. As in some of the species dealt with above Drumming also occurs after adults have fed the nestlings. The availability of an instrument seems to exert strong stimulation. Often well-resonating, artificial instruments (e.g., telegraph poles) are used, and there can be interspecific picid competition for such sites. This also is demonstrated anecdotally by a male caught in the roosting hole and put in a special, resonant-sounding box; he performed Drumming in about one hour after his capture despite being in complete darkness! Common reactions to Drumming are approach, searching flights, frequent Call Notes, and Drumming. Great Spotted Woodpeckers react to the Drumming of *minor* (Radermacher, 1971; personal observ.), *syriacus* (Winkler, 1971a), *tridactylus* (Ruge, 1968, 1971), *Picus canus* (Radermacher, 1971; Winkler, personal observ.), *Dryocopus martius* (W. Walter, personal commun.), and artificial Drums (Richards, 1957). The first effort at Drumming occurs in the first week after fledging; it ceases some weeks after that and reappears in winter. The diurnal course of Drumming frequency was described by Pynnönen (1939) and Langelott (1957).

Situations: A1, 3 (1); B1 (1); C2a, 4a, 5e, 8, 9a; D6; E1; G1; H
Seasonal occurrence: 1 to *4* to 6, 8, 9, *11*, 12

mixtus. Its Drumming is like that of *scalaris* and *pubescens* (Short, 1970).

scalaris. Ladder-backed Woodpeckers seem to Drum only rarely (Short, 1971a). Its desert habitat often lacks suitable instruments for Drumming, which may have the effect of rendering it of less importance in this species. The rolls apparently are shorter than in *pubescens* and have about 30 beats per second (Short, 1971a, 1974a). Ladder-backs react to the Drumming of *nuttallii*.

Situations: C4, 8; E5
Seasonal occurrence: (2-4)

nuttallii. Both female and male Drum, the male more frequently (Miller and Bock, 1972). The Drumming is quite variable due to the diverse circumstances in which it takes place (Short, 1971a). Hence geographical variation is likely to be concealed (see fig. 38A, B). As one average about 21 taps per roll are given, but longer rolls with 28 beats also are found (N=58; Short, 1971a and 1974a, data from Baja California). A male in California (south of Los Angeles area) Drummed rolls with an average of 16.6 beats (range 11-30, N=34) after being confronted with playbacks of its own Rattle and Drumming. Drumming (rather playback of Drumming) elicits approach, Drumming interspersed with Rattles, Call Notes, and Double Calls in males, and Kweeks in females (see Miller and Bock, 1972). According to Miller and Bock (1972, graph) Drumming increases slightly during the egg-laying period.

Situations: B1; C4, 8; H
Seasonal occurrence: 1 to *3* to 6, 11

pubescens. The Drumming (fig. 38C) of this species (both sexes Drum) consists of about 13 beats per roll which are about 0.9 sec. in duration (Short, 1971a, 1974a; see also Lawrence, 1967). Kilham (1962) wrote of rolls lasting 1.5 sec. They are given at rates between nine and 16 per minute; in "intense" (unfortunately not defined by the authors) situations up to 24 short rolls per minute are delivered (Kilham, 1962, p. 126; see also Lawrence, 1967). According to the latter author Drumming may slow down to a Tapping. With regard to the situations of occurrence some information exists (Kilham, 1962, 1974a, 1974b; Lawrence, 1967). Drumming often is associated with special signal posts. Males respond to each other's Drumming with Drumming (for more about this see Kilham, 1974b). It is also often performed near the nest, especially during the time of nest-demonstration behavior (Lawrence, 1967; Kilham, 1962, 1974a, b). A newly widowered male resumed frequent Drumming (Lawrence, 1967) typical of unmated birds earlier in the year. Downy Woodpeckers react to Drumming or playbacks of Drumming with Drumming, Rattles, approach, inspecting holes near the Drumming site, searching flights, and displays (Crest Raising, Tail Spreading near the tape recorder). Winkler also has observed flickers (*Colaptes*) reacting to the Drumming of *pubescens*. Rattles sometimes are interspersed with Drumming.

Situations: A3 (1); B1 (1); C2a, 8a, 8b, 9a, 9b; D6; H Seasonal occurrence: 1-8, 12

borealis. Ligon (1970) published some observations about the relatively rare and low Drumming, which is accomplished by both sexes. It seems to be confined to the colony according to our observations.

Situations: A1; B1; C3, 4, 8; E
Seasonal occurrence: (5)

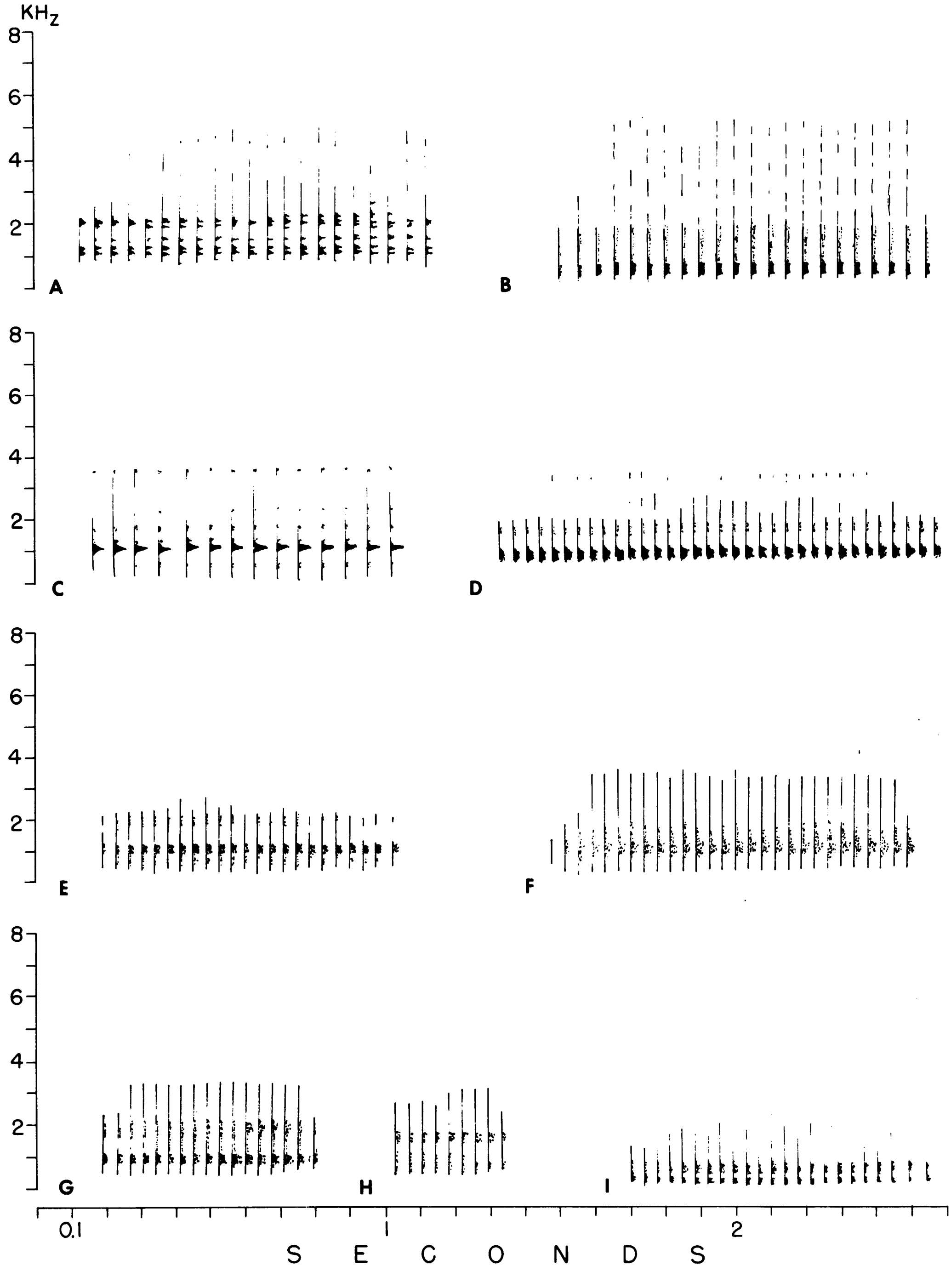

FIG. 38. Wide-band sonagrams of Drumming of some pied woodpeckers. A. *P nuttallii*; Baja California. B. *P. nuttallii* , adult male; California. C. *P. pubescens*; New Jersey. D. *P. stricklandi*, adult male: Arizona. E. *P. stricklandi*, adult male (different from individual of (D)); Arizona. F. *P. stricklandi*, adult female; Arizona. G. *P. stricklandi*, presumably the same male as in (D) before an encounter; Arizona. H. *P. stricklandi*, presumably the same male as in (E), during disturbance at the nest (eggs within nest); Arizona. I. *P. villosus*, male; New York.

stricklandi. Both sexes Drum, the male more often and in longer series. The variation is considerable (fig. 38D to H) between series, but within a series it is far less. Drummings at often used signal posts (usually high treetops) are loud, given in very long series (more than 50 in a sequence), and sometimes are interspersed with Rattles (often a Rattle is the last signal of a series). Drumming has no obvious external stimulus, and it occurs mainly in the morning. Drumming of this sort consists of about 21.5 beats in a roll (N=204 rolls). Drumming is performed frequently in the prebreeding season at various sites and in many different situations. Of 313 minutes (field notes with the aid of a stopwatch) of Drumming, usually 3.5 (median figure) bouts per minute were delivered. However, long and loud series may be uttered at rates of about five to seven rolls per minute. On three occasions a bird Drummed at 11 rolls per minute. Not included are Drummings which were given by a male during disturbance at the nest (plastic dummy placed at entrance of hole) in the nest tree (fig. 38H). Of 21 minutes of recording, two (9.5 percent) contained 11 rolls per minute, and the median was at six rolls per minute. These rolls had about 11.8 beats (N=75) each. Reaction to the Drums (or playbacks) include Drumming, approach, Call Notes, Rattles, and especially Kweeks. The last were uttered by the female exclusively, and regularly in apparently established pairs.

Situations: A3 (1); B1; D6; E5; H
Seasonal occurrence: (3-5)

villosus. Both sexes Drum, males usually more so (Kilham, 1960, 1966a). The Drumming (fig. 38 I) is quite variable, making it at times difficult to distinguish from that of *pubescens* (Lawrence, 1967; see also Short, 1974a, p. 15). From four to 11 or more (Kilham, 1966a); two to five (Lawrence, 1967); or one to nine (median 3.5, N=17 minutes, February in New Jersey; Winkler, personal observ.) rolls per minute are given. When disturbed at the nest, 16 to 20 rolls per minute can be heard (Kilham, 1968). On the average, a roll that lasts 0.9 second has 23 beats (N=10; Short, 1974a). The change in tempo is small, and involves a slight (0 to 5 percent) slowdown (Short, 1974a). Special signal posts often are used but Drumming, depending on the situation, may take place at various sites. It is often heard combined with Rattles, given either by the signaling bird or by a receiver, and with Kweeks (probably mainly as a reaction to Drumming). Drumming is elicited by Drumming after territorial encounters, when adults are disturbed at the nesting hole after having fed the young, and in many other situations (Lawrence, 1967; Kilham, 1960, 1966a, 1968). There are accounts of interspecific reactions in Short (1971a).

Situations: A3 (1); B1; C2a, 4a, 8a, 9a; E5
Seasonal occurrence: (1-5)

albolarvatus. We have few recordings of Drumming that occurred other than in some very long series of rolls. Five rolls had 26, 30, 25, 28, and 26 beats; another uneven roll only had seven beats (fig. 39A). Tempo changes are not well expressed. Drumming is performed high in a tree (see also Robinson, 1957). According to our observations, it is given by the male after territorial encounters. No reactions to it were observed either by us or by Robinson (1957) who heard it only once when the birds obviously were engaged in pair-formation activities.

