VOCALIZATIONS OF THE GREEN AND SOLITARY SANDPIPERS*

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FEW areas of ornithology have developed as rapidly and along such exciting lines as the study of avian vocalizations. Logically much of this work deals with passeriforms, for it is on members of this group that many of the classical discussions of song variation, development, function, and learning were based. Certain non-passeriform groups, too, are well suited for studies of this type. Within the Scolopacidae, for example, the relative dependence upon vocal as compared to visual communication varies enormously. The Ruff (*Philomachus pugnax*) is silent (Hogan-Warburg, 1966) and the Buff-breasted Sandpiper (*Tryngites subruficollis*) nearly so (Oring, 1964). Though other calidridines are more vocal, as a group their repertoires are simple. Ferdinand (1966) described spectrographically the complex vocalizations of the Great Snipe (*Capella media*). Similar analysis of the Long-billed Curlew (*Numenius americanus*) (Forsythe, 1967), as well as written descriptions of Black-tailed Godwit (*Limosa limosa*) (Lind, 1961), and Greenshank (*Tringa nebularia*) (Nethersole-Thompson, 1951) vocalizations, indicate that tringines too have well developed vocal powers. Indeed, personal observations of the Eurasian Curlew (*N. arquata*) indicate that its aerial advertisement song may be more complex and variable than the songs of many passerines. The intra-familial voice range described above, coupled with relatively simple voice structures, would seem to make the scolopacids excellent subjects for evolutionary studies of avian sounds.

Of approximately 85 scolopacid species, only the Solitary Sandpiper (*Tringa solitaria*) of the Nearctic and Green Sandpiper (*T. ochropus*) of the Palearctic lay their eggs in arboreal nests—most often in old nests of certain passeriform species. Both *solitaria* and *ochropus* are solitary and territorial the year-round. The Wood Sandpiper (*T. glareola*), a close relative of *solitaria* and *ochropus*, is wide-ranging, utilizes a variety of nest-sites including old arboreal nests, is gregarious to some extent all year, and shows relatively little intraspecific aggression. A comparative behavioral study of this threesome was begun in an effort to gain insight into the adaptive significance of behavioral patterns as shown by close relatives occupying similar (*ochropus* vs. *solitaria*) and markedly different (*ochropus* and *solitaria* vs. *glareola*) ecological niches. This report attempts to describe and compare the vocalizations of *T. ochropus* and *T. solitaria*. Stress has been placed upon the evolution of these vocalizations, their adaptive significance, and their integration into the overall be-

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SOLITARY SANDPIPER *(Tringa solitaria)* chick, one day old. Painted direct from life 22 June 1968, by Walter J. Breckenridge. The egg, taken when fresh from a nest in central Alberta, was hatched in an incubator in Minnesota.

havioral schemes of the two species. Subsequent papers will deal with other aspects of behavior as well as with the phylogeny of *Tringa*.

STUDY AREA AND METHODS

From 5 April to 3 July 1966 and 10 March to 1 July 1967, I studied *T. ochropus* in Halle-Hunneberg National Forest, 10 km east of Vänersborg, Västergötland, Sweden. One brood was reared in captivity from 31 May to 3 July 1966 after which it was observed in the Copenhagen zoo. *T. solitaria* was studied from 4 to 13 May 1968 at Riding Mountain National Park, Wasagaming, Manitoba, Canada and from 15 to 26 May 1968 at Crimson Lake Provincial Park, 12 km NW of Rocky Mountain House, Alberta, Canada. One clutch, transported from Alberta to Minnesota, later hatched. These young were studied from 21 June to 12 July.

The vocalizations of five pairs of both species were tape recorded with a Uher 514 microphone and 4000L tape recorder at the speed of 19 cm/second. Recordings of adults were aided by the use of a ½m fiberglass parabola. Vocalizations were played at normal speed into a Kay Electric Co. Sonograph machine, model 6061A, at H-S and wide band settings. Frequency measurements were made from narrow band sonograms. Vocalizations were played back in the field through a National Panasonic portable radio model RF885L. Sexes were differentiated only during copulation and egg-laying. In a few cases, members of a pair differed in minor morphological features adequate for individual recognition.

DESCRIPTION OF VOCALIZATIONS

I have called those vocalizations which seem dependent upon sex hormones, which are relatively complex in structure and long in duration, and which function in territory establishment and defense, songs. All others have been designated as calls. An attempt to classify the vocalizations of *T. ochropus* and *T. solitaria* has led to the recognition of two song types and five types of calls in both species. Only those adult vocalizations restricted to the reproductive season appear to be highly stereotyped. Three types of calls are arbitrarily recognized for *ochropus* juveniles and six for *solitaria* young. In the juvenile calls of both species frequency continuums exist with modes apparent at the extremes. All of the juvenile calls of *ochropus* are about 1.5 kc higher than those of *solitaria* whereas the reverse is true of adult vocalizations. Though songs and "epigamic" calls were more frequently given by males than females, all adult vocalizations of both species were given by both sexes. No consistent individual variation was noted. Though some variation in frequency and duration of vocalizations can be accounted for by chance, my data indicate that frequency is influenced by volume (and hence syringeal tension)—louder sounds being slightly higher in pitch. A
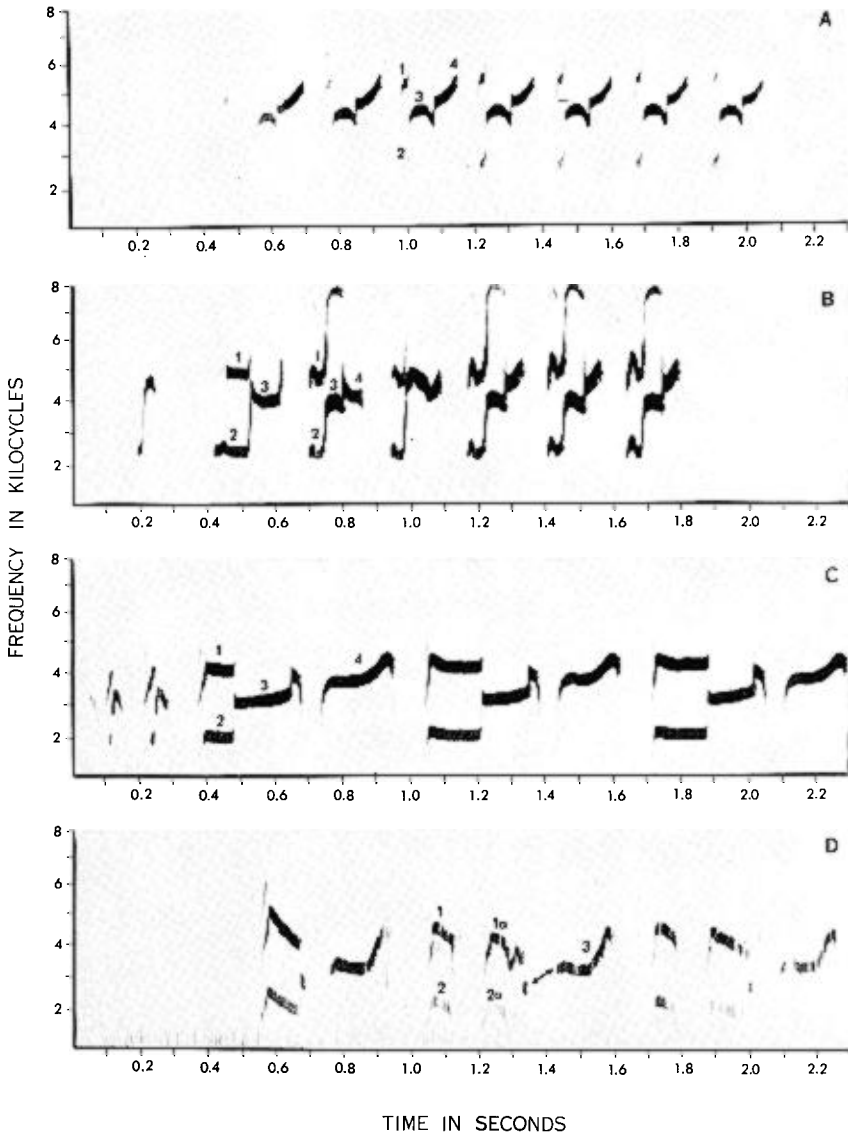
TIME IN SECONDS

FIG. 1. Spectrograms of *T. solitaria* (A–B) and *T. ochropus* (C–D) songs: A, simple "Type II"; B, first unit is simple "Type I"; second and third are intermediate, and the remainder complex "Type II"; C, "Type I"; and D, "Type II" (first unit aberrant). Numbers above song units pertain to individual subunits referred to in the text. Subunits with like numbers are probably homologous.

