

# THE STRUCTURE OF AERIAL DISPLAYS IN THREE SPECIES OF CALIDRIDINAE (SCOLOPACIDAE)

EDWARD H. MILLER

*Vertebrate Zoology Division, British Columbia Provincial Museum,  
Victoria, British Columbia V8V 1X4, Canada, and  
Biology Department, University of Victoria,  
Victoria, British Columbia V8W 2Y2, Canada*

**ABSTRACT.**—Sandpipers in the subfamily Calidridinae (Scolopacidae) breed in the Arctic and Subarctic. In all species, unpaired males engage in distinctive aerial displays. Such displays are described for three species: Dunlin (*Calidris alpina* L.), Semipalmated Sandpiper (*Calidris pusilla* L.), and Stilt Sandpiper (*Calidris himantopus* Bonaparte). In each of the species, displays last several minutes, during which simple monotonous calls are emitted; more complex calls (including "Song") also occur. *C. himantopus* has a unique flight mode, which is considered as apomorphous (derived) within the subfamily. *C. alpina* is apomorphous for the buzziness of the main vocalization emitted in aerial display and *C. pusilla* for loss of the same vocalization and elaboration of another. The ancestral/derived status and systematic value of these and other display components are discussed, with reference to information available for other calidridine species. Received 2 August 1982, accepted 10 December 1982.

BIRD behavior has provided remarkably little insight into systematic relationships. Numerous comparative studies have documented patterns of behavioral similarity among related taxa, but a phylogenetic interpretation of these patterns is difficult because of problems in standardizing and quantifying behavioral attributes and because behavior is so variable even within individuals. These problems are acute in bioacoustics, for vocal learning is widespread, and many vocalizations are highly graded and variable in order to express minor variations in a signaller's behavioral state over short distances. Clearly, the systematic value of acoustic characteristics will be greatest for taxa with little sound-learning and that employ stereotyped sounds in long-distance communication (Mundinger 1979). This study documents long-distance, stereotyped calls in several related species that are presumed to have a small learned component to their vocalizations because of the low levels of structural variation in calls both within populations and across the geographic range of certain species (see Concluding comments).

The Calidridinae (Scolopacidae) consists of 24 closely related species of sandpipers that nest in open habitat in the Arctic and Subarctic (Pitelka et al. 1974). Their ecological similarities and close affinities make them ideal for the study of adaptive radiation and homologies of display behavior in a nonpasserine group. A

good candidate for such study is the aerial display, which is well developed in open-country birds in general and occurs in numerous species of Charadriiformes, including Calidridinae (Armstrong 1963, Pitelka et al. 1974, Miller in press a). This paper's purposes are to describe aerial displays in three calidridine species and to evaluate display components for their significance in pointing to affinities among these and related species. The species are Dunlin (*Calidris alpina* L.), Semipalmated Sandpiper (*Calidris pusilla* L.), and Stilt Sandpiper (*Calidris himantopus* Bonaparte). A detailed account of aerial display in the Least Sandpiper (*Calidris minutilla*) is available elsewhere (Miller 1979, in press b).

The study species are monogamous. Males occupy the nesting grounds each spring ahead of females and establish ephemeral territories over which they give display flights. Males stop displaying when they acquire a mate, although they nest in the area over which they displayed. Both sexes incubate and care for the brood, but adults and chicks generally feed in undefended areas distant from the nesting grounds. The male assumes an increasing role in incubation as it proceeds and is mainly responsible for raising the brood. The aerial displays of unpaired males in these species are therefore very restricted in occurrence and function: a male may engage in display flights for only a few days each spring, and these ap-

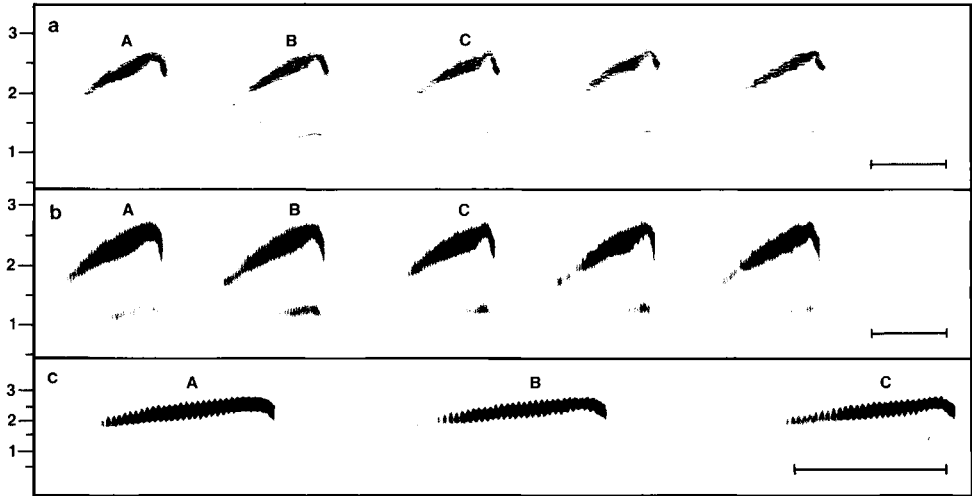


Fig. 1. Sound spectrograms of Rhythmically Repeated Calls of *Calidris himantopus*. A sequence is shown in narrow (*a*) and wide-band (*b*, *c*) representations. Calls marked "A," "B," and "C" correspond to the oscillograms marked the same in Fig. 3. These letters also correspond to the same calls in panels *a*, *b*, and *c* of this figure. The time marker in the bottom right corner of each panel represents 500 ms. The frequency scale is in kHz. Analyzing filter bandwidths are 45 Hz (narrow) and 300 Hz (wide).

pear to function solely to attract a female to a suitable nesting area, while simultaneously repelling competing unpaired males. *C. alpina* deviates most from this general outline.

#### MATERIALS AND METHODS

*Calidris alpina*, *C. pusilla*, and *C. himantopus* were studied near Churchill, Manitoba (58°24'N, 94°24'W), from 24 May to 6 July 1978. *C. alpina* and *C. pusilla* were also studied on the Alaskan north slope, near the mouth of the Canning River (70°10'N, 145°50'W), from 8 to 13 June 1979. Display flights were timed with a stopwatch. Vocalizations were taped at 19 cm/s on Scotch tape 208 matched to a Nagra IS tape recorder with a Sennheiser MKH816 "shotgun" microphone covered with a wind sock.