Situation: H Seasonal occurrence: (1, 4)

tridactylus. Drumming is known from either sex (fig. 39B, C). Central European males Drummed an average of 19.7 beats (N=52) in a roll, and females, 21.2 beats (N=53). Rolls lasted 0.8 to 1.8 seconds (Ruge, 1968, 1975). Long rolls especially are heard during pair-formation and before the onset of breeding (Ruge, 1975). The rolls speed up toward the end (Ruge, 1968, 1975). The considerable variation in the pitch caused by the nature of the substrate was noted by Murr (1956) and by Ruge (1968, 1975), among others. Even power line poles are used as sounding instruments (Zimmerman, 1956). Short (1974a) analyzed the Drumming of North American *tridactylus*: rolls had a duration of 1.24 seconds and contained 16 beats (average values, N=35). He found three categories concerning the speed of the Drumming, but most Drummings are fast and

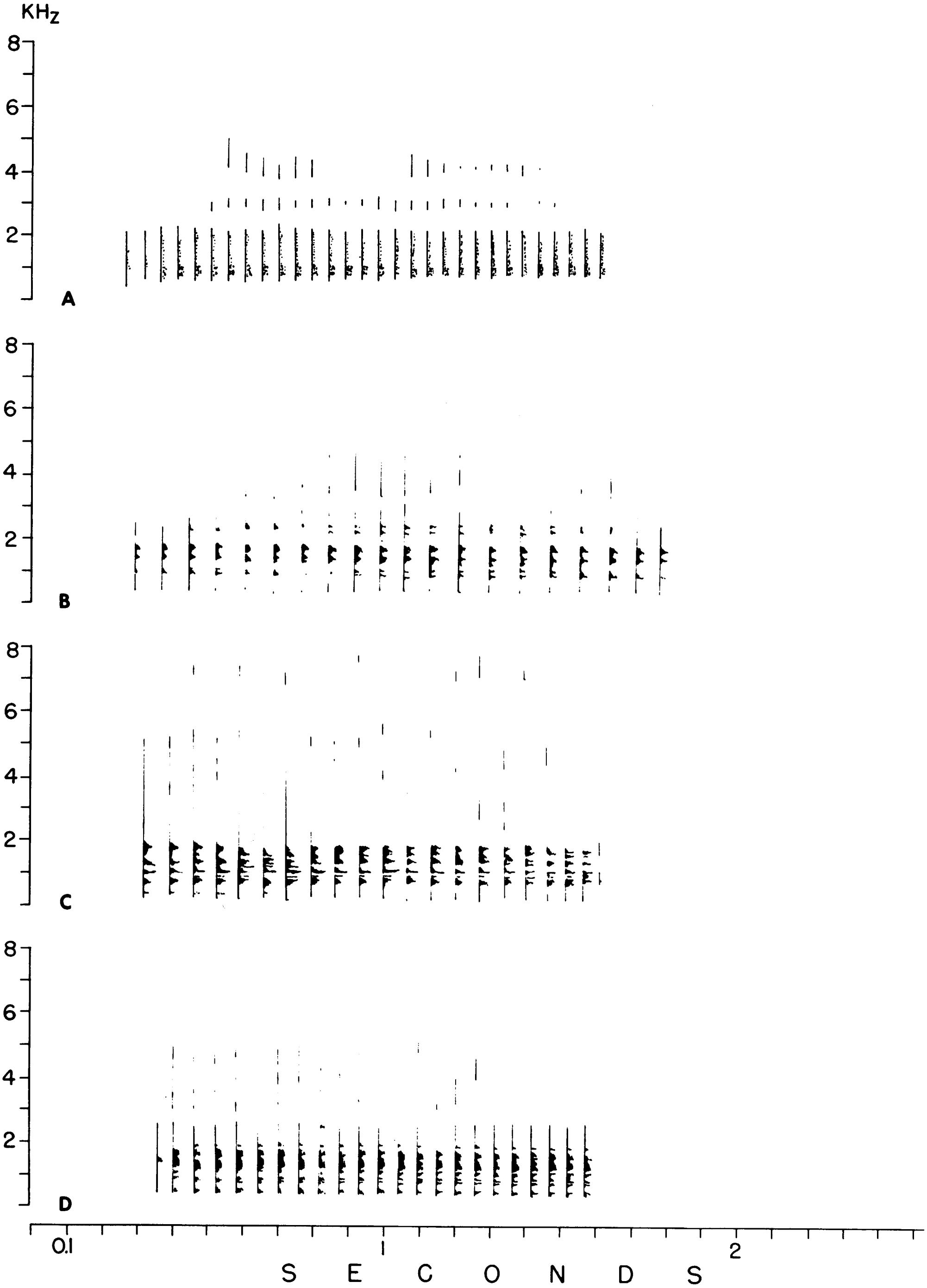

FIG. 39. Wide-band sonagrams of Drumming of some pied woodpeckers. A. *P. albolarvatus*, male; California. B. *P. tridactylus*, female; New York. C. *P. tridactylus*, female; Germany. D. *P. arcticus*, male; New York.

show a terminal speedup. The variation seemed to be correlated with the situation. Fast Drums occur in response to the signal of either conspecifics, or toward woodpeckers of other species (*P. arcticus*); slow Drums are exchanged only between members of a pair. Interspecific reactions also were noted by Ruge (1968) toward *major* and by Schubert (1969) toward *leucotos*. Special signal posts may be used. Noteworthy also is Ruge's observation of Drumming when the birds were disturbed at the nest.

Situations: A3; B1; C2a, 8; D6; E
Seasonal occurrence: (4-8)

arcticus. Short (1974a) studied the Drumming extensively; however, most of the Drummings (fig. 39D) available to him were of birds at the nest. The birds presumably reacted, at least in part, to the presence of the observer. Either sex Drums, females seem to average more beats in a roll, namely 19.95 beats, and males, 18.01. A speedup is characteristic of the *arcticus* Drum. Females seem to Drum less than males according to Short's observations, and more according to Kilham's (1966b) less sustained observations. Drumming may be performed at special signal posts and at various other places. No apparent variation was found as in *tridactylus*, *villosus*, and *stricklandi*, perhaps due to the relatively uniform situation in Short's study, namely that of slight disturbance near the nest (if this effect is correct one would expect the Drumming at the time of pair-formation to be quite long). Black-backed Woodpeckers were found to react to Drumming of Common Flickers (*Colaptes auratus*, Short, 1974a).

Situations: C1a, 4a, 4c, 5a, 5e, 5f, 7b; E4, 5
Seasonal occurrence: (4-6)

Summary. Drumming, a far-carrying instrumental signal, is employed regularly by the pied woodpeckers, the only exception apparently being *medius*. It is conducted at suitably resonant sites, mostly on dead limbs or stubs but also other (sometimes better) objects. Drumming consists of fast strokes, which form groups or rolls, which are organized into series with quite regular intervals. Most species Drum in rolls of about 15 to 30 beats. The shortest rolls are dellivered by *major* (European subspecies) which regularly has less than 15 strokes in a roll. Variation is great, and is attributable to various sources. Therefore, geographical variation is difficult to assess, though undoubtedly present. The signal often is given quite spontaneously in the prebreeding season, it is used in connection with nest-demonstration, and it can take the form of a duet, mainly with extraterritorial birds (but also among members of a pair, and, remarkably, for many species both intraspecifically and interspecifically). A second group of situations concerns activities around the nesting hole where all sorts of disturbance including hatching, presence of competitors, and presence of humans may cause the birds to Drum. In at least three species (*leucotos*, *stricklandi*, *villosus*) it is substantiated that the Drumming in the last-mentioned situations differs markedly from that occurring at other times.

SOUNDS MADE WITH THE WINGS

We have space for only a brief survey of such sounds, among the least known of woodpecker acoustical signals.

Information about this aspect of acoustical behavior is scattered, and never has been collected systematically. Two groups of sounds seem to exist: those accompanying flying, and those of perched birds combined with quivering wing movements.

Wing beats of flying pied woodpeckers are almost always audible when the birds apply their long-distance undulating flight. However, there are contexts in which those flights become more irregular (i.e., the "wave length" decreases), and then the wing beats become more conspicuous. Observations include those of *syriacus* near a conspecific individual (personal observ.), and perhaps Kilham (1962, 1966a) referred to the same type of sound in *pubescens* and *villosus*; however, descriptions are insufficiently detailed. Often on landing, birds produce rustling sounds, especially when landing near an opponent. Such observations are published for *scalaris* and *nuttallii* (Short, 1971a), and for *villosus* (Lawrence, 1967). When leaving a mate, leaving a signal post after Drumming (Rattle), and when flushed, Wing Rustles are known in *syriacus*, *major*, *stricklandi* (Winkler, personal observ.), and *villosus* (Kilham, 1966a). During searching flights (in playback experiments) the woodpeckers sometimes veer in a zigzag fashion that also produces significant rustling (see also Short, 1971a). A special type of wing noise seems to accompany Flutter Aerial Displays (*scalaris* and *nuttallii*; Short, 1971a).

Noises from birds making quivering wing movements when meeting another individual were discussed for *medius* by Feindt (1956). In the nesting hole a wing-quiver combined with fluffing the feathers can produce low humming sounds, audible only at very close distance in captive *minor*, *syriacus*, and *major* (Winkler, 1972). Perhaps Lawrence's (1967) observation of similar sounds in *villosus* belong here as well. Oppressed in the roosting hole, *major* may give hard short rhythmic series of wing beats which, beating the wood, produce an appropriate sound (Winkler, 1972).

THE ELEMENTS OF THE CALLS

We would like to discuss the possibility of subdividing the units described in the foregoing account into a lesser number of integral, smaller component units. If we borrow from linguistic terminology the calls can then be seen as morphemes, and the elements we shall attempt to abstract as phonemes. There are, of course, many problems involved; however, we believe that a beginning should be made.

Three such elementary sounds may be circumscribed: (1) a clicking element; (2) a squeaking element; and (3) an ascending element.

Clicking Element. A further subdivision can be made by separating a double click, which consists of a rising and a falling part, and a single click, which is but a very brief acoustical event covering a wide range of frequencies. Those noiselike elements that usually precede and follow a clicking element are worth mentioning, but it is doubtful that they have any significance for the perception, function, and meaning of the signal. They probably represent side effects such as those commonly accompanying the switch-on and switch-off of oscillators.

Squeaking Element. There are several subdivisions within the squeaking element. First there are long and short signal elements, although these are not in every case distinct. Both of these tentative subgroups could be further divided into a modulated and an unmodulated group, the former allowing a still further division into those elements that are regularly, and those irregularly modulated. In its ideal form the squeaking element is represented on the sonagram as a horizontal line accompanied by a series of harmonic tones. The irregular frequency modulation sonagraphically ranges from slight aberrations from the horizontal line, to wide blurred bars hardly showing any dominant frequencies (=noise). Interestingly, regular frequency modulations commonly have modulation frequencies of about 60 Hz. However, there seems to be variation with respect to the parallel amplitude modulation (Greenewalt, 1968). On the one hand amplitude modulation (with some shift in phase) may exactly mirror frequency modulation, whereas in the other case a peak in frequency corresponds to a double peak in amplitude modulation (fig. 20). Further studies are necessary to ascertain whether this difference is perceived by the bird, and if it is caused by different song-producing mechanisms (cf. Greenewalt, 1968; Gaunt and Wells, 1973).

Ascending Element. The third element can be conceived as intermediate between the other two, but bearing more resemblance to the squeaking element. It is sonagraphically a moderately (compared to the click) rising, mainly concave sound event with harmonic tones. Noteworthy is the lack of a "symmetrical" counterpart for this element (a possible exception may be the central element of the Call Note of *scalaris* and *syriacus*). At the present stage there is no heuristic value in discussing the problem posed by the connections of these elements; however, we note that they are not simply put together like mechanical components. Later we discuss how these elements are combined in the calls. In order to carry the abstraction further let us denote the click as K, the squeak as I, and the rising element as U. Thus the Call Note generally could be modelled as KIK, a Kweek perhaps as KIKUKIK. It can be seen that appreciation of the subdivisions of the elements would permit even better denotations of certain calls. However, we shall not pursue this matter any further; we merely indicate that there exists a wide-open field of research.

REPERTOIRES, GROUPS, AND COMBINATIONS OF CALLS

Some brief remarks are in order concerning aspects of higher levels of organization, with the view, alluded to above, of stimulating future investigations. The starting point for our considerations is the repertoire, the set of calls available to any species. There are several aspects of the repertoire to be treated. The more important ones are: (1) the number and quality of the calls; (2) their discreteness versus fuzziness and distinctiveness; (3) the overall tendencies in call structure; (4) the relative frequency of calls; and (5) the combinations of calls.

