VOCALIZATIONS OF THE WHIMBREL ON ITS BREEDING GROUNDS

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Information on the vocalizations of the Whimbrel (Numenius phaeopus), a circumboreal breeder, is scanty and incomplete. A few calls are described in general accounts of the breeding biology of the North American race (N). p. hudsonicus; Bent 1929, Stout 1967), and slightly more description of some vocalizations is given for the European race (N. p. phaeopus) in the only study of this species (Williamson 1946). Some calls have not been previously described, and none have been analyzed spectrographically. Within Numenius, vocalizations of the Long-billed Curlew (N. americanus) have been analyzed spectrographically (Forsythe 1970), and the vocalizations of the Eurasian Curlew (N. arquata) have been described phonetically (von Frisch 1956).

My purpose here is to describe and analyze Whimbrel vocalizations. A description of the behavioral context of the vocalizations is presented, and possible functions are postulated.

METHODS AND MATERIALS

I studied a population of over 30 breeding pairs of Whimbrels near Churchill, Manitoba. The area is characterized by low rounded cliffs along the coast of Hudson Bay and, just inland, a diversity of habitats in which tundra intergrades with stunted spruce-tamarack forest. Although Whimbrels often forage among the lichens of the coastal cliffs, their nesting is restricted to hummock-bog, sedge-meadow, and dry heath-tundra areas. Most of my data on vocalizations and associated behavior were collected from 17 May to 26 July 1973, and from 11 May to 20 August 1974. Observations were also made from 10 June to 3 July 1975 and from 12 June to 1 July 1976 while I was studying other aspects of the Whimbrel's biology.

Vocalizations were recorded with a 4000 Report-L Uher tape recorder at a tape speed of 19 cm/s, and a M537 Uher microphone. The microphone was mounted on a 72-cm diameter aluminum parabolic reflector. For all vocalizations I recorded as many individual adults as possible throughout the breeding season. Young were recorded at the nest soon after hatching, and up to a week of age, but none were recaptured after this age.

In the laboratory, tapes were played on a Studer tape recorder at a tape speed of 19 cm/s. Audio-spectrograms were made with a Kay Electric 6061 Sona-Graph using a wide-band filter. Time and frequency measurements were made with an overlay marked into divisions of 0.01 s and 1.0 kHz. The acoustical terminology is that of Mulligan (1963: 276).

RESULTS

ADULT VOCALIZATIONS

Low whistle call. This call (Fig. 1A) is uttered as a steady note usually two to five times, but I have heard it as many as 20 consecutive times. The last time the whistle is given during a sequence, it fluctuates in frequency towards the end and then breaks into a long trill. The low and high frequency of the low whistle call, before any vibrato or trill, ranged from 0.8 to 1.3 kHz. The duration of each whistle note varied from 0.15 to 1.59 s ($\bar{x} = 0.87 \pm 0.138$ s, n = 10), with intervals of 0.08 to 0.23 s ($\bar{x} = 0.13 \pm 0.0246$ s, n = 8) between notes.

I heard the *low whistle call* throughout the day, from the arrival of Whimbrels at the area in late May until early June. At this time, I heard it only in association with the aerial display (described below). Around the second or third week of July I heard this call again, infrequently but regularly, during the late afternoon and evening, and the early and late morning hours. I could not see a Whimbrel during these calls, but heard the calls coming from high in the sky.

Low trill calls. These calls are composed of one, two, or three phrases. When only one phrase is given, it invariably is a trill. However, when two or three phrases are given, the first part of one, two, or three of the phrases is a whistle or vibrato, similar to the low whistle call. In the low whistle call the frequency of the note remains constant, whereas in the low trill call the frequency of the whistle wavers.

The frequency of the first phrase (a whistle) of a two- or three-phrase call (Fig. 1B) is low, ranging from 0.9 to 1.6 kHz (\bar{x} low and high = 1.0 and 1.4 kHz, n=8). On one occasion this first phrase was a vibrato with a frequency between 1.4 and 2.0 kHz. The second phrase of a three-phrase call (Fig. 1C) is a vibrato, although it may begin as a whistle, with the low and high frequency of the vibrato ranging from 0.9 to 2.2 kHz (\bar{x} low and high = 1.3 and 1.9 kHz, n=7).

The final trill for a one-, two-, or three-phrase call (Fig. 1D) consists of between 17 and 80 notes ($\bar{x} = 41.6 \pm 5.48$ s, n = 13). The low

and high frequency of the trill notes usually lies between 1.0 and 2.3 kHz (\bar{x} low and high = 1.3 and 2.2 kHz, n=12 phrases). Once, after a Whimbrel had chased a Herring Gull (Larus argentatus) the frequency was between 1.3 and 2.7 kHz. Each trill note lasted between 0.03 and 0.06 s ($\bar{x}=0.045\pm0.0072$ s, n=15 notes from each of 10 phrases), with short intervals of 0.01 to 0.05 s ($\bar{x}=0.030\pm0.0082$ s, n=15 intervals from each of 10 phrases) between notes. Usually the shortest notes and intervals occurred at the beginning of the phrase.