TABLE 1

NUMERICAL DESCRIPTION OF ADULT VOCALIZATIONS*

	Tringa solitaria			T. ochropus		
	N	x̄	S.D.	N	x̄	S.D.
Song "Type I"						
Duration in seconds	12	0.189	±0.026	44	0.652	±0.076
Interval to preceding song unit in seconds	2	0.140	±0.028	37	0.110	±0.019
Maximum frequency in kc/sec	10	5.51	±0.35	44	4.57	±0.15
Minimum frequency in kc/sec	12	2.38	±0.11	44	1.80	±0.15
Song "Type II"						
Duration in seconds	78	0.159	±0.016	21	0.601	±0.054
Interval to preceding song unit in seconds	76	0.065	±0.009	16	0.121	±0.018
Maximum frequency in kc/sec	78	5.90	±0.30	21	4.89	±0.16
Minimum frequency in kc/sec	78	2.55	±0.41	21	1.80	±0.05
"Contact" call						
Duration in seconds	9	0.045	±0.005	45	0.043	±0.012
Interval to preceding call in seconds	8	0.188	±0.042	35	0.146	±0.042
Average frequency in kc/sec	9	4.70	±0.26	45	3.28	±0.23
"Alarm-attack" call						
Duration in seconds	23	0.050	±0.002	33	0.082	±0.018
Interval to preceding call in seconds	18	0.366	±0.126	23	0.072	±0.041
Average frequency in kc/sec	23	4.77	±0.06	33	3.22	±0.18
"Epigamic" chatter call						
Duration in seconds	26	0.046	±0.021	47	0.078	±0.017
Interval to preceding call in seconds	16	0.088	±0.074	35	0.074	±0.036
Average frequency in kc/sec	26	4.65	±0.23	47	3.18	±0.25
"Epigamic" long whistle call						
Duration in seconds	24	0.083	±0.010	22	0.279	±0.057
Interval to preceding call in seconds	17	0.117	±0.014	21	0.091	±0.019
Maximum frequency in kc/sec	24	5.32	±0.44	22	4.34	±0.24
Minimum frequency in kc/sec	24	3.12	±0.66	22	2.40	±0.27
Average frequency in kc/sec	24	4.81	±0.15			
"Alarm-flee" call						
Duration in seconds	15	0.097	±0.028	30	0.152	±0.051
Interval to preceding call in seconds	10	0.144	±0.061	22	0.093	±0.011
Maximum frequency in kc/sec	15	5.17	±0.24	30	4.50	±0.20
Minimum frequency in kc/sec	15	4.23	±0.12	30	3.08	±0.10

* N = sample size; x̄ = mean; S.D. = standard deviation. Average frequencies were determined subjectively by estimation of the frequency on either side of which lies half of the sound energy.

similar phenomenon occurs in man as volume and laryngeal tension increase. In *Tringa*, higher frequencies seem to be lost when recordings are made over great distances as Marler and Isaac (1960) suggested might be the case in their study of the Chipping Sparrow (*Spizella passerina*). I did not investigate geographical variation.
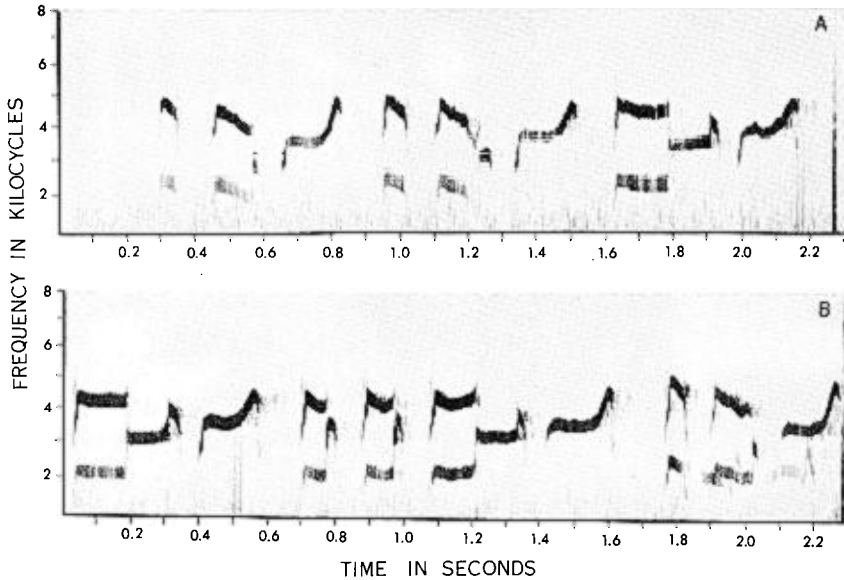
FIG. 2. Spectrograms of *T. ochropus* songs showing change-over: (A) from "Type II"
to "Type I"; and (B) "Type I" to "Type II." Units in the middle are aberrant.

T. ochropus: Physical description of songs.—Songs are normally composed of one or
both of two basic structural units, hereafter designated "Type I" and "Type II" (Fig.
1 C–D, Table 1). "Type I" units are composed of four main subunits which I refer to
as "1" (mean of the duration = 0.160 sec, standard deviation = ±0.018 sec; mean of the
average frequency = 4.02 kc/sec, standard deviation = ±0.27 kc/sec), "2" (0.160 ±
0.018 sec, 2.04 ± 0.17 kc/sec), "3" (0.195 ± 0.023 sec, 3.07 ± 0.23 kc/sec), and "4"
(0.229 ± 0.050 sec, 3.62 ± 0.28 kc/sec). A harmonic is present above "1" at about 6 kc.
Subunits "1" and "2" occur simultaneously and are linked to "3." To the human ear,
the combination of "1," "2," and "3" sounds like a clear whistle abruptly lowering in
frequency at the midway point. After an almost indiscernible pause (0.065 ± 0.010 sec),
subunit "4" ascends as a musical whistle from the point where "3" leaves off.

"Type II" units contain five main subunits which will be called "1" (0.075 ± 0.008 sec,
4.39 ± 0.16 kc/sec), "2" (0.075 ± 0.008 sec, 2.28 ± 0.06 kc/sec), "1a" (0.152 ± 0.015
sec, 4.02 ± 0.18 kc/sec), "2a" (0.152 ± 0.015 sec, 2.10 ± 0.11 kc/sec), and "3" (0.209 ±
0.035 sec, 3.40 ± 0.21 kc/sec). Harmonics are present above subunit "1" at about 6.8 kc
and above "1a" at about 6.4 kc. "1" and "2" occur simultaneously as do "1a" and "2a."
The two pairs are separated by an interval of 0.077 ± 0.011 sec. "1a" and "2a" are, in
turn, separated from "3" by a pause of 0.089 ± 0.021 sec. A "Type II" unit, because of
its two pauses, as well as the relative shortness and great frequency range of its sub-
units, is not as musical as is "Type I."

The two unit types described above are given 1 to 19 times to form a song. The median
number of unit repetitions in songs composed of all "Type I" units is 4 (extremes 1–9);
in songs composed solely of "Type II" units 6 (extremes 2–19). "Type I" units are oc-

casionally given singly, intermixed with "epigamic" calls. Any one song may be composed of all "Type I" units, all "Type II" units, or a combination of the two. A change-over from "Type I" to "Type II" may occur at any point within a song but it is more likely to occur between songs, hence most songs contain only one of the two types. Of 230 songs recorded during 1967, 69 percent contained only "Type I" components, 25 percent only "Type II," and 6 percent both types.

Songs may be separated by long periods of time or they may be so close together (about 0.1 seconds) that it is nearly impossible to say when one ends and another begins. Up to 67 units in 12 songs have been recorded in a minute; and 148 units in five minutes.

Vocal units are remarkably uniform as regards spectrographic configuration. Of the 148 mentioned above, 145 represented the normal stereotyped structure of "Type II" and three contained an extra preliminary note. Aberrant units sometimes occur at the start of a song (Fig. 1D) but most often are found when a bird changes from one unit type to another in the middle of a song. These usually include characteristics of both normal types (see Fig. 2).

T. ochropus: Biological description of songs.—Songs occur from the time birds arrive on the breeding ground until about when young are fledged. Peak occurrence is from arrival of females until the first egg is laid and, to a lesser degree, during egg-laying and hatching. "Type I" songs may continue until the start of southbound migration and occasionally occur south of the breeding ground during northward migration.