Number and Quality. The first stage of all analyses has to be a mere description of the repertoire. Difficulties arise from the problem of "completeness," i.e., the question of whether and how one can be certain that all calls of a species have been investigated. The answer to this question is crucial for all comparative studies as outlined in later sections. In our practice it proved useful either to investigate a species over many seasons, or, failing that, to extrapolate from the repertoire of closely related species. Bear in mind that the latter method has many pitfalls. Table 11 provides a survey of the calls described earlier in the paper, documenting the type of information available and calling attention to the gaps. Armed with an idea of the number of calls present in the repertoires of some species and following a classification of all calls according to their physical properties, one can advance to a study of other aspects. Even from the available information it is apparent that practically all the species have the same number of call-types.

Discreteness. Related to the problems just noted is the question of whether the calls of any particular repertoire are more apt to show transitions than are those of another species. A further question is whether units, though discrete, are structurally similar to each other. This is important in terms both of the sending apparatus, and of the discriminative ability of the receiving apparatus (we ignore for now other aspects of comparative studies; see below). Again, summarizing the results given in the previous sections, all species of *Picoides* appear to be similar in these respects. The Call Note and the Rattle are discrete units and in their physical structure are more distinct in the larger species than in the smaller ones. The Kweek-Twitter-Wicka complex, together with the Wad, are less discrete in all species, although it seems that New World species are more prone to exhibit what we might call "fuzziness" than are the European species. Least distinct to the human ear among all the repertoires probably is that of *arcticus*, in which calls mainly are distinguished by their time-patterns.

Overall Tendencies in Call Structure. Two outstanding examples of this aspect are *borealis* and *arcticus*. In the former we find a marked tendency toward regular frequency modulation that affects the Call Note, the Rattle Call, and, most interestingly, the Distress Cry. In *arcticus* the remarkable feature of virtually all calls is the omnipresence of clicking sounds. More refined data may yield other examples of correlations between features of different calls in one repertoire.

Relative Frequency of Calls. It is almost a truism that some calls are employed more often than others, although hardly anyone has devoted much attention to this (Schleidt, 1973). The problem has two aspects: how much more often is the most frequent call given than the next most frequent call? etc., and which call is it that ranks first? We have noted that, as a rule, the Call Note seems to be the most common in the larger species, and the Rattle Call is such in the smaller species. All other calls seemingly are rarer, except in *borealis*; this woodpecker has a repertoire showing more equivalence of calling rate from call to call than in any other pied woodpecker. Further, careful comparative studies, allowing for seasonal habitat, population density, social status, and other differences, are needed for many species.

Combinations of Calls. This aspect is concerned with higher levels of organization within the acoustical communication system. In the

TABLE 11

The Repertoires of Pied Woodpeckers[a]

Species	Call Note	Double Call	Rattle	Short Rattle	Mutter	Kweek	Wicka	Twitter	Wad	Soft Notes	Chirp and Loud Chirp	Squeak	Tap	Drum
temminckii	—	—	(+)	—	—	—	—	—	—	—	—	—	—	—
moluccensis	—	—	(+)	—	—	—	—	—	—	—	—	—	—	+
maculatus	(+)	—	(+)	—	—	—	—	—	—	—	—	—	—	—
obsoletus	—	—	—	—	—	+	—	—	—	—	—	—	—	+/
kizuki	—	—	(+)	—	—	(+)	—	—	—	—	—	—	—	(+)
canicapillus	+	+	+	—	—	+	—	(+)	—	—	(+)	—	—	(+)
minor	+	0	+	—	—	+	+/	—	+/	(+)	+	+	+/	+
macei	+	(+)	+	(+)	—	(+)	—	—	—	—	—	—	—	(+)
atratus	—	—	(+)	—	—	—	—	—	—	—	—	—	—	—
auriceps	—	—	(+)	—	—	—	—	—	—	—	—	—	—	(+)
mahrattensis	(+)	—	(+)	—	—	(+)	—	—	—	—	—	—	—	(+)
dorae	(+)	—	+/	—	—	—	—	—	—	—	—	—	—	(+)
hyperythrus	—	—	(+)	—	—	(+)	—	—	—	—	—	—	—	(+)
cathpharius	+	—	—	+	—	(+)	—	—	—	—	—	—	—	—
darjellensis	+	—	(+)	—	—	—	—	—	—	—	(+)	—	—	+
leucotos	+	—	+	+	—	+	—	—	—	—	+	+	—	+
medius	+	—	+	+	—	+	—	—	+/	—	+/	+	(+)	0
himalayensis	(+)	—	(+)	—	—	—	—	—	—	—	+	—	—	(+)
assimilis	—	—	(+)	—	—	—	—	—	—	—	—	—	—	(+)
syriacus	+	0	+	+	+	+	+	+	+	+	+	+	—	+
leucopterus	—	—	—	—	—	—	—	—	—	—	—	—	—	(+)
major	+	0	(+)	+	+	+	—	—	+	(+)	+	+	+	+
mixtus	(+)	—	(+)	—	—	—	—	—	—	—	—	—	—	(+)
lignarius	(+)	—	(+)	—	—	—	—	—	—	—	—	—	—	—
scalaris	+	—	+	+	—	+	—	—	+	—	—	—	—	(+)
nuttallii	+	+	+	(+)	—	+	—	(+)	+	—	—	—	—	+
pubescens	+	+	+	(+)	—	+	—	—	+	(+)	+	+	(+)	+
borealis	+	—	+	+	—	+	+	+	+	(+)	+	—	—	(+)
stricklandi	+	0	+	+	0	+	+	+	+	—	(+)	—	+	+
villosus	+	0	+	+	0	+	(+)	(+)	+	—	+	+	(+)	+
albolarvatus	(+)	+	+	+	—	+	—	+	+	—	—	—	(+)	+
tridactylus	+	—	(+)	+	—	+/	+/	+/	+	—	+	+	—	+
arcticus	+	0	+	+	0	—	(+)	—	+	—	+	—	—	+
major × *syriacus*	+	0	+	—	—	—	(+)	—	—	—	+	—	—	—
scalaris × *nuttallii*	—	—	+	—	—	+	—	—	—	—	—	—	—	—

[a] A plus indicates that a sonagram of the call is presented in this paper; this sign enclosed in parentheses means that only a verbal description is cited. The zero indicates that the particular call is missing or is very rare and of no apparent significance; this notation is only used in species that are well known in that respect. The diagonal indicates that we have sonagrams that are not figured in this report. Not included in this survey are Distress Trill and Distress Cry.

descriptive phase, it is necessary only to register which calls are combined, and which combinations are so regular in occurrence as to merit special consideration. We have undertaken some of this above. The most common, consistent combination, to give an example, is that between the Call Note and the Rattle Call. Within a repertoire, one is interested in comparing calls that are combined with those that are not, and those combined frequently with those combined less often.

This leads us to a general consideration of groupings, combinations, and transition of calls. Such consideration only can follow on the heels of the determination of the existence of any syntactical structures. Very detailed investigations were, and still are being undertaken about such structures in the songs of songbirds, for example. Unfortunately, results have been meager relating to the function, motivation, meaning, and homology of song. Thus, the relatively simple combinations present in woodpecker acoustical signals afford us an opportunity not offered by more complex passerine songs. It is also important, and practically of use, that the picid vocal units also are employed *singly* as signals. Some combinations that are good subjects for an initial study of this kind have been mentioned above, as for instance Call Notes and notes of Rattle Calls, Drummings, Rattle Calls, Kweek Calls, Wad Calls and Tapping, and others. As a second step, one could investigate the structure of acoustical interactions between, say, members of a pair. One might consider here the Rattle Call-Rattle Call dialogue, or the obviously intricate Kweek-Wicka-Twitter-Wad colloquies. Other examples are the Drumming duets, and the Drumming-Kweek Call interplay. In *borealis* the genus has its most colloquial bird; three individuals of this species can utter various calls in rapid series, all apparently simultaneously, affording a most challenging call-system.

All of these suggested studies depend upon the existence of carefully documented repertoires; unfortunately, these generally are incomplete, even in common species. The message of this section thus is that much remains to be accomplished before we can progress in depth along the directions of these five aspects to our goal of a full understanding of acoustical signal communication. However, we hope that the results presented herein will render the tasks ahead much easier.

DISCUSSION

INTRODUCTORY NOTES

The preceding sections dealt with the description of the physical properties of the signals involved in the acoustical communication of the pied woodpeckers. In the following chapters we try to outline aspects of the function, motivation, meaning, and homology of these signals. Neither our data nor the available methods are sufficient to provide a fully "objective" analysis. Thus, this part of the paper more than any other represents the result of our experience with the birds, judgments based on that experience, and our mutual discussions. In the literature dealing with vocalizations of woodpeckers all these aspects usually are mingled with the actual description of the calls. We attempt to disentangle these as much as possible in order to initiate a more straightforward and less circular approach.

Because of the highly subjective, but we believe not necessarily wrong, statements we will make, we note at this point that virtually every sentence below could begin with "in our opinion," "perhaps," and so forth. We omit such flourishes and imply them to be self-evident. Our aim is to couple a framework of working hypotheses with our results to serve as a starting point for further, more thorough investigations.

THE FUNCTION OF THE VOCALIZATIONS

General Notes

With the term "function" we try to circumscribe those aspects of woodpecker vocalizations that are related to the question: what effect have the vocalizations in the life of the species? and, of what biological advantage are they? Thus there is a close relation of function to "meaning." To indicate the difference more emphatically one could say that we here consider what role the meanings serve. In an example: A call may mean to a particular intruder "leave this place," and the call therefore would work as a spacing mechanism that is thought to afford some advantage to the species. A serious problem is that the function of a call often can be understood only if the accompanying behavior is understood functionally, too. As an example there are, at least in some species, frequent noisy encounters between pairs, yet encounters involving serious fights actually are surprisingly silent. If we interpret the former as territorial behavior the accompanying calls would have to be classified accordingly. But if this behavior is more complex than that, as many facts make it seem likely, then the functional interpretation poses some problems, at least on this general level. It should be noted that the term function used here includes mainly the "biological role," but also at times the function in the sense of Bock and von Wahlert (1965; e.g., in the discussion of locatability, and in the case of the interspecific action of some calls).

Call Note, Double Call, Scolding Call

One apparent function of the Call Note is to establish and maintain contact between the members of a pair or family. This was first suggested by Steinfatt (1937) in studies of *P. major*. Through these calls the birds are apprised of each other's postition, and perhaps in a rough way, motivational situation. Therefore, this call is important for synchronization and timing of the actions of woodpeckers. This call-type also serves to announce that a certain area is already inhabited by a woodpecker. The frequent delivery of this call near the roosting hole before entering it for the night (*major:* Blume, 1968; *syriacus*: Winkler, 1972) also suggests this function. In the nonbreeding season the Call Note may be almost the only indication of the occurrence of a woodpecker in an area. The only call serving similarly is the Rattle Call of some species (see p. 87). The Call Note also may act as an alarm or warning call, as when a bird is disturbed by a possible predator (e.g., man), but is not so alarmed as to flee, mob, or attack. The Call Note probably is most important in spacing individuals, and in maintaining contact in paired birds.

Because of their functions, the Call Notes are important candidates for acting as powerful isolating mechanisms. This is established in one case (*major*, *syriacus*), in which it also was shown that the Call Note affords a better species discriminating signal than does Drumming (Winkler, 1971a). The differences in Call Notes between such species as *scalaris* and *nuttallii*, which hybridize limitedly, also may operate in the same way (Short, 1971a).

The Double Call seems akin to the Call Note. It may in some cases be a more aggressive version of the latter, and therefore may emphasize the spacing and territorial function.

The Call Note of fledged young serves to attract the parents to find and feed them.

Scolding acts similarly to the Call Notes of alarmed birds, but can be seen as a well-defined functional entity. On one hand it summons the parents and helps attract them to defend their young. It also seems related to the mobbing reaction of passerine birds.