Sound spectrograms were prepared on a Kay Electronics Sona-Graph 7029A. Oscillograms were prepared on a Honeywell Visicorder system 1858. Power spectra were traced from plots obtained from a Princeton Applied Research Model 4513 FFT, and each is based on 2–5 s of tape recordings.

The vocalizations discussed below fall into three classes on the basis of physical characteristics and the social contexts in which they occur: Rhythmically Repeated Calls, Song, and Chattering. The major optical characteristic mentioned is mode of flight. Other optical display components are recognizable in various species of Calidridinae, but they merit separate, special study (see Drury 1961; Miller in press *a*, *b*).

#### RESULTS

##### STILT SANDPIPER, *CALIDRIS HIMANTOPUS*

Display Flights (DF's) start spontaneously, in association with DF's of nearby males or following interactions with females. Once maximal altitude is reached, the displaying male remains there throughout most of the DF, hovering over one area ("treading"), then letting the wind carry him to another area over which treading is resumed, and so on. Throughout the DF, and except when gliding (see next paragraph), *C. himantopus* beats its wings almost continuously in a rapid, relatively deep loose flutter, unlike the other two species. Of the species considered here, this species' DF's are highest in altitude [30–50 m; other estimates are 20–60 m (Jehl 1973) and 30–200 ft or more, averaging 75–100 ft (Parmelee et al. 1967)]. Durations of 24 DF's averaged 1.58 min (median = 1.03 min, SE of mean = 0.327). Jehl (1973) reported that flights last up to 8 min, and Parmelee et al. (1967: 126) mention a duration of "three to four minutes."

Three main types of vocalizations are associated with DF's in this species. One is a harsh, grating series of pulses (Chattering). This call type often precedes the most complex utter-

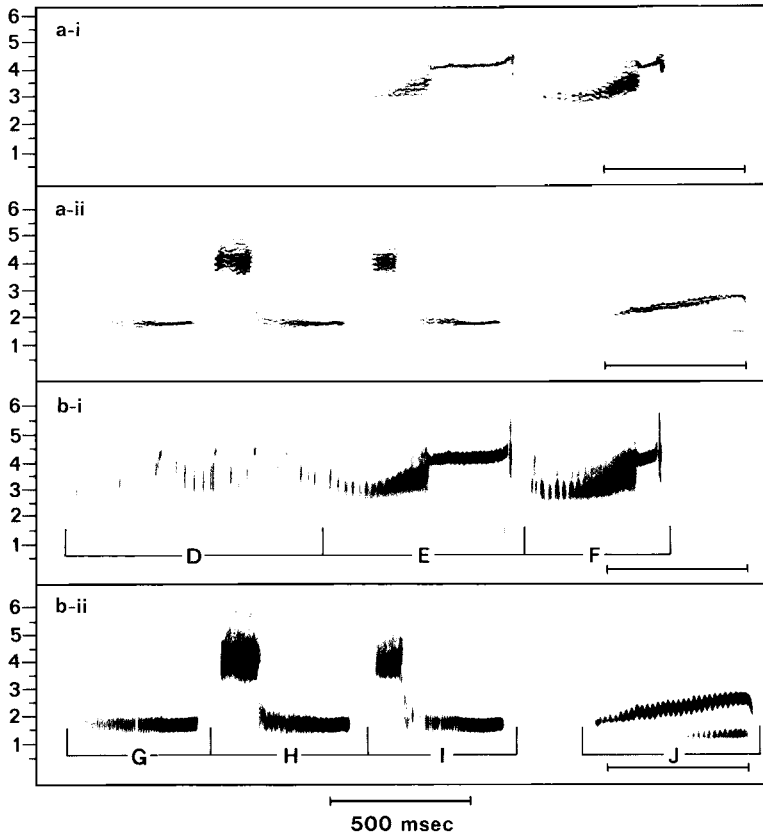


Fig. 2. Sound spectrograms of Song of *Calidris himantopus*, shown in narrow (a) and wide-band (b) representations. Panel a-i corresponds to b-i, and a-ii to b-ii; the uninterrupted temporal arrangement of this Song is apparent in Fig. 3c, d. Parts marked "D" to "J" correspond to the oscillograms marked the same in Fig. 3. The frequency scale is in kHz. Analyzing filter bandwidths are 45 Hz (narrow) and 300 Hz (wide).

ance, Song. The most common call is the stereotyped Rhythmically Repeated Call (RRC), which is emitted throughout most of a DF. RRC's occur in brief sequences followed by Song or by a brief silence; then they resume. Song is invariably uttered when birds sail with wings extended about 30° above the horizontal during DF's (alone or during interactions) and also during aerial pursuit of other birds, during fights, and when newly paired males follow their mates in brief flights (e.g. when changing feeding locations). Song is also often given spontaneously, with no detectable stimulus or change in flight pattern, and usually accompanies descent from a DF. Examples of typical sequences of RRC's and Songs follow; the numbers represent the number of RRC's given in rhythmic sequence and are separated

from other numbers when a break in rhythm occurred (Silence = longer silence than that typical of a break in rhythm):

- (1) 18-19-3-15-3- Song -8- Silence -3- Song
- (2) 5-5-4-6-24-5-4-5-5-16-5
- (3) 12-3-5-26-25-22
- (4) 6-33-14-37-6- Song
- (5) Song -4-9- Song -12- Silence -2-7- Song -3-4.