Birds sing "Type I" songs from the ground, elevated singing perches such as rocks or trees, or in the air. When in the air, they may be part of advertisement displays—most often when the bird is taking off or landing—or they may be given during direct flight. When on the ground, singing birds often raise and spread their tails. When both members of a pair are at the nest prior to the laying of eggs, whisper singing (Lister, 1953) is not uncommon. Song "Type II" occurs as part of a complex advertisement and territorial defense display which includes an undulating flight and steep dives. This display is performed over feeding and nesting territories as well as over intervening areas when the two territories are not adjacent most often during early morning and evening. During pair formation and copulation, a similar display of small amplitude is sometimes directed over the female. Occasionally a "Type II" unit is tacked onto a series of "Type I" units during direct flight.

Singing is elicited by the "epigamic" calling or singing of another bird in the vicinity of the territory. The sight of and/or sounds from pipping eggs and newly hatched young also elicit singing. Songs may be given spontaneously. They function in stimulating the female during pair formation and copulation situations, in advertisement and defense of territories, as well as in pair bond maintenance.

Vocalizations preceding and following songs are most often reciprocal song types and "epigamic" calls (see Figure 3 for flow pattern of vocalizations given during sexual and agonistic encounters). In addition to those
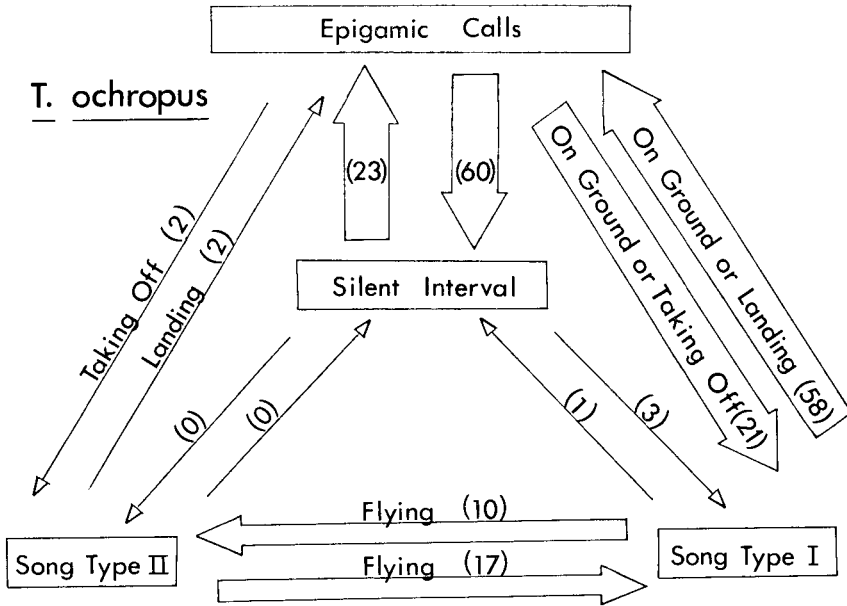
FIG. 3. Flow pattern of *T. ochropus* vocalizations given on the ground and in the air during sexual and agonistic encounters on feeding and nesting territories. Arrow thickness indicates relative frequency of a particular sequence. My sample was biased because recordings were frequently not begun until a bird was already calling or singing. Numbers from "silent interval" to "epigamic calls" to "song Type I" to "song Type II" are thus smaller than normally expected. Song types on this illustration refer to entire songs.

sequences diagramed in Fig. 3, songs are also preceded by "alarm-flee" calls during the pre-incubation period when a bird flies over its nest.

Conspecifics respond to songs as follows: those believed to be unpaired females join in aerial advertisement; mates of displaying males may ignore them or move toward them while uttering "alarm-attack" or "epigamic" calls; and those thought to be unpaired males join in display. The latter eventually leave or are chased. Pairs from nearby territories frequently join in display and chases may follow. When a bird sings in another bird's territory, the host may respond by uttering "alarm-flee" calls from a high perch (sometimes the nest bowl). When far apart, mates may keep track of each other by singing back and forth. Table 2 summarizes the results of song playback experiments.

T. solitaria: Physical description of songs.—These too are composed of one or both of two basic structural units or components again designated "Type I" and "Type II" (Fig. 1 A–B, Table 1). "Type I" units include three main subunits hereafter called "1" (0.094 ± 0.029 sec, 5.12 ± 0.26 kc/sec), "2" (0.094 ± 0.029 sec, 2.64 ± 0.16 kc/sec), and "3" (0.083 ± 0.016 sec, 4.63 ± 0.27 kc/sec). Subunits "1" and "2" occur simultaneously.

TABLE 2

REACTION OF *T. OCHROPUS* ADULTS TO REPEATEDLY PLAYED TAPE RECORDINGS OF
"TYPE I" AND "TYPE II" SONGS OF CONSPECIFICS

Date	Classification of subject	Area No.	Activity and location of subject	Reaction
1 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew toward tape recorder, displayed over it more than one minute.
2 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew toward tape recorder, displayed over it less than one minute.
4 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew away uttering "Type I" songs.
5 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew away uttering "alarm-flee" calls.
9 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew toward tape recorder, flew away uttering "alarm-flee" calls, displayed over marsh—all repeated.
10 April (First day ♀'s were in area)	Unpaired ♂ ?	1	Feeding within 50 m	Flew away uttering "alarm-flee" calls; returned to alternately display over recorder, sing above it, and walk to it, tail raised.
12 April	Paired ♀	1	In trees within 50 m	No reaction.
12 April	Paired ♀	1	Feeding within 50 m	No reaction.
12 April	Paired ♂	1	Feeding 500 m away	Flew to mate; both displayed over marsh, then answered each other with "epigamic" calls and "Type I" songs on ground.
20 April	Paired ♀ prior to 1st egg	1	On nest within 50 m	Flew away uttering "alarm-flee" calls; then sang in distance.
20 April	Paired ♂ prior to 1st egg	1	Feeding within 50 m	Flew toward tape recorder, then ran to within 5 m of it, tail partly raised.
17 April	Unpaired ♂ and ♀	2	Pair-formation within 50 m	♂ raised and fanned tail, ♀ raised unfanned tail; pair took off displaying out of sight.
28 May	Paired ♂ and ♀	2	Unsuccessful copulation within 50 m	♀ ignored it, ♂ flew toward tape recorder displaying near it for less than one minute.

In seven of nine cases, they were connected to "3" without a pause; in the remaining cases the pause averaged 0.140 ± 0.028 sec. Subunit "3" is quite variable in spectrographic form but usually is U-shaped—ascending sharply at the end. In one case a constant frequency was maintained. "Type I" units sound like a short, high-pitched whistle abruptly increasing in frequency about the middle.

"Type II" units are composed of four main subunits which will be referred to as "1" (0.031 ± 0.014 sec, 5.32 ± 0.30 kc/sec), "2" (0.031 ± 0.014 sec, 2.69 ± 0.16 kc/sec), "3" (0.065 ± 0.009 sec, 4.21 ± 0.26 kc/sec), and "4" (0.066 ± 0.013 sec, 4.82 ± 0.15 kc/sec). "1" and "2" are N-shaped and occur simultaneously. A fairly strong harmonic occurs above them at about 8 kc. Subunit "3" is continuous with "1" and "2" but at frequencies intermediate between them. Subunit "4" begins at a frequency level intermediate between "1" and "3" and rises sharply. "Type II" units appear to the human ear as high-pitched, short and rapidly ascending whistles.

The two unit types described above are repeated 3 to 12 times to form a song. Any one song may be composed of all "Type I" units, all "Type II" units, or a combination of the two. "Type I" units hardly ever follow a "Type II" unit when they are both part of the same song. The one possible exception recorded is pictured in Figure 1B where song unit composition is I, II, I, II, II, II; but even here, the second and third song units may be considered intermediates. Occasionally, "Type I" units are given singly with "epigamic" calls. Of 28 songs recorded in 1968, two were composed of all "Type I" units, 10 were made up of a combination of the two types, and 16 contained only "Type II" elements. Songs may be separated by long periods of time as is the usual case, or they may be repeated with only about 0.2 second intervals. The greatest number of units recorded in a minute was 24 in two songs.

Vocal units are not nearly so uniform as in *ochropus*. "Type I" units may or may not have a pause in the middle. Subunit "3," while U-shaped in all but one case, is quite variable in configuration. "Type II" varies a great deal with regard to the duration and energy pattern of subunits "1" and "2." Extremes are illustrated in Figure 1 A–B.