We have already mentioned observations showing that the scolding of *P. major* also elicited warning calls from tits, drawing their attention, and shortly this attracted a gathering of small passerines. On the other hand *P. major* reacts to alarm calls of Chaffinches (*Fringilla coelebs*; Fleuster, 1973). Also the Scolding of *P. pubescens* attracted a Tufted Titmouse to it. The same result was achieved by playing back the Scolding of a Downy Woodpecker. A second functional response is the reaction shown by nestlings that become less noisy (*major*). The situation of occurrence, appearance, and effects of this signal make it reasonable to designate it as the vocal component of a mobbing reaction. The instances in which a conspecific intruder seems to elicit this reaction indicate that mobbing as an antipredator behavior and mobbing toward an intruder have something in common, probably serving to summon the mate. Whereas in the first situation mobbing continues, in the second case other behavior is likely to follow when the summons has succeeded. There is as yet no account of two birds mobbing an intruder with Scolding Calls. Secondarily, the signal serves not only as an antipredator behavior in the above sense, but also in warning the nestlings, and thus lessening their vulnerability.

Rattle Call

Generally the function of the Rattle Call is similar to that of the Call Note discussed above. The Rattle seems to be more of a communicational aid in setting up territories than is the Call Note. The ever loud and long-lasting sound of the Rattle makes it easy to detect, and renders easy the localization of its source. The great number of high-pitched elements with a wide frequency range, or a high frequency modulation also may serve to carry the message a long distance, and, mainly, to make it easier to locate the signaler (see Marler, 1956; Erulkar, 1972). The long notes of *minor* may have functional properties different from those of the other species. The Rattle Call in many ways resembles the song of passerine birds, an aspect usually neglected by investigators who center their attention on the more peculiar Drumming (see p. 90). As in the song of songbirds, however, the function of the Rattle in territorial defense has not been proven (see Thielcke, 1970). Experiments nevertheless show that the Rattle elicits teriritorial (or at least aggressive) behavior in established owners of a territory. A further indication of its territorial aspects is the fact that this call frequently is given from a prominent point within the home range. In at least one case (*stricklandi*) this call acts also as a contact call. Observations of *scalaris* and *nuttallii* (Short, 1971a) indicate the same function (besides the territorial one) for these species. Nothing experimental is known about the Rattle serving as a possible isolating mechanism, which might be very important (Short, 1971a). Future studies of isolating mechanisms within the genus ought to focus on this point.

Quite obvious are the aggressive and localization connotations of the Juvenile Rattle Call in those species which employ it frequently (*canicapillus*, *minor*, *pubescens*, *borealis*).

More than any other vocalization of *Picoides* woodpeckers the Rattle Call is a distinct unit. A clear trait of all Rattles is the capability of carrying a certain message over a long distance without loss of information. This is achieved by its loudness, serial structure, and stability of form. Other than the more specialized Drumming, the Rattle is the major long-distance signal of pied woodpeckers. Because of this and its specific action this call is the most promising vocalization for extended comparative, functional and phylogenetic studies within the whole family and, for comparative aspects of the second of these, even beyond it (for instance, in the Dendrocolaptidae, see sonagrams in Davis, 1964; and also in other groups such as Alcedinidae, which have Rattle Calls very like those of woodpeckers, see Short, 1971b, pp. 91-92).

Short Rattle Call

If what we have designated as the Short Rattle Call is a discrete unit, then its function lies somewhere within the "triangle" of Call Note, Scolding Call, and Rattle Call. Its exact position in this framework varies with the species in question. To stimulate a low intensity mobbing reaction is probably its common effect in *syriacus*, *major*, *pubescens*, *borealis*, and *villosus*. If we extend the concept of mobbing to conspecific intruders, then we can include as well *cathpharius*, *scalaris*, *stricklandi*, *albolarvatus*, and *arcticus*. If we take into consideration all its other situations of occurrence, the best, all-round functional description of this call is that it chiefly is a summons addressed either to the mate, for territorial defense, or to the parent, for feeding. In many cases the individual to be summoned seems to be nearby. Thus, in terms of distance effects, this call would fit into the category of a medium-range vocalization.

Mistle Thrush Call

Information about this call is insufficient to give a complete picture of its function. Its situations apparently are within the range of those of the Mutter Call and the Short Rattle Call. It seems to represent a short-range signal that is easily detectable.

Mutter Call

This is another short-distance signal. It characteristically accompanies a Head Swinging Display. Hence, it is functionally a part of that display, rendering it usable even when the woodpeckers are not in visual contact. Often this occurs when quarreling birds are on opposite sides of a limb or trunk. The function of both the visual and the acoustical signal is to indicate the beginning of an attack, or intended attack, by the signaler. This seems to be of some adaptive value because it can prevent possibly dangerous surprises. Thus, it is mostly employed in ritualized fights rather than in serious ones that are often unaccompanied by vocal signals. The call seems to be functionally identical with the Twitter (see below).

Kweek Call

With the probable exception of *borealis* this call of pied woodpeckers represents the main long-distance signal related to interactions of the sexes. In many species if not in all, except *medius*, it is the main signal of the female in the breeding season. The male may use it near the nest especially before incubation (cf. *stricklandi*). It seems the appropriate response of a female to the Drumming of a male signaling readiness for pairing. The Kweek Call probably functions mainly to diminish aggression of the receiver and to enhance sexual behavior. The sexual aspect is expressed in its seasonal occurrence: no other signal is so confined to the mating season. Other signals that are more territorially oriented usually start earlier and seem to have a lesser autumnal peak. The Kweek Call of *medius* seems to have a broader function, being territorial-sexual, as also is indicated by the fact that in this species the call is mainly or exclusively uttered by males (Conrads, 1975). It often is argued that the Kweek of *medius* has assumed the function of the Drumming, which does not occur in this species. This argument of Ferry (1962) was based on its seasonal occurrence, which is quite similar in both *medius* and *major* (the latter was the species used for comparison). As indicated this argument does not hold because such similarities occur in other species too. The picture would be different if its seasonal occurrence were broadened beyond the spring one that Ferry used exclusively. However, it seems reasonable that in fact the Kweek of *medius* has some of the Drumming function as a territorial proclamation (there seem to be no experiments on this aspect), and as an attraction to females. The latter function is easily deduced from the situation in other species, but careful investigation is needed in the case of the territorial function, for this tends to contradict an appeasing function. The last-mentioned function is clearly evident in the other exceptional species, *borealis*. Here a signal of sexual appeasement among the members of the pair is generalized to function in social appeasement in the group. Therefore, its seasonal occurrence has changed accordingly.

The antithesis between challenging and sexual (appeasing) behavior is also found in the Type II Kweek Call (see p. 54). In consideration of all the situations in which Kweeks occur, it seems appropriate to designate this call as a long-distance appeasing-rally call. In other words the Kweek serves as a means of getting the partner to approach, to follow, or even to stay and, when approached, to "persuade" the approacher to be peaceable. Hence, it can function as part of nest demonstration, together with aerial displays, to end an encounter between pairs, and, in an aspect not yet considered, to insure peaceable interactions with fledglings. Into this conceptual framework there fit the combinations with the Rattle and the Wicka.

Wicka Call

This medium-distance signal, sometimes also used in close-range contexts, can be conceived as a vocal supplanting attack. Thus the function could be described as distance-enhancing. Its adaptive value would be to render less physically harmful the actual attack about to commence, or underway, by giving the opponent an opportunity to flee before a physical attack ensues.

The combination or rather transitions from the Type II Kweek Call to the Wicka can be considered as sign of the change from a more peaceable (appeasing), compromising approach to an aggressive one. This situation can arise after the addressee is identified, which can occur only after its signals are perceived.

Twitter Call

Most Twitter Calls are uttered in situations involving two birds close together. Those Twitters that accompany Head Swinging Displays as in *stricklandi*, *villosus*, *albolarvatus*, and *tridactylus* form a functionally uniform group. They relate precisely to the rhythm of the movements, and mirror acoustically this important visual display. Thus they serve the same function as does the Mutter (see above), i.e., as a means of duplicating the visual display over a second "channel." The apparent vocal variation also reflects the motivational variation (see Motivation section), even more than does the Mutter. Hence, the most important function of these calls may be to transmit the motivational state of the sending bird at close distance showing the agonistic conflict between approach and retreat. It is not surprising (both for the investigator and the receiving bird) that Twitters commonly grade into Wicka and Wad Calls.

Wad Call

Most birds have intra-pair vocalizations that often are soft and difficult to study. The function of these calls, however, is rarely evaluated (Thielcke, 1970). Often the same call is found in situations in which the pair meets ("greeting"), or one partner tries to attract the other (often "tidbit"-calls), or during copulation. In the pied woodpeckers this sort of call is represented by the Wad. Its amplitude only allows it to be employed at close range, and only the harsher Wad Calls can be detected at medium distances. This latter type mainly is used when the bird is approaching a cavity either to demonstrate it, or simply to indicate the approach itself. In the other situations it appears meaningful to employ an appeasing call, especially during that closest of contacts made by birds, copulation. The farther apart the two woodpeckers are, the more it seems that the call shifts to a smacking type, perhaps for reasons associated with the transmission of the signal over various distances, and the actual location of the sender. The tentative functional category of medium to short range, location and appeasing call may be assigned to this vocalization.

Nestling Calls (Soft Notes, Distress Trill, Chirp, Loud Chirp, Screech)

The functions of the nestling calls might be categorized according to the addresses of the signals, the siblings, the parents, and enemies. For the first group all questions are open for lack of any experimental evidence. One might think of mutual stimulation in the case of the Chirp Call. The Chirps may help to direct the parents to the nest (see p. 64). More data are needed to prove a correlation between the occurrence and loudness of Chirps when no parent is at the hole, and the structure of the habitat, i.e., the facility with which the nest-tree may be found. It is noteworthy, for example, that *arcticus* and *tridactylus*, which live in very uniform forest habitat, have almost incessant Chirp Calls of nestlings. An important function of the Chirp and the Loud Chirp calls, not yet proved experimentally, is to control feeding of the young by the adults. The Loud Chirp Call also serves to appease the parents during the act of feeding. This function becomes important also for the fledged young of *borealis*, which probably allows a longer bond between parents and young. Soft Notes and Distress Trills allow control of the brooding of the parent and may prevent injury of the young by careless movements of an adult. Because of the scarcity of information concerning the calls of the embryos prior to hatching (*syriacus*: Ruge, 1969), it is mere speculation at this time to assume that this is a means of changing the parents' behavior in response to the demands of the new developmental stage of the young. The Screech Call might be a vocal mimicry of a snake, as found in (adult) titmice threatened in the breeding hole, and as shown for tits, with mention of flickers (*Colaptes*) by Sibley (1955).

Squeak Call

The apparent function of this group of vocalizations is the appeasement of the parents by the young birds. This becomes necessary especially when the young have reached, or nearly reached adult size, for their activities in securing food from the parents are rough and potentially threatening to the latter. During the last part of the nestling period the parent going to the nest with food comes face to face with a practically full-sized woodpecker in the confined space of the hole. The lunging of hungry woodpeckers at that stage must resemble an aggressive act to the approaching parent; it is noteworthy that in some species (e.g., *arcticus*) the adult females, which are smaller than males and perhaps smaller than their near-fledging young, often feed the young less frequently at that stage, or even cease altogether, leaving the larger male to perform most or all of the feeding chores. Although aggression of the adults generally is minimal during the period when they are feeding young, it seems necessary for the employment of mechanisms to prevent violent actions. The necessity is even greater after fledging, when the mobile young may represent intruders in the territory of the parents. Indeed, there is ample evidence that the parents become more aggressive toward the young as the post-fledging period progresses and the young birds become ever more independent. Interestingly, the young of *borealis* seem to lack a characteristic Squeak Call—intraspecific aggression in this species apparently is buffered by other means.

Distress Cry

One can only guess at the function of the Distress Cry because nothing seems to be known about the reactions of conspecifics to this signal. However, it is reasonable to conclude that it has effects similar to those of other birds (see survey by Thielcke, 1970). The Distress Cry of *borealis* is puzzling. In contrast to the same call of other pied woodpeckers, the Distress Cry of *borealis* appears to be easy to locate. Study of the reaction of individuals of this species is needed before it can be ascertained whether the reactions to the call, and thus the function as well, differ from those of other species.