RRC's of *C. himantopus* consist of only one element, which is around 600 ms long, has a fundamental frequency around 1-1.5 kHz, and is separated from adjacent calls by about 500 ms. The carrier frequency rises gently over an RRC, then declines sharply at the end, and it shows marked rhythmic amplitude and fre-

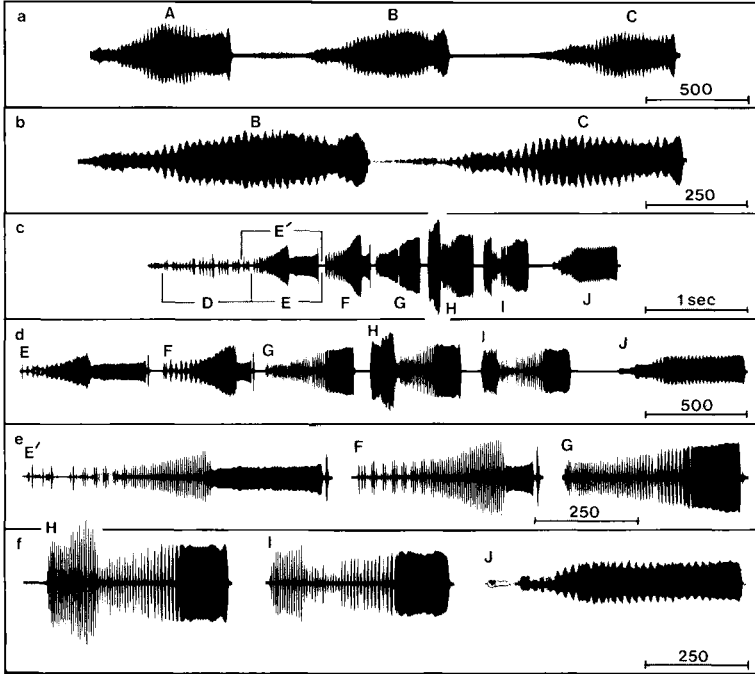


Fig. 3. Oscillograms of Rhythmically Repeated Calls (RRC's) and Song of *Calidris himantopus*. RRC's marked "A," "B," and "C" in panels a and b correspond to the sound spectrograms marked the same in Fig. 1. Song is shown in panels c to f; parts marked "D" to "J" correspond to the sound spectrograms marked the same in Fig. 2. Time markers are in ms, except in panel c.

quency modulation (AM and FM) throughout (Figs. 1, 3, 4). AM and FM are in phase. Overall amplitude declines near the element's end, when the fundamental frequency becomes relatively stronger, then increases right at the end. The fundamental frequency is weak throughout the element, however, and is never as strong as its first harmonic overtone (Fig. 4). There is rarely any detectable energy in higher harmonics on sound spectrograms.

Song in *C. himantopus* consists of several types of elements. The Song shown in Figs. 2 and 3 is preceded by Chattering (marked as D), which merges into a series of pulses of increasing amplitude (start of section E). This pulse series shifts suddenly to a rich tone of constant and lower amplitude about halfway through (second harmonic overtone strongest, fundamental frequency second strongest, first harmonic overtone weakest), and this complex is then repeated (F). The fundamental frequency lies around 1.5–2 kHz. The third major element begins as a low-frequency (1.5–2 kHz), low-amplitude series of pulses and increases gently

in amplitude to end in a nearly pure tone (element G in Figs. 2, 3). This structure is repeated in the terminal parts of the next two elements (H, I), each of which begins with a high-frequency, high-amplitude series of pulses [the last two pairs of notes, H and I, are the *ee-haw* notes of Jehl (1973: 120), like "the braying of a donkey"]. The Song shown ends with an RRC-like call. Females occasionally emit RRC's and Songs (Jehl 1973).

DUNLIN, *CALIDRIS ALPINA*

*Calidris alpina* does not continuously beat the wings like *C. himantopus* during DF but alternates brief glides with rapid, shallow Flutters [Punctuated Fluttering, or PF; these components are termed "Arched-wings-glide" and "Arched-wings-quiver" by Cramp and Simmons (1983: 364)]. Two Manitoba birds averaged 20.4 Flutters per min, based on 1.6 min of sample. Five Alaskan birds averaged 28.6 Flutters per min, based on 3.2 min of sample, and T. A. Sordahl (in litt.) estimated a rate of 19.1

for seven Alaskan samples totalling 6.9 min. Together, these figures yield a weighted estimate of 21.9 [Flutters "every 5–10 s" according to Cramp and Simmons (1983: 364)]. DF's of *C. alpina* are second highest of the species considered here (15–30 m); Holmes (1966) suggests that they average about 50 ft high in northern Alaska (range 10–150 ft), Brown (1962) gives a range of 30–50 ft, Manson-Bahr (1931: 88) states that they "rise to . . . 100–200 ft," and Nelson (1887) mentions an altitude of 15–20 yds. Two DF's lasted 21 and 77 s in Manitoba, and six others (four from T. A. Sordahl in litt.) from Alaska lasted from 26 to 230 s; the overall weighted mean duration is 1.48 min. The longest DF observed by Holmes (1966: 9) was 3.5 min, and he states that they "last from a few seconds to several minutes"; in Finland they last up to 10 min (Cramp and Simmons 1983). Female *C. alpina* sometimes participate in DF's (Sutton 1932, Brown 1938, Holmes 1966). A sketch of *C. alpina* in DF is provided by König (1956: Fig. 2).

There are two main vocalizations associated with DF's of *C. alpina*, and these are emitted in similar social contexts and in a similar pattern to those described for *C. himantopus* (i.e. much arrhythmia and spontaneous Song, and Song during descent). RRC's consist of one element only, which lasts about 600 ms, with intervals between calls of about 200 ms (Figs. 5, 6). Thus, the call is about the same duration as in *C. himantopus* but is given at a faster rate [Heldt (1966: 175) timed 30 calls lasting 24 s for European *C. alpina*]. The fundamental frequency rises gently from about 1–1.2 kHz, and there is a minor terminal drop in frequency and amplitude. The RRC consists entirely of a series of brief pulses. The fundamental frequency is weak throughout the call and is never as strong as its first harmonic overtone (see Fig. 4). There are suggestions of very weak higher harmonics on sound spectrograms. The sound spectrograms for European *C. alpina* in Cramp and Simmons (1983) and Fig. 65A of Glutz von Blotzheim et al. (1975) are very similar.