T. solitaria: Biological description of songs.—Songs occur from the time of arrival on the breeding ground until at least clutch completion and probably to the start of southbound migration. Migrants in Minnesota during early July are not known to sing. Songs are frequent just prior to egg laying as in *ochropus*.

Birds sing from the ground, from elevated singing perches such as treetops, or in the air—either during direct flight or as part of an irregular shallow arc display. Songs are given at feeding and nesting territories and when birds fly between the two, especially during early morning and evening. When singing on the ground, birds may spread their unraised tails and lift their wings overhead.

Singing is elicited by the singing of a strange bird near the territory or by any of a number of vocalizations of a mate. Songs may be given spontaneously. Songs function in an excitatory capacity in sexual situations, in advertisement and defense of territories, and in pair bond maintenance. Vocalizations preceding and following songs are diagramed in Figure 4.

Conspecifics usually respond to songs by singing after the singer is seen.
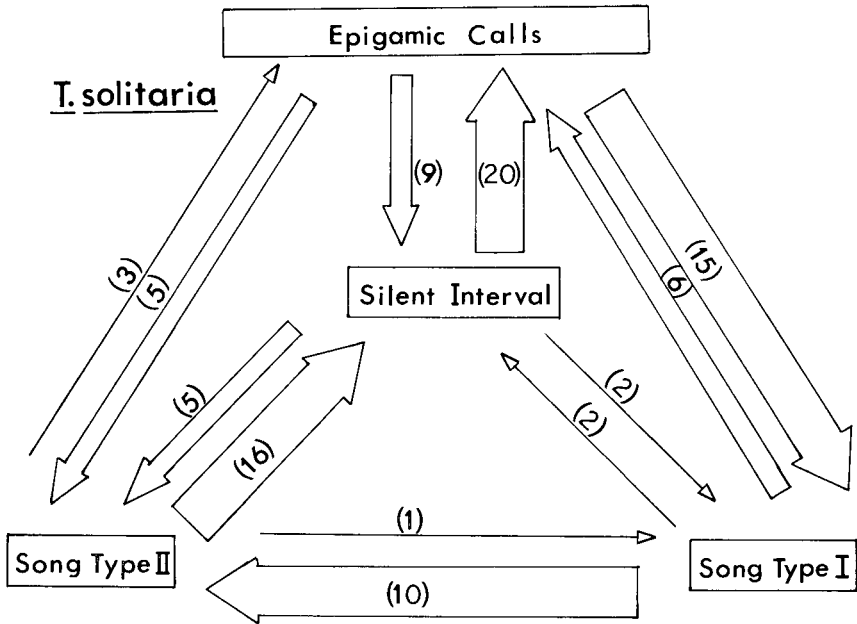
FIG. 4. Flow pattern of *T. solitaria* vocalizations given on the ground during sexual and agonistic encounters at the feeding territory. Thickness of arrows indicates relative frequency of a particular sequence. Song types on this illustration refer to song units rather than to entire songs since songs are not so frequently repeated as in the Green Sandpiper.

Singing intruders are chased from territories just prior to egg laying and perhaps at other times. Members of a pair often maintain contact with each other by singing back and forth. "Type I" and "Type II" songs of *ochropus* were played to *solitaria* at various stages of the breeding season but all results were negative.

T. ochropus: "epigamic" call.—Those vocalizations restricted to the reproductive season but not fitting song criteria of Tinbergen (1939) or Thorpe (1961) have been termed "epigamic" calls. In *ochropus* this includes two structurally different vocalizations which nearly always occur together. They may thus be discussed together when speaking of function but must have separate treatment in discussions of structure. The first of these two types I've designated "epigamic" chatter, the second "epigamic" long whistle.

Chatter is so called because it consists of a noisy, rhythmic series of calls (Fig. 5F, Table 1). These calls, while similar in nature, are always of shorter duration, closer together, and of less frequency range (maximum minus minimum) at the start of the series than at the end. The median number of call repetitions is 4 (extremes 2–10).

In 77 percent of the cases (N = 158), a single long whistle (Fig. 5F, Table 1) followed a series of chatter calls. The name long whistle has been derived from the call's
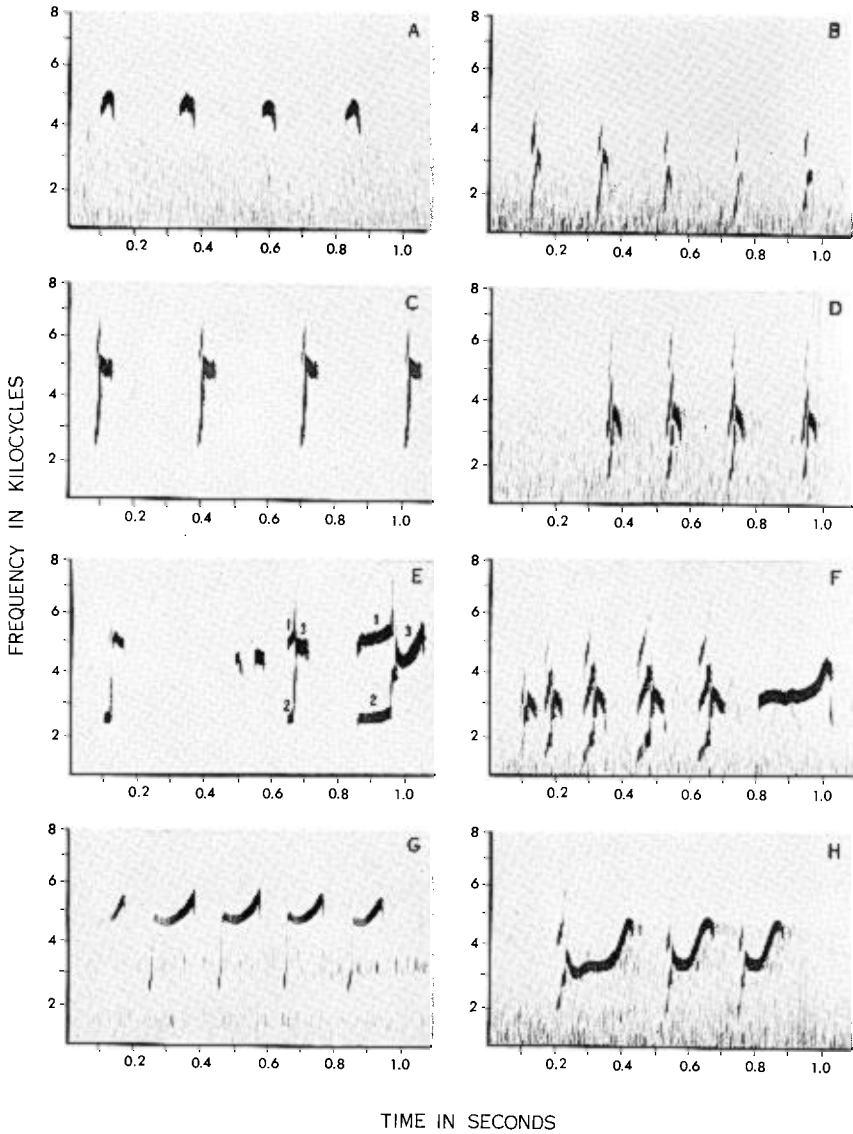
FIG. 5. Spectrograms of *T. solitaria* (left) and *T. ochropus* (right) calls: A–B, "contact"; C–D, "alarm-attack"; E–F, "epigamic"; and G–H, "alarm-flee." Numbers on part E pertain to individual subunits referred to in the text. Subunits with like numbers are probably homologous.

long duration and clear tonal quality. At times, chatter and long whistles are uttered continuously for 15 minutes or more. On rare occasions as many as three long whistles have been repeated in sequence but they nearly always occur singly at the end of chatter.

"Epigamic" calls occur from the time females arrive until the beginning of incubation and briefly when eggs are hatching. Birds call from the ground or elevated perches on the feeding or nesting territory. Calls are elicited by the singing or "epigamic" calling of a mate; or they may be uttered spontaneously. Apparently calls are also elicited by the sight of nest, eggs, or young. These calls function in stimulation of the female during pair formation and copulation situations; and are used by males to entice females to nests. When both members of a pair are at the nest prior to the egg laying period, these calls are often uttered at extremely low volume and are intermingled with whispered "Type I" song. Figure 3 diagrams the relationship between "epigamic" calls and other vocalizations in complex vocal sequences during sexual and agonistic encounters. Conspecifics may, if receptive, move toward a bird giving these calls—sometimes uttering "Type I" songs or "epigamic" calls. When the approach to a calling bird is in the air, it may be accompanied by "alarm-attack" calls.