The duration of the entire call was: one-phrase call, between 1.70 and 6.41 s ($\bar{x} = 3.38$ s, n = 4); two-phrase call, 3.60 and 6.43 s (n = 2); and three-phrase call, between 4.35 and 7.83 s ($\bar{x} = 6.12$ s, n = 7). The call consists of two and three phrases more often than one. I heard the two- and three-phrase calls in all situations, and the one-phrase call in most.

The low trill calls are among the most common vocalizations given by Whimbrels. This call is uttered by both sexes with equal frequency and is heard commonly throughout the breeding season both day and night. As a Whimbrel glides to land, it usually gives a low trill call. An incubating Whimbrel, at intervals of 15 min to several hours, gave this call from the nest; usually the mate did not respond vocally. Low trill calls were also heard regularly from the vicinity of the nest; these were thought to be given by the non-incubating mate. When these calls were heard from within about 100 m of the nest, the incubating bird responded about one-third of the time with the same call.

On all occasions when I witnessed a change of the incubating bird it was accompanied by an exchange of *low trill calls* between the mates. On three occasions the non-incubating bird first gave the call about 30 m from the nest. The incubating bird answered with the same call, then flew from the nest, again giving the call. Once, the incubating bird first gave the call, then flew from the nest. Its mate answered with the same call several times from 10 m away, then walked to the nest and sat on it.

Aerial display song. This song is composed of two distinct calls: the low whistle call, repeated up to 20 times, followed by the three-phrase low trill call. I heard it only with an aerial display.

In the aerial display, the Whimbrel first rose from the ground at about a 45° angle, beating its wings hard until 150 to 300 m in the air. Making circles about 200 m in diameter as it flew, it alternately glided down-

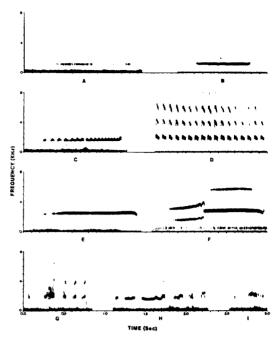


FIGURE 1. Audiospectrograms of various Whimbrel vocalizations. A. low whistle call. B. First phrase of a two- or three-phrase low trill call. C. Second phase of a three-phrase low trill call. D. Final phrase of a one-, two- or three-phrase low trill call. E. Typical whining call. F. Atypical whining call. G, H and I. Various types of notes found in the variable chase call.

wards at a 10° to 15° angle and climbed again at a 45° angle, flapping vigorously as it rose. During the glide, the wings were held stiffly at right angles to the body and curved slightly downwards; the head was erect and drawn back close against the body so that the lower neck projected forward, similar to that described for the Sanderling (Calidris alba; Parmelee 1970). Usually (83% of the time, n = 30) a few seconds after it began to glide, the bird gave the low whistle followed by the low trill call (or just the trill) of the aerial display song. Because of the height of the Whimbrel, I may not have heard the low whistle call every time it was given. During the climb, no vocalizations were uttered. Toward the end of the display, the bird lost altitude, and during the last glide descended at a 45° angle before leveling off about 1 m above the ground and landing. Both wings were raised vertically for about 1 s upon alighting.

Durations of the entire display on the four occasions that I observed it were: 1 min 48 s, 2 min 9 s, 6 min 16 s, and 10 min 10 s. On two other occasions this display lasted for longer than 7 min. Most often I did not see the display until the bird was already singing at some height above the ground. For the above dis-

plays, the average duration of each component (excluding take-off and landing) was: flapping flight—28.0 \pm 3.38 s (range = 7 to 80 s, n=26), and gliding flight—37.4 \pm 3.94 s (range = 7 to 100 s, n=27). When the low trill call was given during gliding, from 2 to 10 s elapsed from the onset of the glide to the start of the call. I could not determine the sex of the bird giving the aerial display song except on one occasion, when I assumed it to be a male because it attempted to copulate with another Whimbrel immediately following the flight.

The aerial display song was first heard in late May, about two to five days after Whimbrels began arriving on the breeding grounds. I commonly heard it throughout the day until early June, after which it occurred much less frequently. In mid-July I still heard this call several times at dusk and dawn.