The Song of *C. alpina* is very different from that of *C. himantopus* (Figs. 5, 6). It consists of a long series of pulses that are distinctively patterned. The Unit of Repetition (UR) in this pattern shows 2 or 3 to as many as 10 brief pulses, followed by a longer pulse. The UR shows several trends over the length of the Song: amplitude declines, the number of brief

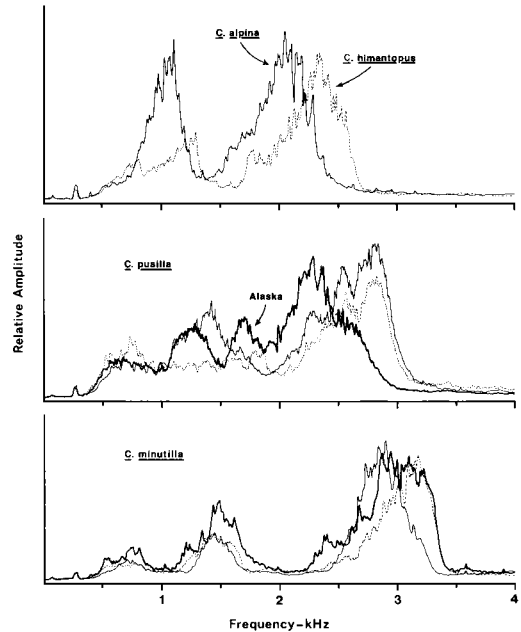


Fig. 4. Power spectra of the prominent vocalizations associated with Display Flights (Motorboat Sound of *Calidris pusilla*; Rhythmically Repeated Calls for the other species); *Calidris minutilla* is included for comparison. All recordings are from Manitoba except for one *C. pusilla*. Three different *C. pusilla* and *C. minutilla* are distinguished.

pulses increases though their individual durations do not change, and the duration of the long pulse increases. The Song lies between about 2 and 3 kHz in frequency. Females sometimes emit Song (Brown 1938, Cramp and Simmons 1983). European *C. alpina* have a very similar song (Fig. 66A of Glutz von Blotzheim et al. 1975, Cramp and Simmons 1983).

No sound resembling Chattering was heard.

#### SEMPALMATED SANDPIPER, *CALIDRIS PUSILLA*

*Calidris pusilla* during DF's exhibits PF. Nineteen records from Manitoba (totalling 28.1 min) give a mean Fluttering rate per minute of 17.9. On the Alaskan north slope, *C. pusilla* averaged 41.2 and 23.5 Flutters per min (based on 12.7 and 2.2 min of samples; the latter were by T. A. Sordahl in litt.). *C. pusilla* has the lowest DF's of the species discussed here (5–10 m high); estimates by Sutton (1932), Dixon (1917), and Parmelee et al. (1967) are 30, 50, and 25–50 ft, respectively. Höhn's (1968) and Irving's (1960) estimates of 50 yds and 200 ft, and Brandt's (1943: 205) comment that they fly

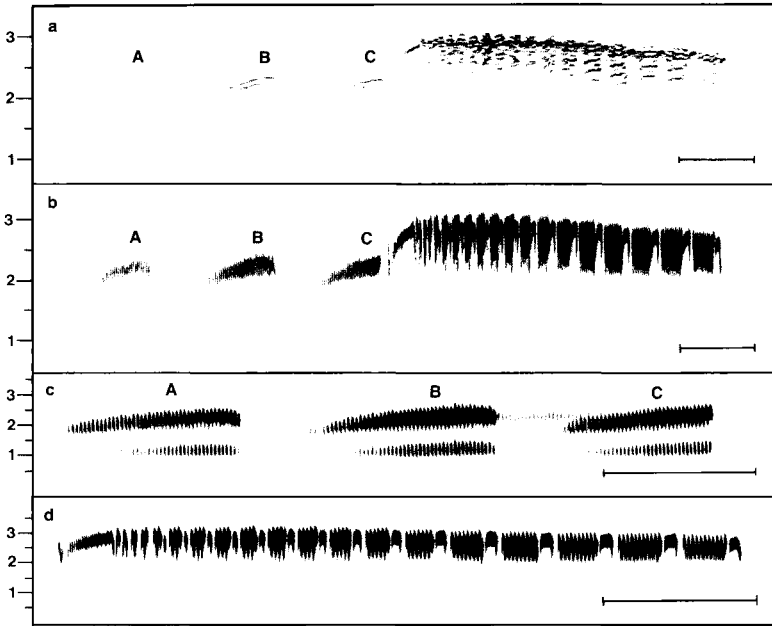


Fig. 5. Sound spectrograms of Rhythmically Repeated Calls (RRC's) and Song of *Calidris alpina*. These are shown in narrow (a) and wide-band (b, c, d) representations. RRC's marked "A," "B," and "C" correspond to the oscillograms marked the same in Fig. 6 and also to the same calls in panels a, b, and c of this figure. A Song follows RRC "C" in panels a and b and is also shown in panel d; the same Song is shown as an oscillogram in Fig. 6a. A weak RRC by another male *C. alpina* is apparent between RRC's "B" and "C" in panel c. The time marker in the bottom right corner of each panel represents 500 ms. The frequency scale is in kHz. Analyzing filter bandwidths are 45 Hz (narrow) and 300 Hz (wide).

"often almost out of sight" are certainly inflated or unusual. Sixty-two DF's in Manitoba averaged 1.56 min in duration (median = 1.48 min, SE of mean = 0.121), and 26 DF's in Alaska averaged 1.68 min (median = 1.42, SE of mean = 0.236).

Vocalizations accompanying DF's of *C. pusilla* are unlike any described so far. *C. pusilla* during DF's emit a "Motorboat" Sound (MS) almost continuously (Figs. 7, 8), and this is less frequently interrupted by Song than in the other species. They sometimes give other calls, all of which also occur in Song (e.g. compare part C of Fig. 7a-i and a-ii, with part A' of Fig. 7b). By designating each of the four pulse elements in the UR of MS by a number (1 = highest frequency, . . . , 4 = lowest frequency), the sequence shown in Fig. 7c can be represented as . . . 342134213421 . . . The corresponding oscillograms reveal that the two pulses with highest frequency also have highest amplitude (Fig. 8b, c). The fundamental frequency of MS is very weak; its first harmonic overtone lies between 2 and 3.5 kHz (Figs. 4, 7).