Tapping

This signal is confined to a single situation and location. From this we infer that it relates functionally to selection of a nest-site. This signal indicates the exact site of a prospective nesting cavity. The signal is directed to the mate and probably stimulates excavation and finally choice of the site. The behavior of selecting a nest site can last a long time if members of a pair are not "agreed" on the site. Maintenance and strengthening of the pair bond, and synchronization of reproduction may also be served through Tapping.

Drumming

Drumming probably is the best known sound produced by woodpeckers. However, it was not until the beginning of this century that Drumming was recognized as a signal rather than as a part of feeding behavior. Various authors have assigned many functions to this signal; we mention only those that seem to apply to the pied woodpeckers. Most emphasis has been given to the function of territorial proclamation and defense (Pynnönen, 1939; Kilham, 1962, 1966a, 1974b; Lawrence, 1967; Short, 1973, 1974a). That Drumming serves as a localization sound for members of a pair also is assumed by many authors (Kilham, 1966a, 1974b; Short, 1974a), as is its role in selection of a nest-site (Kilham, 1966a, 1974b; Blume, 1968). A further group of functions seems to be sexual, specifically including the invitation to copulate, but generally the sexual function is stated in terms of attracting a mate (Pynnönen, 1939; Kilham, 1962, 1966a, 1974b; Blume, 1968; Short, 1973). No functional explanation exists in the literature for Drumming at the nest cavity or near it when the bird is disturbed. We note that many persons seem to accept the occurrence of nonfunctional Drumming, i.e., a behavior performed "for the fun of it." Drumming often is compared with the singing of other birds (see below). This brief summary of possible functions leads to our discussion of those functions that may be attributed to Drumming on the basis of our data.

Two reactions to Drumming seem characteristic of playback experiments—approach to the source and Drumming (often combined with nest hole-demonstration). The former response seems characteristic of already mated birds, for females in many cases fly in calling Kweeks, and males seem by their aggressive actions to expect an intruder. The latter response is generally characteristic of unmated birds, and probably of mated birds, but involves the playback of drumming from a source outside the birds' territory (see Blume, 1968). The basic function of Drumming seems to be to proclaim a certain area, especially one that contains trees suitable for Drumming (and therefore, in principle, for hole excavation). From this follow the functions of attracting mates and keeping rivals away. In terms of the latter, we have to bear in mind that Drumming alone does not suffice to establish and maintain a territory (therefore an experiment devised to test this is not conclusive as noted by Thielcke, 1970). Drumming can be viewed as more specialized for proclaiming an area in territoriality, rather than denoting the owner and serving to locate him, as seems to be the case for the Rattle. Compared with Tapping, it allows a rougher, long-range announcement of a suitable nest site. It has sexual functions to the extent that territorial behavior (or better, behavior related to the hole) plays a role in pair formation, pair-maintenance, and other sexual activities. The often observed "duels" between neighboring males also indicate its function as a spacing mechanism. To this spacing function probably also is related the Drumming of the relieved bird after nest-relief during incubation, and Drumming in fall when roosting holes are being constructed or are occupied. The Drumming of birds disturbed at the nest may function to summon or to warn the mate. It is remarkable that in some of the larger species (e.g., *leucotos*, *stricklandi*) functionally different Drummings also are structurally different.

As noted above, Drumming often is compared with songs of other birds. Unfortunately (because it is confusing and serves no clarifying purpose), Drumming, too, has been compared with various woodpecker vocalizations, especially the Kweek Call (*medius*) and in other genera, similar calls. A major problem is that song is complex, and its function is far from being completely understood. Thielcke (1970) noted that such comparisons are of little value. One common feature of song and Drumming is a manifold combination of functions. Drumming lacks the complex structure of song, and its relation to the hormone testosterone is not evident (some pilot experiments have been conducted with *major*, Winkler, unpubl. data). Moreover, the Rattle and the Kweek calls seem far better candidates for direct comparisons with song, if it be granted that such comparisons are worthwhile at the present state of our knowledge. The unique and probably most important functional aspect of the Drumming signal is that it provides a means of communicating information about certain features (trees suitable for Drumming or nesting) of the territory by means of a corresponding instrument, over a long distance. To our knowledge this capability is not matched by any other avian acoustical signal. Another noteworthy difference is that in many birds, especially in closely related congeners, the song functions in reproductive isolation—Drumming largely fails to do so. This is not to say that Drumming plays no (not even secondary) role in reproductive isolation in some cases, but where it does seem plausible (e.g., *scalaris* does not or rarely Drums, yet interacts with *nuttallii*, which Drums, and *medius* does not Drum in sympatry with Drumming *minor* and *major*), other factors, such as reduction of competition could be involved. We are impressed by the many instances of approach to Drumming, not only by conspecifics, but by distantly related or unrelated woodpeckers (see *major*, *pubescens*, *tridactylus*, *arcticus*). Drumming also varies greatly structurally and functionally within a species, and is affected so much by the Drumming substrate and other ecological parameters, that it is difficult to conceive of it as an optimal signal to serve the role of reproductive isolation.

THE MOTIVATION OF THE VOCALIZATIONS

General Notes

Motivation both as a concept and as a fact is discussed a great deal among ethologists. We therefore briefly outline a framework for the discussion that follows.

Conceptually, one could assign one underlying motivation to each category of call. However, this conceptual level is not the one we treat, because the experimental data are insufficient to permit us to do so. Tentatively, we assume that some hierarchy of motivations is a reality, and that higher categories of motivation do exist. Such categories, not necessarily all at the same organizational level, are arousal in a general sense (see Manning, 1972; Fentress, 1973), aggression, fleeing or escape behavior, sexual behavior, and others. This arrangement of categories more or less emphasizes functional aspects, and it is not unlikely that they are mere constructs of our classifying and interpreting minds. But even if some of them, e.g., fleeing, are not motivational units as such, but only a system of motivations forming a relatively isolated motivational subsystem, the following account, we hope, provides some indications about the real system, whatever that may be.

A few words must be said about aggression. Woodpeckers commonly are regarded as especially aggressive birds (e.g., Short, 1974b). Although there is no quantitative, comparative basis for such opinion, we accept the fact that woodpeckers do exhibit behavior that could in a circumscribed way be defined as "aggressive." The terms aggression and aggressive, however, are used in diverse ways, sometimes having a broad meaning and other times having a narrow meaning. We use aggressive here in the sense of dominance behavior. Therefore, when a woodpecker pecks the finger of a birdbander we do not regard it as aggressive. The functional opposites of aggression as used here are submissive behavior and escape behavior. In more operational terms the categories approach, stay in place, and withdrawal could be employed. However, these are not quite identical respectively with aggression, submissive behavior, and escape behavior. For instance, a female staying in place upon being confronted with an approaching male surely reflects a different motivational basis than the staying in place of an intruder before the attack of the owner of a territory. Another term is self-assertion, which we think to be related to a low level of aggression (dominance behavior), and is, so to speak, confidence in one's own dominance in a possible struggle. It is essentially this dominance system that is the basis for our framework of discussion below. We must omit the less known calls, and those that we cannot analyze because of insufficient information.

Call Note, Scolding Call, Double Call, Rattle Call, and Short Rattle Call

These calls are discussed under three categories of motivation: arousal, aggression, and alarm. None of these call-types can be said to represent purely these rather diverse motivations. We achieve the fit most consistent with the data by allocating the Call Note to arousal, Scolding to alarm, and Rattle to aggression. The wide range of situations with which Call Notes are associated makes it a safe assumption that they are linked with any extant arousal system. The arousal itself, of course, may be caused by various stimuli and therefore may be associated with various other, more specific motivations. States of low arousal are sleep, dozing, and, usually, preening. These are characterized by a fluffed appearance of the plumage associated with a "short neck" and tranquil movements. At the other extreme are a sleek plumage with a "long neck" and many jerky movements. Call Notes almost always are associated with the latter behaviors, whereas high intensity alarm, high intensity aggression, distress, and strong conflict find their expression only in other calls. Thus the above statements have to be refined to the very general statement that "Call Notes are in all species associated with a moderate intensity of arousal and a state of low motivational specificity." As dictated by function there is some variation in motivational structure between species. The function is more closely linked with arousal and alarm in smaller species, and with self-assertion in the larger *Picoides*. In the latter, Call Notes occur more frequently and in bursts (see Hinde, 1953, regarding *major*).

Scolding represents the state of alarm. There seem to be strong similarities with alarm-calls of other birds (see especially Curio, 1975). A common motivational background for the Rattle of all species known so far is aggression or at least dominance within an area. The best example illustrating this is Kilham's observation on Downy Woodpeckers (p. 33). Also our field studies on various species indicate that only well-established birds regularly give this call. In some species Rattles are connected with and closely precede or accompany attacks. For example, this is the case more in *syriacus* than in *major*. In species such as *canicapillus* (Short, 1973), and *medius* (Conrads, personal commun.), the Rattle Call even seems to be associated with initial alarm. The reactions of small *canicapillus* to large *macei* in the latter's presence hint at an alarm motivation being involved in the Rattle Call of the former. That hunger may influence the occurrence of Rattle Calls (most likely mediated by aggression) is shown by the Rattles of hungry fledglings.

Short Rattle Calls may indicate a conflict between tendencies to act aggressively and to flee, caused by the usually rather close proximity of the addressee and the recipient of the signal. Double Calls probably represent either (or both, perhaps varying among the species) very brief Short Rattles (high tendency to flee, e.g., in *syriacus*) or very aggressive Call Notes.

Mutter, Kweek, Twitter, Wicka, and Wad Calls

These calls are set in a framework stretching from aggression, fleeing, and submission at one side to approach, withdrawal, and staying in place on the other side. Two main sources of the observed variation are distance between addresser and addressee(s), and intensity and quality of the conflict among the forementioned motivations. Over a greater distance and/or with more addressees (e.g., in pair-pair encounters), the Kweek and Wicka calls are used. Applying the outlined framework, Type I Kweeks are submissive, and Type II Kweeks and, particularly, Wickas are aggressive. None of these exclusively represents the motivations indicated. Although the Wickas appear to be the most "threatening" signals they cannot be conceived as the signal in which the conflict between fleeing and aggression culminates. This is supposed to be the case in other signal systems (see for examples Eibl-Eibesfeldt, 1967), in which the "most threatening" vocal display is in its form intermediate between the most aggressive and the most submissive calls. Note that in our triangular system submissive is not synonymous with "most ready to flee." Submission includes as well the tendency to remain in place instead of fleeing. The frequent occurrence among species of *Picoides* of calls intermediate between the extremes is viewed as distinctly representing a conflict of motivations. The conflict between fleeing and aggression finds its expression in the Mutter and Twitter, and that between aggression and submission in the Wad. The intensity of the conflict mainly influences the rate of delivery of the calls. The variation in the structure of a call is difficult to understand in the case of the Mutter and the Twitter, and less so in the Wad. We restrict ourselves to discussion of the Wad Call. The most submissive Wads are those of the Kwah-type and the most aggressive ones those of the smacking type. The interrelation between the clicking and the squeaking elements of a particular Wad Call mirrors their respective underlying aggressive and submissive tendencies.

Since a bird usually will move away (flee) from an aggressor, it is evident that appeasement or submission is correlated with sexual behavior, which of course has a strongly seasonal pattern of occurrence. The influence of sexual behavior is reflected in appearance of signals such as Type-I Kweek Calls, and Wad Calls of the Kwah-type, and also calls transitional to the less seasonally influenced aggressive signals. The only exception to this is *borealis* in which the Kweek Calls show a wider social context.

Squeak Call

We believe that this call is uttered by a bird influenced by the two motivations of staying in place and withdrawal (fleeing). A third motivation, hunger, also often is involved. Hunger overwhelms the fleeing tendency and promotes all the actions that make the young bird conspicuous, and so lead to the close contact between parent and young. A parent woodpecker is to its young not only a "food source," but, because of its aggressiveness, also the object of fear. Even when the parent is far away and the hungry young calls for it, demanding food, the young bird also anticipates the coming, fear-inspiring contact, which is expressed in the combinations and transitions between the Call Note and the Squeak Call. The vocalizations reach their extreme form when the conflict between the motivations concerned is most intense, namely during the final phase of the approach immediately preceding the feeding act.