Whining call. This call (Fig. 1E) is a single whistled note, usually of high intensity. Occasionally the whistle will become a vibrato. then break into a low trill call. The frequency of the beginning of the whistle ranged from 1.2 to 2.7 kHz ($\bar{x} = 1.72$ kHz, n = 20). The whistle then increased in frequency, although increases are often slight and are more in intensity than in frequency. The maximum frequency attained by the note varied from 1.6 to 3.0 kHz ($\bar{x} = 2.48$ kHz, n = 20). Occasionally a segment of the note drops in frequency by about 0.5 to 1.0 kHz, or the energy is divided between the fundamental and harmonics (Fig. 1F). The duration of the call was between 0.49 and 2.33 s ($\bar{x} = 1.10 \pm 0.117$ s, n =20).

The whining call was heard from late May until at least mid-July. It was almost always given from the ground, and in a variety of circumstances. In late May, before nesting began, this call was noted continuously throughout the day in areas where Whimbrels later nested. Single Whimbrels (which may have been mated) and both members of a pair gave this call; in the latter case, one adult usually called more often than the other. The calling bird usually spent most of its time on a hummock or high ridge giving the whining call every 10 to 60 s, and occasionally giving a low trill call. This lasted at least 10 min, after which the calls were less frequent. Calling occurred between feeding or preening, and several times was heard to interrupt a low trill call from a neighboring Whimbrel. Often upon landing after an aerial display, Whimbrels gave the whining call several times. On these occasions the bird seemingly leaned forward so that its breast was low and its tail somewhat raised.

Before the onset of nesting, this call was also heard in an area where no nesting, but extensive feeding, occurred (the granitic outcrops along the coast). Here the call was uttered only sporadically. The call was given in two situations: by one of several Whimbrels who were standing on rocks within 20 m of each other, or by a bird immediately after chasing another Whimbrel. Once this call was given in the air by a Whimbrel as it flew up after another Whimbrel that had been standing 10 m away.

In early June the frequency of the *whining call* dropped sharply, although occasional calls were still heard during the day and at night. I did not see the context in which these were given. On 19 June 1974, I saw three Whimbrels land about 10 m from the nest of another Whimbrel. The non-incubating bird flew towards them, causing two of the intruders to leave. The incubating Whimbrel flew from the nest then ran towards the third intruder with its wings raised, giving the *whining call*, which broke into a trill, and repeated this call as the intruder flew away.

I used the whining call in experiments with a mounted Whimbrel (described in Skeel 1976). When this call was played from a speaker beside the mount, 25 m from a Whimbrel's nest, it elicited a strong attack response early in the incubation period from the nesting pair. At one nest the female attacked the mount, at another the male attacked, and at a third the attacker's sex was unknown. When the aerial display song was played from the speaker, it did not elicit such a response. The whining call was heard into mid-July. Once the call was given by one individual, several others called from scattered localities; this lasted several minutes, then was followed by a long period during which this call was not heard.

Variable chase call. This call consists of a series of short and highly variable notes, including short modulated whistles, and buzzes (Figs. 1G, 1H and 1I). The frequency of the fundamental usually lay between 1.0 and 2.5 kHz. The length of individual notes varied between 0.03 and 0.30 s, dependent largely on the type of note. Intervals of 0.04 to 0.44 s occurred between notes. On the two occasions that this call was tape recorded, it lasted 3.92 and 2.72 s.

The five times this call was heard, it was being given by a Whimbrel (sex unknown) in close aerial pursuit of a second Whimbrel.

This call was heard only in late May, and the chases took place above the coastal granitic outcrops where feeding, but no nesting, occurred. The Whimbrel in pursuit landed shortly after giving the call, and upon landing uttered the *whining call*.

Settling call. This call (Fig. 2A) consists of a very soft whistle, audible by me only up to 10 m. Occasionally this call is given twice or is followed by a one- or two-phrase low trill call. The frequency of the settling call lies between 1.1 and 2.5 kHz (\bar{x} low and high = 1.4 and 2.1 kHz, n=7). The frequency of the call was fairly constant, oscillated, or was lower at the start and finish. The whistle lasted between 0.04 and 1.06 s ($\bar{x}=0.591\pm0.0902$ s, n=7). It was given by both members of a pair and was emitted 76% of the time (n=29) a Whimbrel settled onto its nest. This call was not given in any other context.

Whit call. This call is a short, one-syllable note of middle frequency. It was not recorded on tape. On 31 May 1973 it was given three times in succession by one bird as it flew low and rapidly over me. Its mate responded by flying up with a low trill call. The whit call was next heard on 15 July 1974 when a female, feeding beside her nest, gave a "whit" as two of her newly-hatched chicks tumbled from the nest. Immediately after, she gave the adult-to-chick contact call (described below).