The Song of *C. pusilla* occurs in contexts as for the other species. It is a complex buzzy sequence with several distinct parts (Figs. 7, 9). The Song illustrated begins with a Laugh (segment A in Figs. 7, 9), a very common call in other contexts, then merges into the first of four kinds of UR's. The first type (UR-1) consists of two medium-amplitude pulses followed by a low-amplitude pulse, another medium-amplitude pulse, then a longer high-amplitude pulse (segment B in Figs. 7, 9). The last of these shows a strong harmonic structure. UR-2 is represented briefly in this Song: it consists of four or five medium to medium-high amplitude pulses followed by a longer high-amplitude pulse (segment C in Figs. 7, 9). UR-3 is the most complex. It starts with a high-amplitude pulse and is followed by a series of about seven bi-peaked pulses, which increase in amplitude regularly, and a compound high-amplitude pulse (segment D in Figs. 7, 9). The final UR (4) is MS, which starts at seven pulses per unit. This number declines and stabilizes at four, the same as the MS by this male that was not

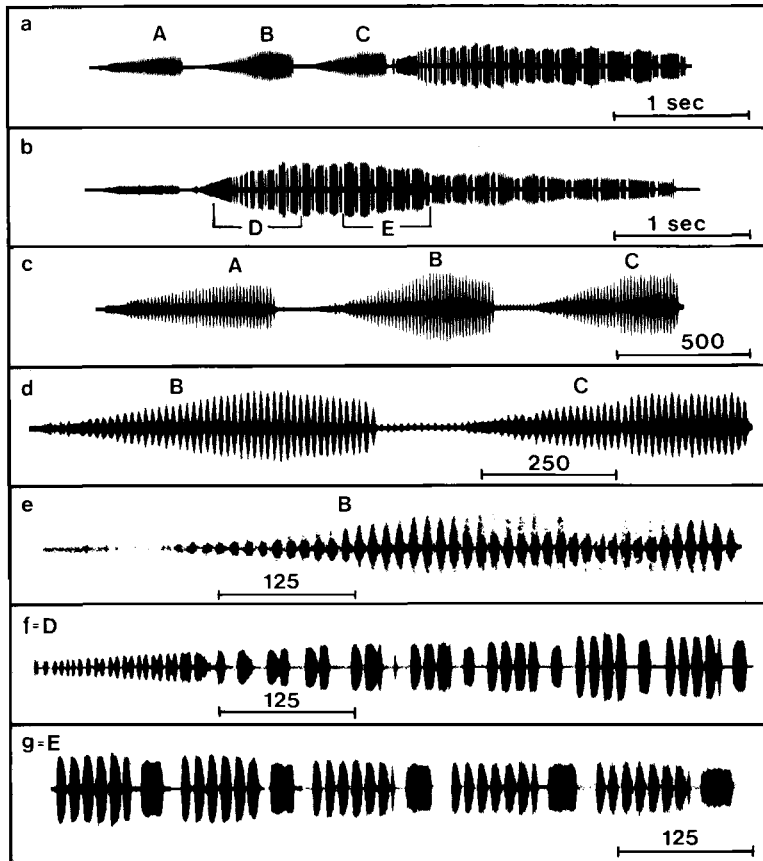


Fig. 6. Oscillograms of Rhythmically Repeated Calls (RRC's) and Song of *Calidris alpina*. RRC's marked "A," "B," and "C" in panels a, c, d, and e correspond to the sound spectrograms marked the same in Fig. 5. The Song that follows RRC "C" in panel a is shown as sound spectrograms in Fig. 5. A different Song (preceded by a weak RRC) is shown in panel b; the parts marked "D" and "E" are also shown in panels f and g. A weak RRC by another male *C. alpina* is apparent between RRC's "B" and "C" in panels a, c, and d. Time markers are in ms, except in panels a and b.

associated with Song (compare Fig. 7*a-i* and *a-ii* with Fig. 7*c*).

#### DISCUSSION

*Flying mode.*—Punctuated Fluttering characterizes DF's of scolopacid species outside the Calidridinae, so it can be considered plesiomorphous (ancestral) in the subfamily (Miller in press b). The flying mode of *C. himantopus* is thus autapomorphic (uniquely derived) among the three species studied. It is shared with the Surfbird (*Aphriza virgata*) and Baird's Sandpiper (*Calidris bairdii*), however (E. H. Miller, W. W. H. Gunn, and S. F. Maclean, Jr. unpubl. data). Quantitative differences in Punctuated Fluttering of different species may

shed some light on affinities, but virtually no data on this easily measured behavior are available. PF of *C. alpina* and *C. pusilla* differs only quantitatively from that of *C. minutilla* (Miller in press b).

*Chattering.*—Chattering of *C. himantopus* and the Motorboat Sound of *C. pusilla* are similar to a call type of *C. minutilla* (Miller in press b). In all species, this call type: (a) typically precedes Song, (b) consists of brief elements, (c) exhibits sequential grading in frequency and amplitude, and (d) has a weak fundamental frequency and most energy in the first harmonic overtone. In *C. himantopus* it differs most strongly in the rapid delivery and extremely brief duration of its elements. The elements of Motorboat Sound in *C. pusilla* are intermediate

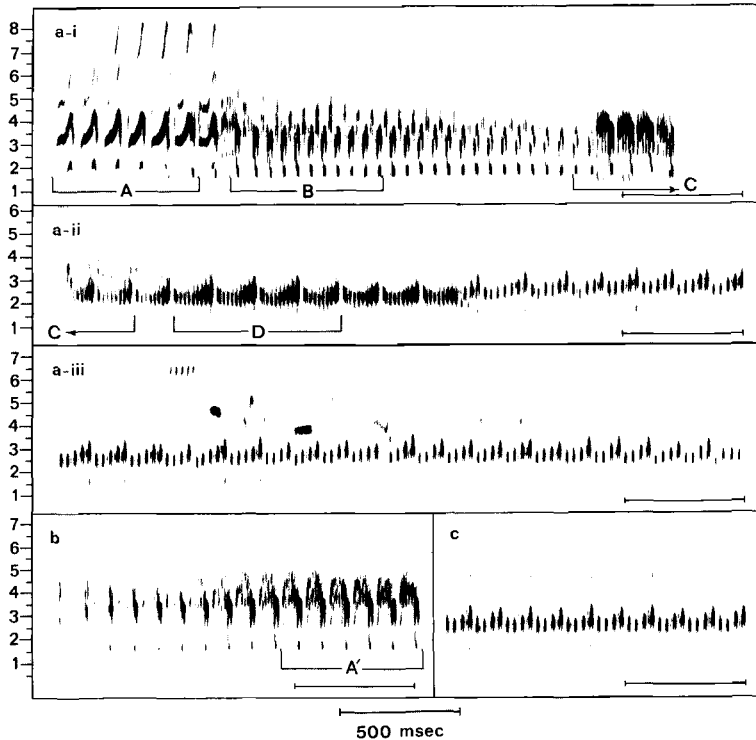


Fig. 7. Sound spectrograms of Song, Motorboat Sound (MS), and a Song-like call of *Calidris pusilla*. All calls are from one male. The uninterrupted temporal arrangement of the Song (panel series *a*) is apparent in Fig. 9*a*. Parts of the Song marked "A" to "D" correspond to the oscillograms marked the same in Fig. 9. Panel *a-iii* shows a later part of the MS series, which terminates the Song. The beginning of a series of calls that resemble one type of Song unit is shown in panel *b*; this sequence is shown as an oscillogram in Fig. 8*d*. The segment marked "A'" corresponds to the oscillogram marked the same in Fig. 8*e*. Part of an MS series is shown in panel *c*. This corresponds to part of the oscillogram shown in Fig. 8*a*. The frequency scale is in kHz. Analyzing filter bandwidth is 300 Hz.