T. solitaria: "epigamic" call.—As in *ochropus*, there are vocalizations which do not fit the classical definition of song but which are restricted to the breeding season. These calls are highly variable in configuration but seem to have a like function. For comparative purposes, I have retained the terms "chatter" and "long whistle" applied to *ochropus* though they are not descriptively accurate for *solitaria*.

The various short notes, here referred to as chatter, are repeated an average of 4.5 times in a series (see left ⅔ Fig. 5E; Table 1). As many as five series in a row, each separated by only a 0.2 second pause, have been recorded. One or two of the individual call notes include a considerable amount of noise; the others are spread over a narrow frequency range and are produced at very low volume.

Long whistles occur in similar situations to chatter though the two do not occur together in a definite and predictable series as in *ochropus*. Whistles have been recorded in groups of 2, 3, 3, 3, 3, 4, and 4. Characteristically they drop in frequency at the end. Whistles are very closely related to chatter in configuration but have been expanded a good deal in duration (Table 1). Because of this similarity to chatter, they are not illustrated.

The seasonal duration of calls, location of calling birds, eliciting stimuli, function, and reaction of conspecifics seem to be the same as for *ochropus*. Because I left the breeding grounds at the completion of clutches I do not know if these calls are given after that time. The relationship of these calls to other vocalizations within complex vocal sequences is diagramed in Figure 4. The headings song "Type I" and "Type II" refer to individual song units and not to entire songs.

T. ochropus: "alarm-attack" call.—These harsh, rapidly repeated calls are characterized by their short duration, constant between call intervals, and wide frequency range (Fig. 5D, Table 1).

This call type is given in a number of situations: (1) when danger is apparent but not imminent, perhaps to attract the attention of a predator for distraction purposes; (2) when young are threatened, at which time the median number of call repetitions is 4; (3) during short flights on the feeding or nesting territory, especially during approach to the nest when the median number of call repetitions is 10; (4) just prior to leaving for or from the nest when the median number of call repetitions is 4; and (5) during attack in aerial chases. Table 3 summarizes data pertinent to this and other calls of both species.

TABLE 3

Synopsis of *Tringa ochropus* and *T. solitaria* Vocalizations Not Specifically Related to Sexual Situations

| Species and call	Period of occurrence	Place of occurrence	Eliciting stimulus	Function	Reaction by conspecifics	Associated call
T. ochropus "alarm-flee"	At least Mar.–Sept.; probably all year	Anywhere	Impending danger	Warn conspecifics	Flee	"alarm-attack"
T. ochropus "alarm-attack"	At least Mar.–Sept.; probably all year	Anywhere	Impending danger	Warn conspecifics; attract predators	Flee, alert, or hide (young)	"alarm-flee"
T. ochropus "contact"	At least Apr.–Sept.	Anywhere	Brood and/or hatching eggs	Intra-familial contact	Answer with like calls	————
T. solitaria "alarm-flee"	At least Apr.–Sept.; probably all year	Anywhere	Impending danger	Warn conspecifics	Flee	"alarm-attack"
T. solitaria "alarm-attack"	At least Apr.–Sept.; probably all year	Anywhere	Impending danger	Warn conspecifics; attract predators	Flee, alert, or hide (young)	"alarm-flee"
T. solitaria "contact"	At least May–Sept.	Anywhere	Mate; probably as in *ochropus*	Intra-familial contact	Answer with like calls	————
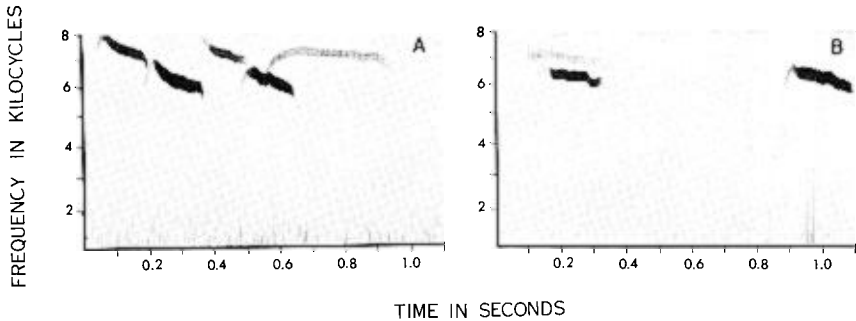
FIG. 6. Spectrograms of the calls of day-old *T. ochropus*: A, "mild distress" (left) and "content" (right); B, "content" (above) and intermediate between "mild distress" and "content" (below and right).

T. solitaria: "alarm-attack" call.—These calls appear as short, harsh, metallic tones (Fig. 5C, Table 1). Like comparable calls of *ochropus*, they are characterized by a certain amount of noise. "Alarm-attack" calls occur in the same situations as in *ochropus*. When an intruder is near the young, the median number of repetitions is 6 (extremes 1–80).

T. ochropus: "contact" call.—These are low volume calls with a relatively small musical element and a relatively great amount of noise. They are the shortest of all *ochropus* vocalizations in duration; and individual calls are nearly twice as far apart as in the "alarm-attack" or "epigamic" chatter (see Fig. 5B, D, and F for a comparison of the three types; Table 1). The median number of call repetitions before and after hatching is 3 (extremes 2–15).

These calls occur in the following situations: (1) between members of a pair while they are feeding separately or are otherwise separated by fairly short distances; (2) between members of a pair while at their nest, mixed at extremely low intensity with whisper "epigamic" calls; (3) during the entire pipping and hatching periods by the sitting adult at various intensities, mostly very low, until the young are dry—at which time the intensity increases and the calls are uttered from the ground—seemingly to induce young to jump; and (4) as follow calls on the ground until the young are fledged. When an adult calls its brood over a great distance, volume and the number of call repetitions increase; but intervals between calls remain the same. This and other calls are summarized in Table 3.

T. solitaria: "contact" call.—As in *ochropus*, these are low volume calls. Their configuration is that of an inverted V; and they have no significant element of noise (Fig. 5A, Table 1). The median number of call repetitions is 3 (extremes 1–17).

These calls have been noted in the first two situations as listed above for *ochropus* and probably occur in all four. See Table 3 for a comparison to other calls.

T. ochropus: "alarm-flee" call.—These are sharply ascending calls characteristically possessing an element of noise at the start (Fig. 5H, Table 1). "Alarm-flee" calls given from the air are usually single whereas a series of three or four is normal when given from a stationary perch. When several calls are given in series, the first is invariably the longest and has the lowest minimum frequency. The duration of successive calls becomes less and less but the frequency usually remains the same or nearly so after the second call. These calls are loud from start to finish and are shrill to the human ear.

The "alarm-flee" call has been recorded from four situations: (1) in flight any time

TABLE 4

SYNOPSIS OF CALLS OF *TRINGA SOLITARIA* AND *T. OCHROPUS* CHICKS*

Species and call	Age when first recorded	Age when last recorded	Associated behavior	Connotation
T. solitaria "contact"	10 hours	17 days (last day birds were healthy)	Laying, sitting, standing, or feeding	contact
T. solitaria "contact" (intense)	2 days	17 days	walking, running, or feeding	contact; intermediate between content and distress
T. solitaria "content-moving"	5 hours	17 days	walking and/ or feeding	satisfaction
T. solitaria "content-still"	6 hours	17 days	sitting or standing	satisfaction
T. solitaria "mild distress"	5 hours	17 days	restlessness, searching for food	hunger or cold
T. solitaria "intense distress"	5 hours	17 days	running and pecking	hunger, cold, or pain
T. ochropus "content"	5 hours	22 days	sitting or standing	satisfaction
T. ochropus "mild distress"	5 hours	35 days (beginning of transition to adult "alarm-flee")	restlessness, searching for food	hunger or cold
T. ochropus "intense distress"	3 days	35 days (beginning of transition to adult "alarm-flee")	running and pecking	hunger, cold, or pain

* Table form adopted from Forsythe (1967).

an adult or its brood is directly threatened with danger, the median number of repetitions being 3 (extremes 1–5); (2) when a bird takes off spontaneously; (3) as a bird flies by or from its nest prior to the start of incubation; and (4) when a strange pair attempts to establish itself in the territory of another pair—whether it be the nesting or feeding territory, the median number of repetitions being 1 (extremes 1–3). In the latter case, the female of the established pair repeatedly utters volleys of "alarm-flee" calls from the nest bowl or a perch above the feeding territory while her mate displays in the air. The latter is the only known situation in which these calls are given by a stationary bird.