Short predator alarm call. This (Fig. 2B) is a slow, short trill composed of four to eight syllables. The range of a note was between 1.8 and 2.4 kHz to 3.0 and 3.5 kHz, and the frequency of a sequence of notes remained fairly constant. The average low and high frequencies were 2.36 and 3.19 kHz (n = 48 notes from 8 calls). The duration of individual notes also remained fairly constant within a call, although the first or last note may be more variable in length. Notes ranged from 0.030 to 0.080 s in duration ($\bar{x} = 0.064 \pm 0.0094$ s, n =48 notes from 8 calls), with intervals of from 0.030 to 0.065 s ($\bar{x} = 0.043 \pm 0.00169$ s, n = 40intervals from 8 calls) between notes. On only one occasion an unusual variation of this call was heard and recorded. It consisted of seven phrases, each having one to three notes. Most of the notes were of the same shape on the sound spectrogram as the typical short predator alarm call, but a few notes contained elements of a slightly higher frequency (0.5 kHz).

The short predator alarm call was heard many times and in only one context—as an alarm call, given by both sexes, when a potential aerial predator was being chased. (Once a Whimbrel gave this call as it flew

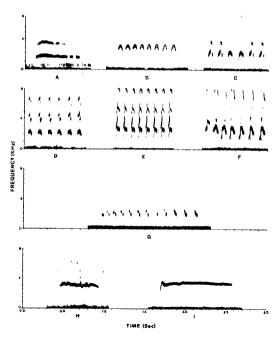


FIGURE 2. Audiospectrograms of various Whimbrel vocalizations. A. Settling call. B. Short predator alarm call. C. Notes found in the long predator alarm call. D. Notes found in the type I scolding trill call. E. Notes found in the type II scolding trill call. F. Notes found in the type III scolding trill call. G. Adult-to-chick contact call. H. Chick peep call. I. Chick wheee call.

towards me, then immediately began to give the scolding trill call.) The call was uttered on all occasions after chase of the potential aerial predator began and once while the Whimbrel was still on the ground. Usually intervals of 8 to 10 s separated the calls for the duration of the chase. I heard Whimbrels give this call as they flew after Herring Gulls. Thayer's Gulls (Larus thayeri), Common Ravens (Corvus corax), Parasitic Jaegers (Stercorarius parasiticus), and a Marsh Hawk (Circus cyaneus). However, these species were not chased every time they flew over Whimbrel territories. Three times I saw a Short-eared Owl (Asio flammeus) fly low over an area in which Whimbrels were nesting: it was not chased. As a Whimbrel chased the potential predator, it dived downward from a rear and slightly higher level, going just below the level of the predator, then swooped upward just below the tail of the intruder. The Whimbrel then repeated this attack. During the ascending part of its flight the Whimbrel gave the short predator alarm call up to three times, and continued its chase for up to five consecutive dives.

I first heard the *short predator alarm call* in late May, a few days after most of the Whim-

TABLE 1. Characteristics of scolding trill calls.

Characteristic	Call type		
	I	II	III
\bar{x} low and high frequency ¹ range of frequency ¹ no. of calls	1.7–2.5 1.5–2.8 7	1.3–2.8 1.0–3.4 15	1.4–3.8 1.2–4.2 15
$ \bar{x} $ length of each note ² range no. of notes	0.053 ± 0.0010 0.040-0.065 15 from each of 7 calls	0.054 ± 0.0030 0.040-0.060 10 from each of 15 calls	0.068 ± 0.000 0.060-0.080 118 from 15 calls
\tilde{x} length of each interval ² range no. of intervals	0.071 ± 0.0015 0.035-0.145 15 from each of 7 calls	0.075 ± 0.0323 0.045-0.125 10 from each of 15 calls	0.0507 ± 0.001 0.030-0.085 103 from 15 calls
\bar{x} length of a call ² range no. of calls	$\begin{array}{c} 2.94 \pm 0.275 \\ 2.04 - 4.05 \\ 7 \end{array}$	1.79 ± 0.129 $0.36-4.98$ 58	$\begin{array}{c} 0.95 \pm 0.065 \\ 0.32 - 1.48 \\ 26 \end{array}$
\tilde{x} no. of notes/call range no. of calls	$24.6 \pm 2.50 \ 17 - 35 \ 7$	14.3 ± 0.98 $3-35$ 58	8.2 ± 0.54 $2-12$ 26

¹ In kHz. ² In seconds.

brels had arrived in the study area, and heard it regularly until late July. The incidence of this call was greatest in late May and early June, before most of the eggs were laid. At this time, as many as six Whimbrels at once could be seen in pursuit of the same potential aerial predator. After nesting began, this dropped to one Whimbrel at a time, although a second Whimbrel sometimes took up the chase once the first one turned away. A Whimbrel might continue the chase for as far as 500 m, flying over territories of other Whimbrels as well as its own.