in duration. The Motorboat Sound also shares with Chattering the tendency to have a greater number of elements per unit of repetition just after (and before?) Song; I do not know if this is also true of *C. himantopus*. In any case, Chattering and its apparent homologues occur in *C. minutilla*, *C. pusilla*, and *C. himantopus* but not in *C. alpina*. In *C. himantopus* it is used mostly to introduce Song; indeed, Jehl (1973: 120) discusses this call ("xxree") only as the introductory portion of Song. Chattering of *C. minutilla* is tied much less closely to Song and frequently occurs by itself in aggressive contexts (Miller in press *b*). In *C. pusilla* it is bound to Song even less and is the dominant vocal component of DF's. The possible adaptive significance of these differences and the evolutionary pathways that led to them are obscure at present.

The Song of the Curlew Sandpiper (*Calidris*

*ferruginea*) may begin with a homologue of Chattering: "most songs begin with a brief chatter of 5 to 10 staccato chit-chit sounds" (Holmes and Pitelka 1964: 367). A sound spectrogram of "territorial song" of the Little Stint (*Calidris minuta*) is suggestive of chattering (Fig. 1E of Tikhonov and Fokin 1981). It is more difficult to judge from other published descriptions of calidridine calls how widespread this call type is, although Parmelee (1970: 109) notes that "chattering notes" often accompany descent from DF's in the Sanderling (*Calidris alba*) and that the notes "were of a familiar type given by non-performing birds." Løvenskiold (1963: 201) writes similarly of descent: "the male makes a short, steep, downward flight, simultaneously uttering a loud 'churring' noise." Male western Sandpipers (*Calidris mauri*) emit a "harsh, prolonged grat-



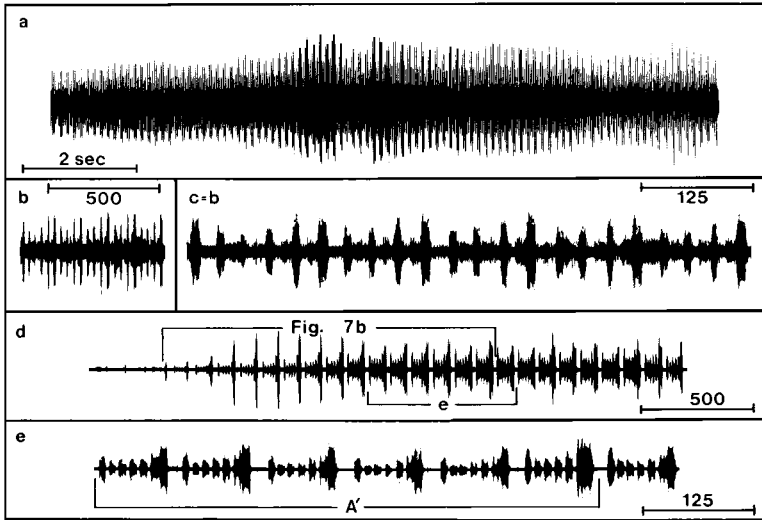


Fig. 8. Oscillograms of Motorboat Sound (MS) and a Song-like call of *Calidris pusilla*. Part of the MS series in panel *a* is shown as a sound spectrogram in Fig. 7c. A segment of the series is shown on different time scales in panels *b* and *c*. The beginning of a series of calls that resemble one type of Song unit is shown in panel *d*; part of this is shown in panel *e*, and part corresponds to the sound spectrogram of Fig. 7b. The portion marked "A" corresponds to the part of that sound spectrogram marked the same. Time markers are in ms, except in panel *a*.

ing note" during intraspecific clashes (Brown 1962: 2). Finally, a "chattering sound" accompanies short-range agonistic displays in male Buff-breasted Sandpipers (*Tryngites subruficollis*) during spring migration (Oring 1964: 86); this is a lekking species, which does not possess DF's like the other calidridines mentioned.

These observations suggest that a Chatter-like "aggressive" call is widespread in calidridines and is more or less associated with Song in those species possessing Song. Its widespread occurrence suggests that it may be plesiomorphous, although I know of no evidence suggesting that it exists outside the Calidridinae. As a working hypothesis, I suggest that the absence of a recognizable homologue of Chattering in *C. alpina* and the extreme elaboration of this call type in *C. pusilla* are different apomorphous (derived) conditions. Descriptive and sonographic evidence points to an elaboration of Chattering in Temminck's Stint (*Calidris temminckii*) like that in *C. pusilla* (Haviland 1916, Southern and Lewis 1938, Fig. 66E of Glutz von Blotzheim et al. 1975, Cramp and Simmons 1983).

*Rhythmically Repeated Calls.*—RRC's are present in *C. alpina*, *C. minutilla*, and *C. himantopus* (Miller in press b). They are the sim-

plest and most common calls used in DF's of these species. RRC's have the most energy in the first harmonic overtone of the fundamental in all the species (Fig. 4), they show a gentle rise in amplitude and frequency over their course (both decline near the end), and they are emitted rhythmically in long series.