Drumming

This signal does not fit into either of the above used motivational frameworks. It can be linked to some extent with them, but not fully so. Drumming often is correlated with low levels of arousal as indicated by the frequently interspersed preening and the bird's usually relaxed posture. In situations of great arousal and in some conflicts, Drumming becomes irregular (Blume, 1961). It is easy to elicit Drumming by a human tapping on a tree, and it is likely that the acoustical properties of the substrate, as well as other acoustical signals, trigger Drumming. Drumming often evokes the same action in response; usually this is not true of vocalizations. It seems that there is a low threshold for Drumming, easily elicited even by extraneous noises or the Drumming of other species of picids.

Drumming thus appears to relate to a special category of motivation of its own, rather than being the outcome of the usually ascribed motivations.

THE MEANING OF THE VOCALIZATIONS

General Notes

The meaning of a signal depends on the information content of the message, further influenced by the context (Smith, 1965), and on the repertoire of referents available to the sender and the receiver. The information content can be deduced by careful observation of the circumstances surrounding the occurrence of a particular call, and its correlation with external and internal parameters of the communicator. It is more difficult to determine the preciseness with which the receiver can retrieve the original information content of a message. Only its reactions can provide clues helpful for analysis. The set of fundamental referents seems to be very small (Smith, 1969). However, it is quite difficult to establish such referents; those Smith chose are fairly heterogeneous, and they also include some functional aspects of the signal. We prefer not to describe distinct, basic meanings, ordering the various calls after them. Rather, we provide a brief discussion about their likely meanings. We classify the possible information carried by a vocalization as follows: (1) information about the sender; (2) information about the environment of the sender (including sender-environment relations, such as position); and (3) information to influence the receiver. Every call carries information of all three classes but the relative significance of these may vary between and even within the call-types.

The meaning depends on the information content of the call. This can be established by looking at the physical structure, which limits the amount of information transferable, and at its correlation with certain situations around and within the sender. The difficulties involve mainly the fact that the immediate response to a signal is not in itself a measure of meaning (for a theoretical discussion see MacKay, 1969), and also that the meaning depends upon the previous history of interactions of the receiving and sending individuals (see Simpson, 1973). As a starting point we suggest some ideas that should be testable as working hypotheses. It should be taken for granted that, although we are exclusively treating acoustical signals here, concomitant visual displays often are associated with vocalizations (e.g., the Kweek Call, which see, and associated display flights), and the overall meaning or meanings of such a display complex requires an understanding of all its aspects, visual and acoustical.

Call Note, Double Call, and Scolding Call

These signals mainly transmit information about the general state of arousal of the sender. For the receiver, this can be an important indication of the mood of the other bird. It is self evident that every call is an indication of the existence and, in the case of woodpecker calls, also the location of the sender. The Call Note announces the location of the sender as demonstrated by the fact that this call is delivered most often during, and especially shortly after, major changes of position. It is also the call given by fledglings still being fed by their parents. Experiments (Winkler, 1971a) with *major* and *syriacus* showed that this call attracts conspecific birds and stimulates them to seek the sender. In Scolding, all classes of information are important parts of the message: the announcement of the extreme motivational state, and hence the information that there is something causing the excitement, and information to induce the receiver to join the sender (adults), or to be quiet (nestlings). There might be an additional influence on the adult receiver. Alarm calls or Scolding are uttered not only in alarm due to disturbance in the nesting area, but also when the female encounters a strange male (see pp. 19, 24; *syriacus*, *pubescens*). Moreover, the alarm Scolding increases when the Scolding bird is joined by its mate. Thus, the call may involve a goading or inciting of the receiver (see also under "function"). An example of a similar case is the agitation movement ("inciting") of female ducks (Lorenz, 1941). Correlated with the variation in motivation of this call is a variation in its meaning. This involves both an announcement of location and a readiness to defend position or location. This meaning is related to aggression, and therefore those species that more frequently employ the Rattle Call use the latter for transmitting this information. The Double Call has about the same information content as the Call Note described above.

Rattle Call

The rather considerable ritualization of this call precludes it being a fine and sensitive indicator of emotional states of the signaler. But the apparent variation in length and rate of delivery may play a certain role in coding this type of information. Certainly, the basic aggressive motivation behind this vocalization usually is detected by the receiver. The call gets its specific role mainly through the combination of this information with the information which tells the place of the signaler. So the basic message is a self-confident statement about the presence, and to some extent the location (hence often uttered after alighting) of the signaler and its readiness to maintain its position. The diverse context of this call offers a rich set of possible meanings for the receiver. As an example, the previously sketched meaning becomes quite definite during encounters. As an answer to a Rattle given by the perceiver it simply signals an acknowledgment of the presence and location of the signaler. For the mated receiver this might mean that he may continue to feed, or it may tell him that he must proceed in a certain direction if he intends to start courtship behavior, and that he has to overcome a certain aggressiveness. In other situations the receiver can interpret this message as a challenge to answer, or to approach and make himself visible. Of special interest are the not infrequent combinations of the Rattle Call with Drumming or with the Kweek Call (see p. 23ff.). The close relation to the Call Note also is shown by the regular combination of these two calls. As discussed above (p. 87) these calls to some degree may replace each other in certain species. Thus, in a given species part of the field of meaning may be covered by one or by the other call. In species such as *syriacus*, *major*, *stricklandi*, and *villosus* the aggressive, challenging aspect is of greater importance than it is in *minor*, *medius*, and *pubescens*. These last three species, *canicapillus*, and especially *borealis* use this call also in the fledgling stage. The presence of the juvenile characters, compared with the full Rattle Call (pp. 23, 26) gives additional information; thus for the parents the call means there is a youngster to be fed, and that caution is needed because of the size and aggressiveness of the young bird. It is noteworthy that the ontogenetic development of the Rattle Call permits its use just when the young are of sufficient size and physical capability to pose an aggressive threat of some magnitude.

More information is needed about other species, and especially about *borealis*, for which the available information is too sparse to establish the (probably quite specific) meaning of the adult Rattle Call.

Short Rattle Call

It is somewhat difficult to find a common denominator for the meaning of this call. The Short Rattle obviously contains some information about the location of the sender; this is suggested by its similarity to the Rattle. This information also is meaningful for the intended receiver (most clearly so when young birds are calling) for whom it means to approach. Most Short Rattles are given by birds in a high state of alarm (in a very general sense). Thus, for the receiver it means that if it approaches the calling bird it will have an alarmed woodpecker with which to cope, with all the consequences of that situation.

Mistle Thrush Call

The available information does not permit any conclusion at this time.

Mutter, Kweek, Wicka, and Twitter Calls

This set of calls, as already discussed in the previous sections, comprises a functionally and motivationally interrelated system. The same can be assumed for their meaning. The main information of all these calls lies in the precise indication of the sender's motivational state. Their actual meaning derives from the accompanying actions of the sender and from the motivational state of the receiver, too, who accordingly is influenced to take appropriate action. This strong interdependence between the sender and the receiver, and the context and the structural diversity of the signals make possible a great range of meanings. In order to understand fully these meanings, and to conduct a thorough analysis, it is particularly important to achieve a comprehension of the social relations between the interacting individuals, including the history of their foregoing relations and encounters. The most interesting species for such an analysis would be *borealis*.

Wad Call

The information about the sender of the Wad Call is twofold. The call can express more or less submission, and it can give clues regarding the identity of the sender. Also, in many cases, a change is indicated in the distance between the recipient or its hole and the sender. Hence the recipient should be influenced not to flee, or to become aggressive. The information "moving" seems to be encoded mainly in the smacking sound, the information "submissive" and "staying here" in the middle part. An example would be the changing quality of the calls during the events involved in copulatory behavior. During incubation the call means to the receiver that the partner is approaching to relieve it, and hence that the hole has to be vacated. There is good reason to believe (see p. 59) that in at least some species this call also contains information about the individuality of the sender. For example, if a strange bird (intruder) should call at the nesting cavity, this would mean to the incubating bird "stay," and even "get ready to defend the nest." The mate, on the other hand, is readily accepted by the incubating bird.

Nesting Calls

These calls include Soft Notes, the Distress Trill, the Chirp Call and the Loud Chirp Call. Soft Notes and the Distress Trill can be seen as opposite extremes. They contain the information that the sender has experienced a pleasant change (Soft Notes) or a distressing one (Distress Trill). The basic meaning for the receiver, therefore, is to continue its present behavior if it receives Soft Notes, or to change it quickly if it hears a Distress Trill.

The Chirp Call means that there are young to be fed at a certain point in the home range. The Chirp also is capable of transmitting information about the developmental stage of the nestlings. The Loud Chirp Call carries this same information and additionally assures the feeding parent that the young is willing to accept food. It is interesting to note that the first point of information, that about the developmental status of the bird, is different in the Red-cockaded Woodpecker (see p. 66).

Squeak Call

The Squeak Call identifies the transmitter as a young woodpecker, which is not likely to attack. The diverse motivational states of the bird are encoded chiefly in the length of the call, which varies more than the pitch of the squeaking element. The call also contains the information necessary to control the parents' aggressiveness.

Distress Cry

The strong correlation between the utterance of this call and a specific situation leads us to the conclusion that the only information it contains is that the sender is in great distress, most likely because it has been seized by something harmful. Because of the lack of experiments, however, it is not clear whether this means that the receiving individual should seek information about what has happened, or what caused the trouble, or should simply flee. Perhaps the length, loudness, and repetition rate of the calls code more, differential, significant information for the receiving woodpecker.

Similar considerations probably hold for the Screech of which too few facts are known to allow more speculation.

Tapping and Drumming

These two instrumental signals are discussed under the same heading because it appears from the standpoint of information content that they are more akin than the functional diversity of the Drumming (at least as commonly held, see p. 90) may suggest. Both signals have something to do with the nest hole.

First let us consider Tapping. As far as evidence is available Tapping almost always is performed at the entrance of a newly started (nesting) cavity. So, the prevailing information on the signal is that a hole or an initial hole exists at a particular site. So this signal is the most significant of the woodpecker's repertoire with respect to information about a "thing" in the environment. It also has information to influence the receiver in two ways, namely to show him the precise location of the hole and to invite him to participate in the finishing or preparing of the hole for breeding. Anthropomorphically speaking, this could be summarized by the word "hole" and simultaneously pointing at it.

Compared with Tapping, Drumming is louder, more redundant (frequent repetition) and seemingly less specific. What it apparently lacks is the immediate relation to a hole. One could venture to say that this signal represents a step further toward abstraction, i.e., it is less ikonic. Tapping requires that the object be present; Drumming can be regarded as conveying the notion of the object, namely the hole. Thus we can put forward the hypothesis that in anthropomorphic terms Drumming means generally "hole!" with no indication of a precise site. We will shortly test whether this fits the various observations. First it is mainly performed, at least in the better known species, in the vicinity of a hole (a nesting hole, roosting hole, or an unused old hole) and very often in a dead or partly dead tree that would at least allow excavation of a hole. "Hole!" is an announcement that can function both as a territorial claim and as an invitation for a potential mate. Even the situation in which an enemy has come near the hole can be captured in this meaning (translated here as "hole!"). Structural differences in Drumming as are present in some species (e.g., *villosus* group) can be expressed by tonal differences; to stay in the anthropomorphic realm one can simply add exclamation marks. If such transliterations are to be tolerated at all, it is Tapping and Drumming that are the only signals so deserving. Compared with vocal signals, these instrumental signals are unusual in blending averbal, emotional utterances and abstract entities, as human words so perfectly do.

Sounds Made with the Wings

This acoustical signal apparently gives the information that a woodpecker is taking off, veering from course, or landing. This signal especially seems to be employed when a close contact has to be broken off, or else established. A very speculative hypothesis would be that the signal means to the receiver "move and thus reveal yourself." In *Colaptes auratus* wing sounds may play a role as alarm signals to nearby young or a mate (Short, unpubl. data), but such seems not to be the case in *Picoides*.

Call Elements

At the level of the elements there is no reason at all to assume that they possess any meaningful information. There role lies in the transport of information as such and in their ability to encode information by their combination into meaningful calls. One still could argue that at some level of perception the element as such could yield information about basic motivational states of the sender (see p. 94). Without the existence of relevant experiments the discussion of the problem cannot be pursued. Of course, if one considers not their quality, but presence or absence and numbers, then collectively these can have meaning, e.g., the number of elements of the three distinct parts of the complex Rattle Call of *arcticus*, and the omission completely of elements of one of these three parts from a Rattle obviously conveys a message, but this is not evidence that any individual element has meaning in itself.