Long predator alarm call. This (Fig. 2C) trill was recorded twice. Two types of notes occur in the call in a variable sequence. One of these note types is very similar to the notes of the short predator alarm call; 10 of the 44 and 14 of the 24 notes in the two calls recorded were of this type, and ranged in frequency from 1.5 to 2.7 kHz. The second type of note ranged from 1.6 to 4.0 kHz. Notes ranged from 0.45 to 0.6 s in duration ($\bar{x} = 0.614 \pm 0.0107$ s, n = 66). The entire length of the call lasted 5.22 and 2.73 s.

The long predator alarm call was given by a Whimbrel, presumably of either sex, as it flew from the vicinity of its nest low along the ground toward a human intruder while the intruder was 50 to 250 m distant. Upon landing about 30 m from the intruder, scolding trill calls (see below) were uttered. I noted the long predator alarm call most often during my first few visits to a particular nest-site; on subsequent visits scolding trill calls were more common.

Scolding trill calls. These calls comprised a trill, but were variable in several features probably depending on differences in the situation, the motivational state of the bird, and the individual giving the call. Three basic notes were recorded; depending on their note type, scolding trill calls were classified as type I, II and III (Figs. 2D, 2E and 2F, respectively). All the notes within the type I call were usually similar, whereas in the type II call, the initial note(s) usually resembled the notes of a type I call (on a few occasions several middle notes were of type I), and in the type III call the initial notes usually resembled the notes of a type I or II call. Harmonics were a prominent feature of these calls.

Comparisons of frequency and time parameters of the three call types were made (Table 1). The type I call was recorded eight times, although heard more often. Once I recorded a two-note version (not included in the analysis because of the rarity of its occurrence). The frequency of the calls becomes progressively higher from types I to III, and the number of notes (and total length of the call) progressively shorter. The mean length of notes and intervals is about the same for types I and II, but for type III the notes are longer and the intervals shorter.

Like the long predator alarm call, the scolding trill calls were only heard when directed towards humans, never towards birds. I never had an opportunity to hear whether these calls were directed towards other mammals. In general, the type I calls were emitted in low

intensity situations. This call was given throughout the incubation period, although infrequently, when I was 1 to 50 m from the nest. The type I call was given more often just after I entered a blind placed 6 to 15 m from the nest, at which time the bird would walk back and forth about 20 m from the blind.

The type II scolding trill call was by far the commonest, and was heard in all situations. When the long predator alarm call was not used, this was the alarm call given. It was also uttered when I was at the nest-site, both when eggs or chicks were in the nest. When I was holding the chicks or they were hiding near the nest-site the type II call was given, although often the calls were type I or type III. The type II call was also given just after I entered a blind near the nest.

The type III call was heard only when a Whimbrel appeared to be extremely excited while I was at the nest. This call was always given (sometimes interspersed with type II calls) with a display similar to the distraction and/or lure displays described for some other Scolopacidae (e.g., Simmons 1955). During this display, the Whimbrel would droop its wings so that the leading edge was almost parallel to the ground. Simultaneously, the bird would fan its tail, sometimes slightly and at other times so that up to a 110° angle was formed. Usually the tail was held low to the ground when spread, but occasionally was twisted so that the fan faced towards me. Only one Whimbrel at each of four different nests was seen to give an exaggerated form of this display. At one nest, the display was given during the first week of June, but not afterwards, and at the other nests the display was given only during the latter half of incubation. Several other individuals displayed less intensely.

Adult-to-chick contact call. This (Fig. 2G) is a low gurgling trill, audible to me at 30 m. The frequency of the first type of note in the call, which may make up a small or large portion of the entire trill, varied from 1.5 to 4.0 kHz, a single note sometimes encompassing the entire range. The last notes of the call are very similar to the trill notes given in the low trill calls. Each note (discounting the faint "stem") had a frequency varying between 1.2 to 2.1 and 1.6 to 2.6 kHz (\bar{x} low and high = 1.46 and 2.41 kHz, n = 15 calls). The lowest part of the "stem" was as low as 0.8 kHz. The length of the trill notes (discounting the first one which was sometimes as short as 0.2 s) ranged from 0.04 to 0.07 s ($\bar{x} = 0.055 \pm 0.00066$ s, n = 174 notes from 15 calls). Intervals of 0.02 to 0.09 s ($\bar{x} = 0.051 \pm 0.00096$ s, n = 174 intervals from 15 calls) separated the notes. An entire call lasted from 0.85 to 1.96 s ($\bar{x} = 1.14 \pm 0.059$ s, n = 22) and contained 8 to 19 ($\bar{x} = 11.5 \pm 0.58$ s, n = 22) notes.

This call was given by an adult female after her first chick had hatched and wandered about 0.5 m from her. The adult continued to give this call periodically after all the eggs had hatched, sometimes in response to cries from the chicks, which were feeding or walking near the nest with the female, and sometimes just before brooding the chicks. The male was not present during the hatching of this nest.