    T. solitaria: "alarm-flee" call.—As in *ochropus*, these calls rise sharply in frequency after an initial noise element (Fig. 5G, Table 1). There is no predictable pattern to changes in duration and frequency of successive calls of a series.

    These calls have been noted whenever danger is impending. They were repeatedly given

TABLE 5

NUMERICAL DESCRIPTION OF CHICK CALLS*

T. solitaria	"contact"			"contact" intense		
	N	x̄	S.D.	N	x̄	S.D.
Duration in seconds	12	0.041	±0.007	29	0.065	±0.009
Interval to preceding call in seconds	10	0.249	±0.055	24	0.250	±0.029
Maximum frequency in kc/sec	12	5.29	±0.20	29	5.83	±0.35
Minimum frequency in kc/sec	12	4.63	±0.14	29	4.50	±0.23

T. solitaria	"content" moving			"content" still		
	N	x̄	S.D.	N	x̄	S.D.
Duration in seconds	12	0.119	±0.013	10	0.201	±0.044
Interval to preceding call in seconds	10	0.216	±0.037	—	—	—
Maximum frequency in kc/sec	12	6.04	±0.24	10	5.20	±0.15
Minimum frequency in kc/sec	12	4.73	±0.35	10	4.38	±0.19

T. solitaria	"mild distress"			"intense distress"		
	N	x̄	S.D.	N	x̄	S.D.
Duration in seconds	22	0.113	±0.012	12	0.143	±0.015
Interval to preceding call in seconds	13	0.099	±0.018	10	0.240	±0.024
Maximum frequency in kc/sec	22	6.33	±0.35	12	5.48	±0.19
Minimium frequency in kc/sec	22	4.60	±0.32	12	4.27	±0.11

T. ochropus	"mild distress"			"content"		
	N	x̄	S.D.	N	x̄	S.D.
Duration in seconds	24	0.192	±0.026	10	0.33	±0.042
Maximum frequency in kc/sec	24	7.33	±0.48	10	7.36	±0.22
Minimium frequency in kc/sec	24	6.18	±0.37	10	6.42	±0.25

N = sample size; x̄ = mean; S.D. = standard deviation.

by birds flushed from complete sets of eggs in contrast to *ochropus*. In this situation, the median number of call repetitions was 2 (extremes 1–5).

Calls of T. ochropus chicks.—Three types of calls were noted: (1) "content," (2) "mild distress," and (3) "intense distress." The first two are illustrated in Figure 6 along with intermediates between "content" and "mild distress." "Intense distress" calls were not tape recorded but basically differed from "mild distress" only by their being louder and more repetitious. A summary of pertinent information is given in Table 4; descriptive statistics are included in Table 5. Table 6 summarizes the reactions of chicks to the vocalizations of adults.

Calls of T. solitaria chicks.—These young produced a number of different vocalizations. It is problematical as to how many should be given different names since a continuum from shortest to longest occurred. Modes were apparent at the two ends of this continuum. For the purposes of this paper I have recognized six types—illustrated in Fig. 7A–F. Numerical descriptions of these calls can be found in Table 5 and a summary of pertinent data sufficient for present purposes can be found in Table 4.

TABLE 6

REACTION OF *TRINGA OCHROPUS* CHICKS TO VOCALIZATIONS OF ADULTS

Location	Age	Vocalization	Source	No. Brood Observations	Reaction
Wild	1 day	"contact" call	Parent	2	Jump from nest, move toward parent; "content" call given; one separated from siblings gave "mild distress"
Wild	1 day	"alarm-attack" call	Parent	2	Crouch silently
Wild	1 day	"alarm-flee" call	Parent	2	Scatter, crouch (perhaps in response to "alarm-attack" calls)
Paper bag near nest	1 day	"contact" call	Parent	1	Move toward parent; utter "mild distress" calls
Captivity	1 day	"alarm-flee" call	Tape	1	Scatter to corners, crouch
Captivity	1 day	"contact" call	Tape	1	Move toward recorder
Captivity	2 days	"alarm-flee" call	Tape	1	Scatter to corners, crouch
Captivity	6 days	"alarm-flee" call	Tape	1	Scatter to corners, crouch
Captivity	11 days	"Type I" song	Tape	1	No reaction
Captivity	est. 13 days (just caught in wild)	"Type I" song	Tape	1	Cock head; give "mild distress" calls

DISCUSSION

In view of the lack of information available on the vocalizations of scolopacids, I have not been able to compare a great many species. Instead, I have described sounds produced by two closely related species occupying somewhat similar arboreal niches in different zoogeographical areas. Subsequent reports will compare these two species to closely related ground-dwelling forms. Emphasis in this and subsequent reports will be placed upon the evolution of sandpiper vocalizations.

Alarm calls of a number of European passerines have been analyzed spectrographically; and a remarkable similarity was found. They possessed in common a long duration and uniform high pitch (Marler, 1959). It was concluded that they were mutually well adapted to meet predation pressures in that these alarm calls would be extremely poor for binaural or phase location. This same spectrographic pattern is found in the downy young "content-still" calls of both *T. ochropus* and *T. solitaria*. In view of the similarity of
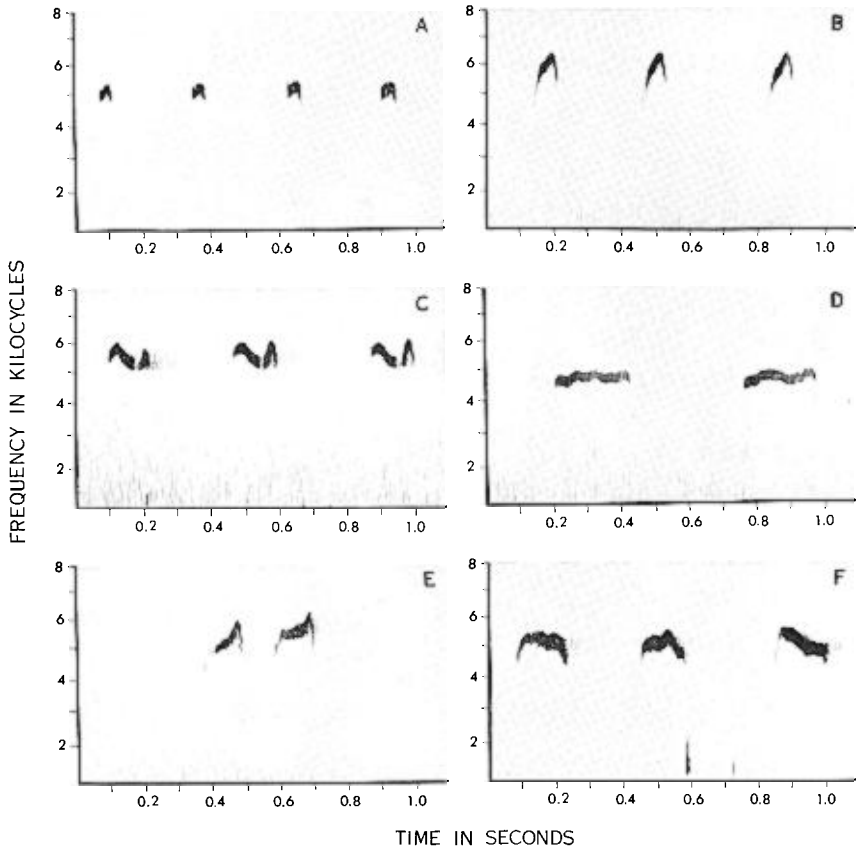
FIG. 7. Spectrograms of the calls of downy *T. solitaria*: A, "contact"; B, "contact" (intense) ; C, "content-moving"; D, "content-still"; E, "mild distress" (hungry or cold) ; and F, "intense distress."

ecological situations, including predators, faced by both species (and by the passerines mentioned above) this call similarity is not surprising.

I do not have data to indicate which adult calls, if any, "content-still" calls evolve into during the course of ontogeny. I do know that shortly after *T. ochropus* young fledge, they have no calls as high in frequency as the young "content" call, and that in early fall only "alarm-flee" and "alarm-attack" calls are heard. Distress calls of these species will probably, when careful analysis is complete, be shown to merge with the "alarm-flee" calls of adults.

No short rhythmic calls were noted in *ochropus* chicks. In *solitaria*, the calls I've called "intense contact" in the young are almost identical spectrograph-

ically to the "contact" calls of adults. Those of the young birds are however longer, separated by greater intervals, and considerably higher in frequency (Figs. 5A and 7, Tables 1 and 5). How much of this difference is due to syrinx maturation is a point for future investigation. The constant intervals between "intense contact" calls, indicate that they are suited for intra-specific phase location. The fact that they possess a greater frequency range than low intensity "contact" calls (Table 5) further indicates a location function. They may well be intermediate between low intensity "contact" calls, and calls produced in slightly distressful situations. Experiments to test this hypothesis are planned. An intermediate motivational state may also be involved in eliciting "content-moving" calls.