Groups and Combinations

Theoretically, the compounding or adding to signals accompanying calls can change or at least influence the meaning of a call. Such effects can be summarized under the heading "context" (see p. 94). A different question is whether a group of calls as such has meaning as a group, one which could not be inferred from the knowledge of the meanings of the individual calls. For the former case some examples can be given, e.g., the combination Drumming-Rattle Call and the combination Kweek Call-Rattle Call. Probably in both cases the meaning of the particular call is narrowed by the presence of the other, but we cannot support this with evidence. A sequence, say, of Drumming, Wad Calls, and finally Tapping is highly organized, but the meaning of it still can be understood by simply stringing out the corresponding individual meanings. Further studies in this field surely would be rewarding because of the relatively slight complexity of the combinations in question.

THE HOMOLOGY OF THE VOCALIZATIONS

General Notes

Homology is an often debated concept of comparative biology. We do not want to enter into this discussion, and we do not ask whether homology is a useful concept. Rather, we follow the classical approach of ethologists in applying the basically morphological concept of homology to behavior. Among the many views of homology we choose to utilize the pattern outlined by Bock (1974, pp. 229-234). We do not treat vocalizations as morphological structures (Atz, 1970), but as similar to them. Also, we believe vocalizations to be equivalent to visual displays, and do not conceive of them as representing a behavioral product akin to a nest, as Atz (1970) does. Both visual and acoustical signals undergo the same amount of transformation until analyzed by the observer: nerve pulses–muscle activity–transmission by light waves or soundwaves–sampled by movie camera or tape recorder–and, analysis through a frame-by-frame analyzer or sonagraph.

Tembrock (1960), believing that such an approach is possible and useful, wrote that there had as yet been few such studies, and this is still true today. The main difficulty in all behavioral studies lies in the evanescence of behavior. Also a certain degree of completeness of the knowledge of the repertoire is necessary for an evaluation of features of any call (some examples will be found in the next section). We use two types of similarities for any analysis, namely similarities of the form of the call (or relation between its least separable units) on the sonagram, and similarities of the relations of a call with other entities (calls, displays, or situations).

Call Note

All the calls mentioned under this heading (p. 9) are considered to be homologous as Call Notes within the genus *Picoides*. These calls bear a close structural similarity, and they occur in similar situations, functionally expressing the presence of a woodpecker (see p. 86). Doubts arise only in the case of the Call Note of *arcticus* and *borealis*. However, the association of these calls with other behavior (see p. 9 ff.), and the structural similarity of their component elements to the Call Notes of other pied woodpeckers permit us to homologize these calls with the Call Note. The most important feature of the Call Note of *arcticus* is the lack of the middle element of the call. Looking at other species we can see that *villosus*, *albolarvatus*, and *tridactylus* exhibit a significant restriction of this element (figs. 3, 4). Moreover these species show a tendency for reduction in the amplitude of the first element (fig. 4). In fact, the sonagraphic structure of the Call Note of *albolarvatus* and *villosus*, both having lost the middle element, shows that they can be regarded as intermediate between typical pied woodpeckers and *arcticus*. The most unusual feature, apparently a derived condition, of the Red-cockaded Woodpecker's call is its strong frequency modulation (see p. 15). The long duration of the call is also extreme among the pied woodpeckers, although connected with the main group through the Call Notes of *stricklandi* and *villosus*.

Scolding Call

The only distinctive character of the Scolding Call is the time-patterning of the notes which always resemble Call Notes, being at the most somewhat louder and higher pitched. This holds for all species known so far. Thus the conclusion that all Scolding Calls have a common phylogenetical root is by no means farfetched. This seems to be the most conservative call with respect to time-patterning; Scolding notes never diverged much from Call Notes.

Double Call

This call is difficult to understand phylogenetically. It seems to bear some resemblance to the Short Rattle Call. Both calls are relatively little known, so later studies may shed light on their relations.

Rattle Call

The Rattle Call seems to have evolved from a series of Call Notes, and in its primitive stage consists only of a group of these notes. This pattern in its typical form mainly is found in some of the smaller Asian species and in *pubescens*. Two changes lead to calls of other species. In *minor* the single notes of the Rattle become longer and squeakier than a single Call Note. In the other species, generally those of larger body size than the aforementioned ones, a shortening of the notes emerges. This tendency is made still more pronounced by the parallel tendency toward frequency modulation; both trends lead to signals covering a wide frequency range and having a fast, regular time pattern. With these statements we anticipate the question of homologizing the various Rattles dealt with in the first section of this report. By so doing it becomes evident that all the Rattles are very easily linked. However, it should be noted that the shortening of the Rattle notes in the larger species could have and, very likely, did emerge independently at different phylogenetic points. Perhaps the best character for revealing the phylogenetic relations among the Rattles is the initial note which, of all notes within a Rattle, most resembles the Call Note of any given species. A somewhat difficult case is the Rattle Call of *arcticus*, in which the Rattle bears no relation to the Call Note. The characters that can be used here are the serial organization and the tendency to become more frequency modulated, and/or that for shorter notes (see fig. 19). This probably is the most derived Rattle Call of all.

Summarizing, we state that the Rattle Call of the extant pied woodpeckers derives from a primitive Rattle comprised mainly of Call Note-like notes showing a separation in structure between the first note and those following, the former remaining like a Call Note.

Short Rattle Call

It is uncertain whether this category is a phylogenetic unit at all. There seem to be two related calls, the Double Call and the Rattle Call. Perhaps we have in this group two types, namely, one stemming from the Double Call, the other from the Rattle. Therefore, we do not suggest any definitive statement about the homology of this call.

Mistle Thrush Call

This strange call seems to have no counterparts in the repertoire of species other than *major*. Hence, one is tempted to reason that it is a specialized form of one of the other categories. Possible candidates are the Short Rattle Call and, less likely, the Twitter Call (or Mutter Call). Until new data are available, no further statement can be made.

Mutter Call

Physical structure would appear at first glance to be of no value in ascertaining the relations of this call. The best starting point seems to be a comparison of the situations in which this call is employed. The only call that could be derived from the same ancestral call with respect to this trait is the Twitter Call. If this is correct the Twitter Call (which see) would be more similar to the ancestral call, because it shows fewer derived features than does the Mutter Call. The initial and closing parts of the Mutter Call have been reduced or even lost, and the central portion has become frequency modulated. There is some tendency toward frequency modulation in Twitter Calls, and a similar trend is found in the Wad Call. Perhaps the distinct and regular frequency modulation of the Mutter Call can be understood as a reaction to the possible misunderstanding of these two otherwise very similar calls. There is also a point that the pitch of the central part of the Twitter Call of various species matches fairly well with the carrying frequency of the Mutter Call. Thus, Mutter and Twitter calls appear homologous through an ancestral Twitter-like call.

Kweek, Wicka, and Twitter Calls

The reason we discuss these three calls together is because they seem to have a similar common structure. If we start from a hypothetical call that has all the features commonly found in this group of calls it would be composed of two Call Notes (forming the first and last parts) connected by a squeaking element (central part). Probably an ancestor of the genus had only one such call; very likely it already showed considerable variation according to motivation. During further evolution, the parts of the continuum became more distinct. The Kweeks are derived from this hypothetical primitive call by reducing the first element and by stressing the second and the third, which also elongates, and perhaps becomes higher pitched, and louder. In the Type I Kweek Call the third part is the most impressive structure, and in the Type II Kweek the second element tends to merge into the rising portion of the last element. So all Kweeks but those of *medius* and *borealis*, which shall be discussed subsequently, can be regarded as homologous, as a "conflict" call and moreover, at the level of the genus, even as distinct Kweeks. The Kweek Calls of *medius* and *borealis* were put in this category in the first chapter because they are the only squeaking calls of adults. This superficial similarity has to be looked at more closely in order to justify homologizing them as Kweek Calls. The forementioned similarity is an argument based on the supposedly sufficient knowledge of the repertoires of both species. Thus, the conclusion is based on two hypotheses, namely that these calls are not entirely new entities, and that our knowledge is complete in this respect. The most difficult case is that of *borealis*, because the Kweek notes are very similar to the usual Call Notes. It could be that there are two types of Call Notes in this species. To this view one can retort that no Call Note is so variable as to allow such a dichotomy so easily. Even more unlikely is the possibility that the Kweek is the Call Note and the Call Note is a Kweek! The fact arguing against this is the presence of the usual combination of Call Note and Rattle. Variability, seriation, and situation make it reasonable to conclude that the Kweek is homologous with the other Kweeks as the Kweek Call. This is also the most parsimonious conclusion at the moment.

The evolution of the Kweek Call of *borealis* can be understood on the basis of the social structure of this species. The context that probably favored the development of such a call is the feeding of fledglings. As there is some evidence that Kweek Calls are employed by adults feeding fledglings, apparently as an appeasement, one can imagine that out of this situation a generalized signal evolved that now plays an important role in group maintenance.

We believe that it is possible to derive the

Kweek Call of *medius* (some of the arguments to be used would also apply to *borealis* above) from a primitive pied woodpecker Kweek Call. In *medius* the similarities between the Call Note and the Kweek Call are so weak that one can safely discard the possibility of the latter being a derivative of the former. We have already noted the tendency of this Kweek Call to become longer, especially in its third part. A fine example of the possible link between primitive Kweek Calls and the derived one of *medius* is provided by that of *canicapillus*. Thus the Kweek Call of *medius*, and very likely that of *borealis* (it is inconceivable that these represent a single phyletic line), are Kweek Calls with reduced first and second parts, and an elongated third part. We observe that both apparently belong to what we might term the most "peaceful" Kweek Calls in the entire assemblage, although the selective reasons for their similarity are different. In the case of *medius* the loss of Drumming favored the expanded development of the Kweek, which is, importantly, the only call having a close connection to Drumming both in its occurrence in certain situations (one should recall the high coincidence of these two signals in other species) and its seasonal distribution through the year. Besides that it is one of the few available long-range vocal signals.

The Wicka has no such spectacular derivatives. Its occurrence within the genus makes it questionable whether primitive *Picoides* ever had a specialized call such as the call here designated the Wicka Call. The Wickas are easily derived from the Type II Kweek Call just by continuing the overall tendency, ending up with the falling leg of the first part and the rising one of the third part separated by a gap which is hardly different from that between the notes in a series. Thus our conclusion is that the Wicka Calls are homologous as specialized conflict-calls related to the Type II Kweek Call; not unlikely they evolved several different times from the Kweek Call in different groups within the genus.

The Twitters, finally, can be visualized as short range, low intensity forms of a primitive conflict call. They show all the features of this hypothetical call. Perhaps their most noteworthy characteristic is that, if they change in the course of phylogeny their reductions occur more symmetrically than in the Kweek; the third element here also seems to be that most resistant to shifts. Similarities in structure, in the way they are combined with other calls and especially with visual displays, and their situations of occurrence provide a firm basis for the conclusion that Twitter Calls are homologous as such, and also as conflict calls. One possible exception is the Twitter series we described for *syriacus*, which perhaps should be excluded from the above statement. This signal remains doubtful in its origin. The reasons why we believe that the Mutter Call and the Twitter Call are homologous as Twitter Calls have been mentioned above.

Wad Call

Based on similarities with respect to physical structure and their situations of occurrence this category probably forms a phylogenetical unit too. There are aspects that make more detailed interpretation difficult. There is the intraspecific variation of this call from a smacking extreme to a plaintive extreme. We have no information about the presumably more primitive species and how their Wad Calls vary. Thus we cannot state whether this call is primitive, or is a relatively new feature that perhaps evolved several times independently. There are some similarities between the Wad Call and the Twitter Call. This possibly hints at a phylogenetic relationship between these calls.

Soft Notes

Although sparse, the data nevertheless indicate a close resemblance in a phylogenetic sense between the Soft Calls of different species. Moreover, the special situations of occurrence and apparent function (p. 89), and their physical character resemble those of vocalizations of species representing not only other woodpeckers but even other orders. It is commonality of function, and in part the early developmental stages of birds that allow the widespread occurrence of a signal such as this. This also suggests that a comparative analysis of this call-type might yield useful information even above the generic level.