Several pairs with chicks up to one week old were seen. Both adults accompanied the young, and both periodically gave this call as they moved with the feeding chicks. At least one adult was always alert and regularly calling to the chicks; the other was sometimes feeding intensely. When the chicks were several days old, they wandered as far as 20 m from the adults.

CHICK VOCALIZATIONS

Peep call. I taped only one good recording of this call (Fig. 2H). It had a frequency of between 2.5 and 3.5 kHz and lasted for 0.51 s. On all other occasions, the call appeared to be of similar frequency and length. This call was given by the chicks just after hatching as they wandered feeding near the adult. It was audible to me up to 15 m and was heard only in the absence of threat, such as human presence. The age at which this call is discontinued was not determined because I heard it only when I was in a blind near a nest in which the eggs were hatching. Later when I watched chicks feeding near their parents, I was beyond range of the call.

Wheee call. This was the only other chick vocalization recorded (Fig. 2I). The frequency changed only slightly within a given call, and ranged from 2.8 to 3.8 kHz and frequency modulated, giving the call a harsh quality. The length of the call varied from 0.86 to 0.95 s ($\bar{x}=0.903\pm0.0202$ s) the four times I recorded it. This call was usually uttered when chicks were disturbed at the nest. Chicks that were recaptured up to the age of one week gave a louder version of the same call.

DISCUSSION

I found the vocal repertoire of adult Whimbrels on the breeding grounds to consist of 10 distinct types of calls. I heard two types of calls given by the chicks from the time of

hatching to one week of age. Forsythe (1970) recorded eight calls of adult Long-billed Curlews and four calls of the chicks. He heard no calls in the wintering areas that were not also heard on the breeding grounds; perhaps this also applies to Whimbrels.

When the low whistle call of the Whimbrel is given as part of the aerial display song it appears to function as self-advertisement. Williamson (1946) described a "koo" note, a whistle during the climb of the display, but I heard no vocalizations at this time and heard the low whistle call only after the Whimbrel began to glide. The function of the low whistle call when given in July is unclear. This call spectrographically resembles the long call of the Long-billed Curlew, the main difference being the slightly lower frequency of the low whistle call. The functions of the long call puzzled Forsythe (1970). It was not associated with a display, but was often given as a Long-billed Curlew glided before landing.

The low trill calls also appear to function in self-advertisement when given as part of the aerial display song. At other times the low trill calls probably serve locative functions among Whimbrels and more importantly, as contact notes between individuals of a pair. This call is probably most similar structurally to the long curluoo call of the Long-billed Curlew, although notes in the latter call are different and average about one quarter as many. The functions of the long curluoo call may be announcement (it was normally given just after the bird landed), territorial defense, and possibly maintenance of the pair bond (Forsythe 1970). This announcement role is similar to that of the low trill calls given by a Whimbrel as it lands, and between an incubating bird and its mate. The long curluoo call differed in that it was only given by males and was associated with agonistic displays between males.

Flight-songs are characteristic of many open-country nesting birds, including most scolopacids, and serve as self-advertisement for mate attraction and/or territorial defense (Armstrong 1963). At the beginning of the breeding season the *aerial display song* appears to function chiefly in self-advertisement. The low frequency of the call indicates the necessary low rate of attenuation. I was not able to determine if it was uttered solely by males, although Rosenberg (1931) believed this to be the case. Forsythe (1970) never observed Long-billed Curlews to give a flight-song.

Von Frisch (1956) described an aerial display for the Eurasian Curlew very similar to

that of the Whimbrel: a male Eurasian Curlew repeatedly ascends steeply, then glides downward, calling at the same time. Once one male starts, those in neighboring territories begin, and all continue the aerial display for several minutes (this did not occur with the Whimbrels). Because a female was often absent or, when present showed no interest in the aerial display of a male, von Frisch believed the display to have no role in courtship, but to function solely in marking the territory. I feel that the aerial display song of the Whimbrel serves both in attracting a mate and in marking an area, part of which will later become its territory. This display does not appear to be essential for either since only a small proportion of Whimbrels did it, particularly in hummock-bog areas where nesting density was highest. High territory and mate fidelity (unpubl. data) may facilitate rapid pairing and eliminate the need of this display for many individuals.