One might argue that "contact," "alarm-attack," and "epigamic" chatter calls of both *solitaria* and *ochropus* adults, are variants of a single call dependent upon changes in the motivational substrate for their identities. Increased structural complexity as well as functional specialization from "contact" to "alarm-attack" to "epigamic" chatter, may be indicative of the phylogeny of this call complex. Certainly their spectrographic forms indicate that they are closely related (Fig. 5A–F). I have preferred, however, to treat them separately in order to emphasize their functional differences. In my opinion, "contact," "alarm-attack," or "epigamic" chatter calls of the two species are homologous and analogous. These three calls, though functioning in different contexts, probably all serve to aid in location of conspecifics. Their structures would seem well adapted for this purpose, for as Marler (in Marler and Hamilton, 1967) pointed out, ". . . low frequencies are best for locating sound by phase differences, and high frequencies are best for intensity difference. The easiest sounds to locate are those that provide cues for all methods, requiring a wide frequency spectrum and sharp discontinuties." In both species, the "contact" call, which is uttered by birds fairly close to each other and which are involved in activities not directly related to the calls, e.g. feeding, possess the poorest location cues. But their shorter duration and smaller frequency range means less sound energy expended and at close range these calls are seemingly adequate for location. "Alarm-attack" and "epigamic" chatter, are more efficient for location purposes according to Marler's criteria. This is not surprising in view of the fact that these calls are functional parts of activities having considerable selective importance.

"Alarm-flee" calls of *solitaria* and *ochropus* are also somewhat similar (both being high pitched and rapidly ascending in frequency) and, I presume, homologous as well as analogous. In both species the calls begin with a noise element not unlike that of "alarm-attack" calls. Whether this structural similarity is indicative of functional and/or evolutionary relationships between the two types is difficult to say. But it is of special interest that all

possible gradients between "alarm-attack" and "alarm-flee" calls occur. They
were noted once for *solitaria*—when an incubating bird was flushed from its
nest but remained near it. While sitting still or moving toward the nest, it
gave "alarm-attack" calls; when fleeing it gave "alarm-flee" calls; and when
flying short distances to other perches equidistant from the nest it gave inter-
mediate calls. In *ochropus* the same thing occurred when parents circled the
fence in which their young were trapped. Calls intermediate between "alarm-
attack" and "alarm-flee" thus occur in both species in intermediate motiva-
tional situations. Variations of this sort are to be expected in calls not involved
in reproductive isolation.

A single "alarm-flee" call such as the first of the series illustrated in Fig.
5 G–H, provides little in the way of location cues. In *ochropus*, one or less
often two of these calls is usually given by a flying bird. "Alarm-flee" calls
do, however, occur in series—the intervals between them being constant. In
particular, this occurs when a stationary female defends a territory from
intrusion by a conspecific. In such a case, the addition of location cues af-
forded by phase differences would seem to be of adaptive significance. In
either case—whether given singly or in series—this call seems to convey the
message "danger—flee."

In Fig. 5F, as one follows the "epigamic" chatter from left to right, it is
noticeable that time intervals as well as call durations increase. This is a
regular phenomenon as chatter progresses toward a song (Fig. 1C) or long
whistle (Fig. 5F). In Fig. 3, it is shown that chatter normally precedes song
"Type I" and that "Type II" is more specialized, occurring primarily in aerial
display. I propose that this sequence—from "epigamic" chatter to "Type I"
to "Type II"—is a recapitulation of *ochropus* song evolution. All of the
elements of "Type I" subunits "1," "2," and "3" including the first harmonic,
can be clearly found in epigamic chatter (Fig. 1C). In addition, spectrograms
of chatter not reproduced here possess greatly expanded elements. Subunit
"4" is strikingly similar to the long whistle (Fig. 5F). The origin of the long
whistle and subunit "4" is open to question. They are apparently closely re-
lated to each other.

"Type II" units, which are more specialized in structure and function,
nevertheless hold clues to their evolutionary origin. If, for example, those
subunits labeled "1" and "1a" are rejoined and those labeled "2" and "2a"
likewise, they are strikingly similar to units "1" and "2" of the "Type I" song
seen in Fig. 1C. And furthermore, if subunit "3" of Fig. 1D is attached to the
small energy blotch visible between and to the right of "1a" and "2a," this
song suddenly becomes nearly identical with subunits "1," "2," and "3" of
song "Type I" (Fig. 1C). What seems to have happened in the course of song
evolution is that "1" and "2" have split giving rise to "1" and "1a"; and "2"

and "2a" respectively; and "3" has broken off from its former connection to "1a" and "2a." It is also possible that "1" and "2" may have arisen secondarily by addition. In either case, a double-pause song highly specialized for aerial displays has evolved. Its characteristics—double pause and increased frequency range—enhance its use as a location cue over great distances.

The songs of *solitaria* have much in common with the basic *ochropus* pattern. As in *ochropus* (Fig. 1C), the three subunits of "Type I" seem to be represented in elements of "epigamic" chatter (Fig. 5E). "Type I" units, and to a lesser extent "Type II" units (Fig. 1A–B), are very much like the "1," "2," and "3" part of "Type I" *ochropus* songs, except that they are shorter in duration and higher in frequency. The series of calls shown in Figure 5E may well be close to repeating the evolutionary history of *solitaria* "Type I" songs. *Solitaria* songs have no intra-unit intervals but inter-unit intervals may be significant aids to location.

In both *ochropus* and *solitaria*, "Type II" units are shorter and have higher maximum frequencies than "Type I" units (less than 5 percent of the time the means of duration and maximum frequency could be expected to overlap). In *solitaria*, the minimum frequency is higher and intervals between songs shorter in "Type II" than in "Type I." In other words, there has been a tendency for the more specialized songs (ones performed at higher intensity) to include more sound energy at higher frequencies per unit of time. The four song types of *solitaria* and *ochropus* all end in clear tones—well suited for conveying species-specific information.

Precise measurements of time spent and energy expended in song production per season are not available. Nevertheless, it is obvious that *ochropus* sings louder and perhaps as much as ten times more often than *solitaria*. Because the two species nest in comparable parts of the boreal forest, lay their eggs most often in old passerine nests, and are solitary year-round, their ecological niches have been presumed nearly identical; but never have dissimilarities been stressed. In southern Sweden, *ochropus* commonly utilizes the nests of three turdid species—the Blackbird (*Turdus merula*), Song Thrush (*T. philomelos*), and Mistle Thrush (*T. viscivorus*). Blackbird and Song Thrush nests are distributed widely throughout the forest wherever stands of immature Norway spruce (*Picea abies*) are located. Though some nest sites were near feeding territories, many were not. Mistle Thrush nests most often were high in Scotch pine (*Pinus sylvestris*), less frequently in Norway spruce. Mature Scotch pines usually are not next to feeding territories as fluctuating water levels periodically kill or damage trees. Thus, nests available for use by *ochropus* are widespread throughout the forest. The closest two used in one year of which I was aware were 400 m apart. On Hunneberg, which includes about 50 sq. km, there were 20–25 breeding pairs. In Alberta, *solitaria* usually

uses nests of Rusty Blackbird (*Euphagus carolinus*), Cedar Waxwing (*Bomby-cilla cedrorum*), and Robin (*Turdus migratorius*). Rusty Blackbirds and Cedar Waxwings breed close to muskeg ponds where *solitaria* feeds. Robin nests are scattered throughout the forest. The nests in which *solitaria* lays its eggs are nearly always close to feeding ponds according to my observations and those of R. Lister and D. Parmelee (pers. comm.). Furthermore, two or more pairs may nest as close as 100 m from each other. Hence the distance over which conspecifics communicate is much less than is normal for *ochropus*. The songs of *ochropus* which are very loud and frequently repeated appear specialized for communication over great distances. The fact that these songs must be effective over long distances may also explain why they are so much lower in frequency than those of *solitaria*, for as I have explained above, there seems to be a tendency for high frequencies to drop out first when re-cordings are made over great distances. This being the case, I would expect the higher frequencies to be selected against during the evolution of species which communicate vocally over great distances.