RRC's with a pulsed or nearly pulsed structure, as in *C. alpina*, are suggested by written descriptions for other species, many of which refer to the buzzy quality of the calls. Included in this group are the White-rumped Sandpiper (*Calidris fuscicollis*; Fig. 91 of Glutz von Blotzheim et al. 1975), Broad-billed Sandpiper (*Limicola falcinellus*; Flint 1973, Fig. 93 of Glutz von Blotzheim et al. 1975, Cramp and Simmons 1983), Spoon-billed Sandpiper (*Eurynorhynchus pygmeus*; Dixon 1918, Portenko 1972), *C. alba* (Manniche 1910, Parmelee 1970, Green 1975), *C. bairdii* (Bailey 1926, Parmelee et al. 1967), and Rock Sandpiper (*Calidris ptilocnemis*; Elliot 1895, Murie 1959, D. R. Paulson in litt.). Other descriptions point to RRC's more like those of *C. minutilla* and *C. himantopus* for the Red Knot (*Calidris canutus*; Manniche 1910, Salomonsen 1950, Rosenberg et al. 1970, Fig. 66C of Glutz von Blotzheim et al. 1975, Cramp and Simmons 1983), *C. minuta* (Fig. 66D of Glutz

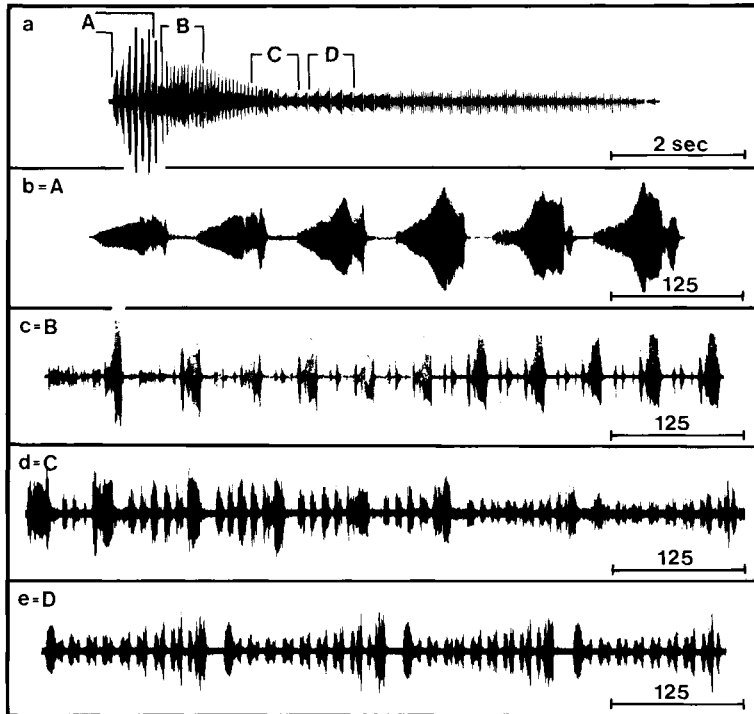


Fig. 9. Oscillograms of song of *Calidris pusilla*. Segments marked "A" to "D" correspond to sound spectrograms marked the same in Fig. 7a and also to the same sequences in panels b to e of this figure. Time markers are in ms, except in panel a.

von Blotzheim et al. 1975, Cramp and Simmons 1983), Long-toed Stint (*Calidris subminuta*; Leonovich 1973), and *C. ferruginea* (Holmes and Pitelka 1964). Conflicting descriptions were found only for the Purple Sandpiper (*Calidris maritima*), a close relative of *C. ptilocnemis* (Soper, cited by Bent 1927: 147; Keith 1938; Swanberg 1945; Tiedemann, cited by Løvenskiold 1963: 188; Uspenski 1969). Considering the presumed affinity between the two species, I accept for now Swanberg's (1945: 123) description of the RRC as "buzzy" (but see Cramp and Simmons 1983).

Sonographic evidence is obviously needed to confirm the trends I have summarized. In the absence of such evidence, I feel that the accounts cited are consistent enough to allow some working hypotheses to be established:

1. RRC's are plesiomorphous within the Calidridinae because of their wide distribution in related Scolopacidae (Miller in press b). Thus, the absence of RRC's in *C. pusilla* and *C. temminckii* (my interpretation; no descriptions or sound spectrograms suggesting RRC's for the latter species are available) is a synapomorphy

(shared derived state). RRC's are absent in lekking species, too, through convergence (Miller in press a).

2. RRC's outside the Calidridinae [except Woodcock (*Scolopax*)] are not pulsed (do not have a buzzy quality), so this character is apomorphic in the subfamily, uniting *C. alba*, *C. alpina*, *C. bairdii*, *C. fuscicollis*, *C. maritima*, *C. ptilocnemis*, *Eurynorhynchus*, and *Limicola*.

*Song*.—The vocalizations I have termed Song for the three species (plus *C. minutilla*; Miller 1979, in press b) occur in remarkably similar circumstances in all, and it seems reasonable to infer their homology. The structural complexity of Song in the four species and the near-absence of adequate descriptions for non-calidridine taxa make identification of ancestral and derived attributes impossible at present.

*Concluding comments*.—Three sound types are easily recognized in nuptial aerial displays of many Calidridinae, based on sound morphology and the contexts in which sounds occur: Rhythmically Repeated Calls, Chattering, and Song. Chattering and RRC's are probably plesiomorphous within the subfamily; pulsing

("buzziness") of RRC's is probably apomorphic. The distinctive flight mode, Punctuated Fluttering, is probably plesiomorphous in the group. Identification of other components of phylogenetic significance must await detailed analyses of vocalizations of other species, particularly of the complex utterance, Song. The ease with which certain sound types can be recognized across species and the remarkable conservatism of these sound types across the broad geographic range of certain species (e.g. *C. alpina*) make it likely that acoustic characteristics will shed much light on phylogenetic relationships within the Calidridinae.

## ACKNOWLEDGMENTS

Many people have helped me by reviewing all or parts of drafts, collecting or analyzing data, and assisting with field work: F. Cooke; D. Fairfield; B. Fenton; R. Gill; C. Handel; O. Hildén; S. Hills; R. Holmes; J. Jehl, Jr.; D. Jenni; K. Kovacs; S. MacLean, Jr.; P. Martin; P. Myers; L. Oring; D. Paulson; S. Pruett-Jones; T. Sordahl; and R. Wood. I am grateful to H. Lundgren, A. Ceska, and B. Culik for their careful help with translations, E. Longprés and H. Hosford for help with the production of diagrams, and the Natural Sciences and Engineering Research Council of Canada for financial support. This research began when I was a faculty member in the Biology Department, York University, Downsview, Ontario.