Bent (1928) attributed a "cur-lew note" to the Whimbrel, as did Larrison and Sonnenberg (1968) during migration. Williamson (1946) did not mention such a call, and I found no two-syllable whistle, like the curluoo call of the Long-billed Curlew (Forsythe 1970), in the vocal repertoire of the Whimbrel at Churchill. The call most likely to be Bent's "cur-lew note" is the whining call. During nesting, and in areas where nesting later occurs, this call appears to function primarily as a contact or warning note in connection with establishing a territory, and as an agonistic note when conflicts occur. Because this call is given by both members of a pair, before and after establishment of their territory, it may also help maintain the pair bond. The function of this call in mid-July once most of the eggs have hatched is enigmatic. At this time Whimbrels no longer remain on their original territories, but are constantly moving with their chicks. Since both parents care for the chicks for at least one or two weeks, this call may increase in importance in maintaining the pair bond. The sound source of this call is difficult to locate because the call is long, of high intensity, and without sharp intensity changes; I do not know the adaptive significance of this except to confuse predators. The whining call appears to serve many of the same functions as the curluoo call of the Long-billed Curlew.

A call similar to the variable chase call of the Whimbrel was not found for the Longbilled Curlew, and Forsythe (1970, 1972) did not mention behavior involving conspecific chases. This call was not noted by Bent (1929) or Williamson (1946). When I noted this call, I could not determine any reason for the onset of the chase. Because of its apparent spontaneity and its occurrence before territories are established (a time of increased tension between males), I feel that this call and chase may be incipient territorial behavior.

The settling call seems to announce settling by an incubating adult. I thought that this sound might be caused by the weight of the bird forcing air from its air sacs as it settled. I have found no reference to this call for other scolopacids.

As with other birds (Collias 1960, Armstrong 1963), Whimbrels appear to have different alarm calls for aerial and ground predators. The Long-billed Curlew also has two alarm calls, but none restricted solely to aerial predators. The arc display call was directed towards human intruders, and the kikeck call towards all types of predators (Forsythe 1970). Aerial predation of Whimbrel eggs in the Churchill area was more common than ground predation—only one clutch was thought to have been taken by a Red Fox (Vulpes vulpes). Therefore, it is not surprising that this specific call has evolved. cause Long-billed Curlews nest farther south than Whimbrels, the abundant ground predators play a more imporant role.

According to Armstrong (1963, after Marler 1955) "warnings of air-borne predators are usually high-pitched and without abrupt phase- or intensity-difference—approximating to pure tones beginning and ending gradually." Thus, it would be difficult for a predator to locate the bird giving the warning. Although the short predator alarm call of the Whimbrel is high pitched, the short abrupt notes would render it and the long predator alarm call easily located. This may be adaptive since the Whimbrel, rather than trying to conceal itself from the predator (which preys upon the eggs, not the adult), actively pursues it.

The scolding trill calls which appear to function as alarm and scolding calls, are very similar spectrographically to the ki-keck call of the Long-billed Curlew (Forsythe 1970), and the alarm-attack calls of the Solitary and Green sandpipers (Tringa solitaria and T. ochropus; Oring 1968). These calls all have "a wide frequency spectrum and sharp discontinuities," and thus are easy sounds to locate (Marler and Hamilton 1967). These characteristics are also true of mobbing calls of many passerine birds (Armstrong 1963).

Next to the variable chase call, the scolding trill calls were the most variable in character and number of notes. However, a general pattern was present. The state of excitement of the scolding bird increased (as indicated by its behavior and the circumstances) from the type I to type III call; associated with this was a progression towards higher frequencies, longer notes and shorter intervals, and fewer notes in the call. The frequency range of the type III call was also greatest, which would tend to make it the easiest to locate. This type was always accompanied by the distraction display, in which the bird presumably wanted to attract attention to itself. Forsythe (1972) described a distraction display of the Longbilled Curlew, observed once. In both species, the display appears to be poorly developed as a predator-reaction; it occurs infrequently, conspicuous plumage features are lacking, and on many occasions diversionary movements (such as tail fanning or twisting) were incomplete or lacking. These curlew species tend to distract a ground predator (e.g. a human) by flying toward and scolding an intruder before it approaches the nest closely. Distracting in this manner, while the predator is still at a distance, would appear to be advantageous for open-country species with large exposed eggs, readily seen from nearby.

A contact call from adult Long-billed Curlews to their chicks was not described by Forsythe (1970), but Graul (1974) described a brood call of the Mountain Plover (Charadrius montanus) which apparently attracts the young. The adult-to-chick contact call of the Whimbrel did not cause the chicks to gather beside the adult, but likely did attract the chicks and, because of its low audibility, function to keep them nearby. The brood call of the Mountain Plover and this call of the Whimbrel consist of a series of short notes spanning a fairly wide frequency range. The location of the call is therefore easily determined by the chicks. The low audibility reduces the possibility of alerting predators.

The two calls of the chicks have characteristics that make the sound source difficult to locate: they were of high frequency, without sharp intensity changes and of long duration. The peep call appears to be a contact note with the adult and possibly the other chicks. It is functionally similar to the peep-beep call of Long-billed Curlew chicks. The wheee call of Whimbrel chicks is likely a distress call, and would be functionally similar to the squeee call of Long-billed Curlew chicks.