Distress Trill

Although data about this call are meager for this genus, it may be expected that it is a call common to all species. It doubtless will be proved that these calls are homologous in *Picoides*. A still more interesting aspect of this call is the possibility of finding homologous calls in other genera, even orders, in which special distress calls of very young birds exist (e.g., Anseriformes, Galliformes). Special attention should be paid by future investigators to its relation with the ontogeny of the Short Rattle Call.

Chirp and Loud Chirp Call

These calls are widespread within the family and the order (e.g., barbets). Within the genus *Picoides* there is no doubt that all the calls put into these two categories are homologous as nestling calls (Chirp Call) and loud nestling and fledgling calls (Loud Chirp Calls), respectively.

Squeak Call

We state that the Squeaks of the pied woodpeckers are homologous as squeaking calls given by fledged birds when fed. Separation from the Loud Chirp Call is not always clear, and in fact ancestrally there may have been even less differentiation of these calls.

Screech Call and Distress Cry

Distress Cries of the pied woodpeckers are homologous as series of notes of long duration, rich with overtones and subject to various degrees of frequency modulation, given in distress. Frequency modulation alone as a prevailing feature is a derived condition and appears in *borealis*. The Screech Call can be regarded as a specialized Distress Cry with strong, irregular frequency modulation (=noise). It remains to be determined whether a more primitive form of a Distress Cry exists in adult three-toed woodpeckers (*tridactylus* and *arcticus*).

Tapping and Drumming

Some authors (e.g., Blume, 1968) think that Drumming evolved from Tapping. However, this process must have taken place well before the radiation of the genus *Picoides*. Therefore this subject is not pursued further. The widespread occurrence of these two signals backs the assumption that each of them corresponds to such a signal in the common ancestor. The apparent lack of Drumming in *medius* has to be considered as a derived condition.

Eibl-Eibesfeldt (1967, p. 121) believed that Drumming evolved from the birds excavating holes. This view is corroborated somewhat by the fact that, starting with excavating for feeding purposes through hole-excavating and finally Drumming, there is evident an increasing tendency to form discrete groups of strokes and to maintain a regular rhythm (Winkler, unpubl. data). There is also the fact that birds other than woodpeckers do not excavate in hardwood and have not evolved Drumming. The apparent shift into different forms of Drumming by some of the New World species is a further derived condition not present in more primitive species.

Homologs in Other Woodpeckers

It is outside the scope of this report to compare the vocalizations we have discussed with those of other woodpeckers, and in fact data are too sparse (especially, too few data are available for numbers of species in any one genus) to permit such an effort. Nevertheless, we note that calls similar in sound and context to those of *Picoides* are found in other picids. Drumming of course is widespread in this family, but variation in its circumstances of occurrence is little known. Further data, much needed, may help to establish homologies, even unsuspected, between other groups of woodpeckers and *Picoides*. We are a long way from attempting a family-wide analysis of the type we have undertaken for *Picoides*. Many, especially large woodpeckers employ a Long Call, a loud, long-distance call that functionally relates to both Drumming and Rattle Calls of *Picoides*; some species using this call Drum, others do so rarely or not at all (see Short, 1972, 1973). There may be relations between the Kweek of *Picoides* and Long Calls of other picids (e.g., *Picus*). Call Notes vary greatly in structure and probably in function in woodpeckers, and they appear to be lacking or are replaced by other calls in some groups. Certainly, they are not homologous throughout the family. Kweek-like calls have been noted by the junior author in many species of picids, but their derivation is unclear. Particularly interesting would be information concerning African *Dendropicos*, which has a vocal repertoire resembling that of *Picoides* (Drumming is minimized and Call Notes are less common in comparison, Short, personal observ.)—this genus is thought by us to contain the closest relatives of *Picoides*.

TAXONOMIC CONSIDERATIONS

We find that certain results of our analyses have bearing on the systematics of the pied woodpeckers. This is not the place to delve into the relationships of these woodpeckers, rather we will consider some instances in which these data are in agreement with, or suggest modifications of, the existing classification of pied woodpeckers (see Peters, 1948; Short, 1971a, 1974a, and MS). Another point to be considered is the relative primitiveness versus specialization (or primitive versus derived condition) of a few call-types indicated by what we know of the vocalization. Of course, it proves that most of the calls are variable, indistinct, or insufficiently known to provide taxonomically useful information at this time.

The Call Note is potentially useful for taxonomy. The New World assemblage shows characters of length of the note and the break in the center of the note that agree well with Short's (1971a) conclusions. There is a high-pitched Call-Note group including at least *pubescens*, *scalaris*, and *nuttallii*. A longer noted, lower pitched group is comprised of *villosus*, *stricklandi*, *albolarvatus*, *tridactylus*, *arcticus*, and *borealis*. A definite break or tendency toward a break in the center of the note characterizes *albolarvatus*, *villosus*, and especially *arcticus*, and to an extent *tridactylus*. Most of the other species that are well-known fall into a short-lengthed, lower pitched cluster.

An attempt was made to relate some parameters of this call to one another and to the environment. We devised a subjective scheme categorizing 15 levels of density of vegetation in the habitats of pied woodpeckers, and assigned values to each species (some species, e.g., *major*, *scalaris*, vary greatly, of course). We also established a size-ranking of species, and compared these rankings, the habitats, and the pitch of the peaks of the Call Notes. We found a weak, statistically insignificant negative correlation between size of the woodpeckers as indicated by wing length and the pitch of the Call Notes (this does not mean that correlation is absent, as we know that intraspecifically the pitch of smaller races is higher than that of larger races, e.g., in *villosus*; Short, personal observ.). There was a positive correlation between the pitch and habitat ranking, that is, woodpeckers of denser habitats give lower-pitched calls. The P-value for significance of the correlation was just above the 0.05 level for all species for which habitat information could be appraised based upon our personal experience, with but three species, *nuttallii*, *pubescens*, and *tridactylus* falling out of line to any great degree (when these three species were removed from consideration the correlation for the remaining species gave a value of P less than 0.01).

Further data are required on Call Notes of Asian species before we can say much about inferences from Call Notes regarding taxonomy (see Appendix 1).

The Rattle Call shows some tendencies that are of importance. More primitive or less derived species of this genus show less distinction between the Call Note and the Rattle Call. All the species having marked Call Note-Rattle Call differences are thought on other bases (e.g., Short, 1971a) to be specialized (for example, *arcticus*, *borealis*, *major*). We noticed a linear relationship between the duration of the note of the Rattle Calls and the intervals between these notes, correlating very well for all species except *minor*, *medius*, and *dorae*. In this feature *medius* and *dorae* are similar and are distinct from both the main group of *Picoides* and also from *minor*. Among Short Rattle Calls, that of *tridactylus* bears resemblance to the Rattle Call of *stricklandi*.

The Kweek Call will prove useful, ultimately, because of its variation. However, more species must be studied in detail. It should be possible to plot the occurrence and variations in the two types of Kweek Calls in various species and species groups. Striking Kweek Calls such as that of *medius* may better be placed in perspective when Kweeks of more Asian species are known.

As calls become better known for more species, gaps will be discovered, doubtless, akin to the absence of Drumming in *medius*. At the moment we cannot be certain that particular calls are actually lacking in many of the species.

The vocal data in their entirety suggest certain points. For example, the evidence corroborates other data in emphasizing the distinctiveness and probable monophyly of the New World group. The relationships within this group as discussed by Short (1971a, 1974a) generally are upheld. These include the close relationship of the three-toed woodpeckers to the *villosus* subgroup, the inclusion of *villosus*, *stricklandi*, *albolarvatus*, *tridactylus*, and *arcticus* in that subgroup, and the relations of *pubescens* with *scalaris* and *nuttallii*. Changes that may be indicated from Short's (1971a) scheme are: (1) *borealis*, rather than being nearer the *pubescens-scalaris* group appears to be vocally more like the *villosus* group; (2) *arcticus* and *tridactylus*, although within the *villosus* subgroup, are more distinctive, and may be related more closely to *albolarvatus* than to *villosus* itself; and (3) *arcticus* is very specialized and probably is less closely related to *tridactylus* than thought previously by Short. Nonetheless, the acoustical analyses show that all the American species are interrelated rather closely.

Applications to the Old World species are more difficult—as shown in Appendix 1, only two of 11 New World species are poorly known vocally, but 12 of 22 Old World species are poorly known. All that can be said at the moment is that: (1) as suggested from other data (Short, MS) *medius* and the *major* group (*major*, *syriacus*, *assimilis*, *himalayensis*, *leucopterus*) appear to be highly derived and specialized; (2) *medius* is more distinct than we had realized earlier, and seems not to be as close to *leucotos* as we previously had thought; (3) from what little data are available, *dorae* and *obsoletus* fit well within the range of variation of *Picoides*; (4) *obsoletus* may be related rather closely to *minor*; and (5) there is agreement with other data (Short, 1971a) that the primitive members of the genus are to be found among Asian species, including relatives of *minor*, *canicapillus*, and *moluccensis*, i.e., that such groups as *medius* itself, the *major* group, and the American group have their common ancestor in an ancestor of some of the Asian species, from which they have differentiated, undergoing specialization. We would welcome acoustical data on such species as the pygmy woodpeckers *maculatus* and *temminckii*, *auriceps*, *mahrattensis*, and *hyperythrus*, particularly the first and last of these, which seem on other bases to be somewhat distinctive. Further data also are required for such species as *obsoletus*, *kizuki*, *atratus*, *dorae*, *cathpharius*, *leucopterus* (or *assimilis*, or *himalayensis*), and *lignarius* both to check the meager results we have so far for some of these species, and to add other species to those known for certain groups so that we are not unduly biased by the single (or two) species of those groups for which data are available.

APPENDIX 1

LIST OF PIED WOODPECKERS AND STATUS OF ACOUSTICAL DATA

SCIENTIFIC NAME[1]	VERNACULAR NAME	AVAILABLE ACOUSTICAL DATA
Picoides temminckii	Temminck's Pygmy Woodpecker	Almost nil
Picoides moluccensis ("nanus")	Brown-capped Woodpecker	Little
Picoides maculatus	Philippine Pygmy Woodpecker	Little
Picoides obsoletus	Brown-backed Woodpecker	Little
Picoides kizuki	Japanese Spotted Woodpecker	Little
Picoides canicapillus	Gray-capped Woodpecker	Fair
Picoides minor	Lesser Spotted Woodpecker	Good
Picoides macei	Streak-bellied Woodpecker	Fair
Picoides atratus	Stripe-breasted Woodpecker	Almost nil
Picoides auriceps	Brown-fronted Woodpecker	Almost nil
Picoides mahrattensis	Yellow-crowned Woodpecker	Little
Picoides dorae	Arabian Woodpecker	Little
Picoides hyperythrus	Rufous-bellied Woodpecker	Almost nil
Picoides cathpharius	Crimson-breasted Woodpecker	Little
Picoides darjellensis	Brown-throated Woodpecker	Little
Picoides medius	Middle Spotted Woodpecker	Good
Picoides leucotos	White-backed Woodpecker	Fair
Picoides himalayensis	Himalayan Woodpecker	Little
Picoides assimilis	Sind Woodpecker	Almost nil
Picoides syriacus	Syrian Woodpecker	Excellent
Picoides leucopterus	White-winged Woodpecker	Almost nil
Picoides major	Great Spotted Woodpecker	Excellent
Picoides mixtus	Checked Woodpecker	Little
Picoides lignarius	Striped Woodpecker	Almost nil
Picoides scalaris	Ladder-backed Woodpecker	Good
Picoides nuttallii	Nuttall's Woodpecker	Good
Picoides pubescens	Downy Woodpecker	Excellent
Picoides borealis	Red-cockaded Woodpecker	Fair
Picoides stricklandi ("arizonae")	Strickland's Woodpecker	Good
Picoides villosus	Hairy Woodpecker	Excellent
Picoides albolarvatus	White-headed Woodpecker	Fair
Picoides tridactylus	Three-toed Woodpecker	Fair-Good
Picoides arcticus	Black-backed Woodpecker	Good

[1]Synonyms sometimes used are in parentheses.

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