T. glareola (Kirchner, 1963) and the Redshank (*Tringa totanus*) (Gross-kopf, 1958), both possess at least two song types as do *solitaria* and *ochropus*. In addition, both *glareola* and *totanus* as well as *T. nebularia* (Nethersole-Thompson, 1951) and other closely related but lesser known forms, have calls which are apparently similar in structure and function to those of *solitaria* and *ochropus*. Comparisons between these species are best reserved until spec-trographic data are available.

In *ochropus* and *solitaria*, as in the entire *Tringa-Totanus* complex, morpho-logical features differ much less than do vocal ones. Vocalizations are prob-ably much more important in species recognition of territorial males than morphological features as Lanyon (1963) reported for *Myiarchus* flycatchers. Smith (1965) pointed out that when songs are employed for stimulation of the female after pair formation, individuality may be important to achieve synchrony between mates; and this distinctiveness may be visual or vocal. In *ochropus* and *solitaria* a need for individuality is overcome by intense chasing of all intruding males from occupied territories and by the fact that resident females rarely leave their territories.

According to Marler (in Marler and Hamilton, 1967), sympatric species are likely to have songs consistently and distinctly divergent when songs func-tion as reproductive isolating mechanisms—as they certainly do in *Tringa*. One might guess that since *ochropus* and *solitaria* are allopatric, so similar in certain aspects of their ecological niches, and indisputably close phylogeneti-cally, that their songs might be much more similar than they are. Personal observations of *T. glareola* indicate that its song (and aerial display) is much more like that of *solitaria* than that of *ochropus*. Songs of *glareola* may be

close to those of parental stock for the entire genus. *Glareola* is sympatric geographically and to some extent ecologically with *ochropus*. Thus, sympatry with a very closely related form has been part of the pressure molding the evolution of *ochropus* songs while it has not been involved in the recent history of *solitaria*. This pressure by a sympatric form may help explain why *ochropus* songs are apparently more stereotyped than those of *solitaria*. On the other hand, evidence from island forms suggests that in the absence of close competitors, variability increases (Marler, 1960)—a situation which may to a lesser extent involve mainland forms facing similar situations such as *solitaria*. In species where song is largely learned, e.g. Chaffinch (*Fringilla coelebs*), the reverse seems to be the case (Thorpe, 1958).

According to Ficken and Ficken (1962), many closely related species of North American warblers have at least two song patterns. One of these, which they call the "accented" song, is highly species-specific; and is used especially in establishing pair bonds and territories. This "accented" song occurs infrequently later in the season when it is replaced by the "unaccented" song— a type which differs little from species to species. An interesting parallel occurs in *ochropus* and *solitaria*. In the former, "Type II" songs occur primarily during pair formation and territorial advertisement; they are very rare in other contexts. "Type I" songs occur frequently both before and after the period of pair formation and territorial advertisement; and though they do occur in these situations, are infrequent during the aerial or highest intensity part of the displays. The two song types of *solitaria* do not fit an "accented"-"unaccented" pattern but rather both occur in a variety of situations. But it is of interest to note that it is the "Type I" pattern of *ochropus* which is most similar to that of *solitaria* (Fig. 1B–C, subunits 1–3). In other words, it is the song which is little involved in pair formation and territorial advertisement that is most similar to that of a very closely related but allopatric species. "Type II" *ochropus* songs, it seems, are roughly equivalent to the "accented" songs of warblers, and "Type I" to the "unaccented."

According to the bird song classification of Hartshorne (1956), the songs of *solitaria* are "discontinuous" (pauses between songs occupying more than 70 percent of the performance time) and "non-versatile" (less than four distinct songs or phrases). This situation is not uncommon among passerines. But according to this same classification, *ochropus* songs are "highly continuous" (pauses between songs occupying less than 50 percent of the performance time) and "non-versatile" (less than four distinct songs or phrases) —a combination which Hartshorne (1956) considered extremely rare. During one minute, e.g., only "Type II" song units occurred and they were repeated 67 times. Excluding all inter-unit and inter-song intervals 40.2 seconds (67 percent) were involved in actual singing. Even when intra-unit intervals are

excluded, leaving only the time when sound energy was being produced, this bird was singing 29.2 seconds per minute or 49.7 percent of the total performance time. Hartshorne (1956) also stated that "Indicative of a low level nervous organization—high threshold, great tolerance for monotony—is a lack of clear musical contrasts within the basic song pattern, as well as in its reiteration without ample pauses or variations. The second deficiency is found only in association with the first." This generalization based upon passerines is deficient with regard to *ochropus* for this species possesses clear musical contrasts in its basic song but lacks "ample pauses or variations."

Songs of *ochropus* and *solitaria* function in territorial establishment and defense, pair formation, and in readying the female for reproduction—as in passerines. Also as in passerines, songs are more or less restricted to the reproductive season. Their structural complexity and duration are greater than in many passerines but less than in others. The single major difference seems to be that in passerines, songs are often given without immediate external stimuli whereas in *solitaria* and *ochropus* songs are nearly always given in response to conspecifics. Some singing does occur, however, in the absence of conspecifics during direct flight.

SUMMARY

Tringa ochropus and *T. solitaria* occupy similar ecological niches in the boreal forests of the Palearctic and Nearctic respectively. In both forms, the calls of chicks are high-pitched—about 6 to 7.5 kc in *ochropus* and 4.5 to 6 kc in *solitaria*. Chick content calls of both species are clear, high-pitched monotones. Distress calls are spread over a considerable frequency range and are shorter than content calls. A number of other calls were recorded in *solitaria*; and it is thought that they may represent intermediate motivational situations.

Whereas the juvenile calls of *ochropus* are substantially higher than those of *solitaria*, the reverse is uniformly true for all adult vocalizations. All adult vocalizations are given by both sexes. Adults of both species utter a number of short duration, frequently repeated calls here named "contact," "alarm-attack" and "epigamic" chatter. These calls are all well adapted for locatability. In *ochropus*, all three possess a considerable noise element but most energy is centered about 3.2 kc. Noise is absent in *solitaria* contact calls but present in "alarm-attack" and "epigamic" chatter. These calls center about 4.8 kc.

Both species possess "alarm-flee" calls which are usually given by flying birds, especially when taking off. These calls ascend rapidly—from 3.1 to 4.4 kc in *ochropus* and 4.3 to 5.1 kc in *solitaria*. They possess noise elements similar to those of "alarm-attack" calls; and intermediates occur in intermediate motivational situations.

Long whistles are vocalizations present only during the breeding season in both species —at about 3.2 kc in *ochropus* and 4.8 kc in *solitaria*. The species-specific information which they are well adapted to convey is apparently enhanced by the location cues of chatter which accompanies them. This combination of long whistles and chatter occurs during pair formation, copulation, and other situations about the nest.

Both species have songs composed of one or both of two basic structural units—"Type I" and "Type II." "Type I" units are less specialized. In both species they show close relationships to "epigamic" chatter. The more specialized units, "Type II," arose by

addition and shift of energy in *solitaria* and by fragmentation in *ochropus*. The songs of *ochropus* are composed of 1 to 19 units each of which is about 0.6 seconds long, is separated from preceding and following units by about 0.1 seconds, and is located from about 1.8 to 4.6 kc. Three to 12 units compose the songs of *solitaria*, the units being about 0.2 seconds long; each separated from preceding and following units by about 0.15 seconds. They are located from about 2.5 to 6 kc. In both species "Type II" units are of shorter duration and higher frequency than "Type I." The structures of "Type II" units are better adapted for location over long distances while retaining clear tonal components for the conveyance of species specific information. The fact that *ochropus* songs are louder, longer, lower, and more frequently repeated than those of *solitaria*, may be related to the much greater territory size of *ochropus*. Selection may therefore have favored vocal characteristics capable of being transmitted and received over great distances.

The songs of *ochropus* are similar to the "accented" and "unaccented" songs of some warblers in that "Type II" songs are restricted to pair formation and territorial advertisement and "Type I" songs occur at other times. In addition, "Type I" songs are the ones showing relationships to *solitaria*. The songs of *solitaria* do not fit an "accented-unaccented" pattern.

Songs of *solitaria* are "discontinuous" and "nonversatile." Those of *ochropus* are "highly continuous" and "nonversatile"—a situation apparently rare or nonexistent in passerines. As many as 67 units/minute with 29.2 seconds of actual sound energy production have been recorded.

Adults of *solitaria* did not respond to playbacks of *ochropus* songs while *ochropus* responded to playbacks of conspecific songs by approaching, singing, and often performing aerial displays. Chicks of *ochropus* responded to "alarm-flee" calls by scattering to corners of a box and crouching; to "contact" calls by moving toward the sound source.

ACKNOWLEDGMENTS

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