On a few occasions in August, I heard vocalizations accompanying flocks of 10 to 15 migrating Whimbrels. The flocks were extremely high, and I was not able to record the sounds.

This vocalization was not included because I do not know if it was a different call from those already described. It consisted of a series of short notes rapidly repeated and was given simultaneously by many in the flock. It appeared to function as a contact note among flock members. The call of migrating Whimbrels has been described by Witherby et al. (1940) as "a rapid tittering." Larrison and Sonnenberg (1968) described "a soft whistled cur-lew, cur-lew during the migration season. Vocalizations off the breeding areas need further investigation

SUMMARY

Vocalizations of adult and young Whimbrels were recorded during the breeding seasons of 1973 and 1974 near Churchill, Manitoba. I was able to distinguish the following 10 adult calls: low whistle, low trill (composed of one, two or three phrases), whining, variable chase, settling, whit, short predator alarm, long predator alarm, scolding trill (three types), and adult-to-chick contact call. A peep and wheee call were distinguished for chicks up to one week of age. The context in which calls were heard is described, and suggestions are made as to the function of the calls. Whimbrels also have an aerial display song; this consists of the low whistle call, repeated up to 20 times, followed by the three-phrase low trill call. The display associated with this is described, and appears to function chiefly in self-advertisement. A distraction display occurs infrequently, and associated with this is the type III scolding trill call.

The adaptive advantage of the physical nature of various calls is discussed, particularly with respect to the ease with which the source of a sound can be located. Calls with short abrupt notes (particularly those spanning a wide frequency range), such as the low trill, short and long predator alarm, scolding trill, and adult-to-chick contact calls would be relatively easy to locate. However, long calls of high frequency without sharp intensity changes, such as the whining call and the two chick calls, would be difficult to locate.

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LITERATURE CITED

- Armstrong, E. A. 1963. A study of bird song. Oxford Univ. Press, London.
- Bent, A. C. 1929. Life histories of North American shore birds. U.S. Natl. Mus. Bull. 146.
- Collias, N. E. 1960. An ecological and functional classification of animal sounds, p. 368-391. In W. E. Lanyon and W. N. Tavolga [eds.], Animal sounds and communication. Am. Inst. Biol. Sci., Washington, D.C.
- Forsythe, D. M. 1970. Vocalizations of the Longbilled Curlew. Condor 72:213-224.
- Forsythe, D. M. 1972. Observations of the nesting biology of the Long-billed Curlew. Great Basin Nat. 32:88–90.
- Graul, W. D. 1974. Vocalizations of the Mountain Plover. Wilson Bull. 86:221-229.
- Larrison, E. J., and K. G. Sonnenberg. 1968. Washington birds, their location and identification. Seattle Audubon Soc., Seattle, Washington.
- MARLER, P. 1955. Characteristics of some animal calls. Nature 176:6-8.
- Marler, P., and W. J. Hamilton. 1967. Mechanisms of animal behavior. John Wiley and Sons, New York.
- Mulligan, J. A. 1963. A description of Song Sparrow song based on instrumental analysis. Proc. 13th Int. Ornithol. Congr. (1962):272-284.
- Oring, L. W. 1968. Vocalizations of the Green and
- Solitary sandpipers. Wilson Bull. 80:395-420. Parmelee, D. F. 1970. Breeding behavior of the Sanderling in the Canadian high arctic. Living Bird 9:97-146.
- ROSENBERG, E. 1931. Etwas vom Brachvogel und seinen flugen. Beitr. Fortpflanzungbiol. Vogel 7:13-15.
- SIMMONS, K. E. L. 1955. The nature of the predator-reactions of waders towards humans, with special reference to the role of the aggressive-, escape-, and brooding-drives. Behaviour 8:130-173.
- Skeel, M. A. 1976. Nesting strategies and other aspects of the breeding biology of the Whimbrel (Numenius phaeopus) at Churchill, Manitoba. M.Sc. diss., Dept. of Zoology, Univ. of Toronto.
- Stout, D. G. [ed.]. 1967. The shorebirds of North America. Viking Press, New York.
- von Frisch, O. 1956. Zur brutbiologie und jungentwicklung des Brachvogels (Numenius arquata L.). Z. Tierpsychol. 13:50-81.
- WILLIAMSON, K. 1946. Field notes on the breeding biology of the Whimbrel. North-western Nat. 21:167-184.
- WITHERBY, H. F. [ed.], F. C. R. JOURDAIN, N. T. TICE-HURST, AND B. W. TUCKER. 1940. The handbook of British birds. Vol. IV. H. F. and G. Witherby, London.

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