## LITERATURE CITED

- ARMSTRONG, E. A. 1963. A study of bird song. London, Oxford Univ. Press.
- BAILEY, A. M. 1926. A report on the birds of northwestern Alaska and regions adjacent to Bering Strait. Part VII. Condor 28: 31-36.
- BENT, A. C. 1927. Life histories of North American shore birds. Part 1. Bull. U.S. Natl. Mus. 142.
- BRANDT, H. 1943. Alaska bird trails. Cleveland, Ohio, Bird Research Foundation.
- BROWN, R. G. B. 1962. The aggressive and distraction behaviour of the western sandpiper *Ereunetes mauri*. Ibis 104: 1-11.
- BROWN, R. H. 1938. Breeding-habits of the dunlin. British Birds 31: 362-366.
- CRAMP, S., & K. E. L. SIMMONS (Eds.). 1983. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic. Vol. 3. Waders to gulls. Oxford, Oxford Univ. Press.
- DIXON, J. 1917. Children of the midnight sun. Bird-Lore 19: 185-192.
- . 1918. The nesting grounds and nesting habits of the Spoon-billed Sandpiper. Auk 35: 387-404.
- DRURY, W. H., JR. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. Auk 78: 176-219.
- ELLIOT, D. G. 1895. North American shore birds. A history of the snipes, sandpipers, plovers and their allies. New York, F. P. Harper.
- FLINT, V. E. 1973. Data on the biology of the broad-billed sandpiper. Pp. 98-100 in Fauna and ecology of waders, Issue 1. Moscow, Moscow Soc. Naturalists.
- GLUTZ VON BLOTZHEIM, U. N., K. M. BAUER, & E. BEZZEL (Eds.). 1975. Handbuch der Vögel Mitteleuropas, Band 6, Charadriiformes (1. Teil). Wiesbaden, West Germany, Akademisch Verlagsgesellschaft.
- GREEN, G. H. 1975. Sanderling, Greenland and colour rings. Bull. Wader Study Group 15: 13-15.
- HAVILAND, M. D. 1916. Notes on the breeding-habits of Temminck's stint. British Birds 10: 157-165.
- HELDT, R. 1966. Zur Brutbiologie des Alpenstrandläufers, *Calidris alpina schinzii*. Corax 1: 173-188.
- HÖHN, E. O. 1968. The birds of the Chesterfield Inlet, District of Keewatin, N.W.T., Canada. Can. Field-Natur. 82: 244-262.
- HOLMES, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in Northern Alaska. Condor 68: 3-46.
- , & F. A. PITELKA. 1964. Breeding behavior and taxonomic relationships of the Curlew Sandpiper. Auk 81: 362-379.
- IRVING, L. 1960. Birds of Anaktuvuk Pass, Kobuk, and Old Crow. A study in Arctic adaptation. Bull. U.S. Natl. Mus. 217.
- JEHL, J. R., JR. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. Wilson Bull. 85: 115-147.
- KEITH, D. B. 1938. Observations on the purple sandpiper in North East Land. Proc. Zool. Soc. London 108: 185-194.
- KÖNIG, D. 1956. Der Alpenstrandläufer (*Calidris alpina schinzii* (Br.)) als Brutvogel an der schleswig-holsteinischen Westküste. Vogelwelt 77: 108-114.
- LEONOVICH, V. V. 1973. The distribution and biology of the long-toed stint. Pp. 78-81 in Fauna and ecology of waders, Issue 1. Moscow, Moscow Soc. Naturalists.
- LØVENSKIOLD, H. L. 1963. Avifauna Svalbardensis, with a discussion on the geographical distribution of the birds in Spitsbergen and adjacent islands. Norsk Polarinstitutt Skrifter 129.
- MANNICHE, A. L. V. 1910. The terrestrial mammals and birds of northeast Greenland. Medd. Grøn. 45: 1-200.
- MANSON-BAHR, P. H. 1931. On the breeding displays of certain waders, with special reference

- to the snipe family. Bull. British Ornithol. Club 57: 84-99.
- MILLER, E. H. 1979. Functions of display flights by males of the Least Sandpiper, *Calidris minutilla* (Vieill.), on Sable Island, Nova Scotia. Can. J. Zool. 57: 876-893.
- . In press a. Communication in breeding shorebirds. In Behavior of marine animals, vol. 5. Shorebirds (J. Burger and B. Olla, Eds.). New York, Plenum Publ. Corp.
- . In press b. Structure of display flights in the Least Sandpiper. Condor.
- MUNDINGER, P. 1979. Call learning in the Carduelinae: ethological and systematic considerations. Syst. Zool. 28: 270-283.
- MURIE, O. J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. North American Fauna 61.
- NELSON, E. W. 1887. Report upon natural history collections made in Alaska between the years 1877 and 1881. Washington, D.C., Government Printing Office.
- ORING, L. W. 1964. Displays of the Buff-breasted Sandpiper at Norman, Oklahoma. Auk 81: 83-86.
- PARMELEE, D. F. 1970. Breeding behavior of the Sanderling in the Canadian high Arctic. Living Bird 9: 97-146.
- , H. A. STEPHENS, & R. H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. Bull. Natl. Mus. Canada 222.
- PITELKA, F. A., R. T. HOLMES, & S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in Arctic sandpipers. Amer. Zool. 14: 185-204.
- PORTENKO, L. A. 1972. Birds of the Chukotskii Peninsula and Wrangel Island, Part I. Leningrad, Nauka.
- ROSENBERG, N. T., N. H. CHRISTENSEN, & B. GENSBOEL. 1970. Bird observations in northeast Greenland. Medd. Grønl. 191: 1-87.
- SALOMONSEN, F. 1950. The birds of Greenland. Copenhagen, Munksgaard.
- SOUTHERN, H. N., & W. A. S. LEWIS. 1938. The breeding behaviour of Temminck's stint. British Birds 31: 314-321.
- SUTTON, G. M. 1932. The exploration of Southampton Island, Hudson Bay. Part II, Zoology. Section 2. The birds of Southampton Island. Mem. Carnegie Mus. 12. Part II, Section 2: 1-275.
- SWANBERG, P. O. 1945. Om skarsnappan, *Calidris m. maritima* (Brünnich), i de svenska fjällen och dess häckningsbiologi. Fauna och Flora 40: 108-133.
- TIKHONOV, A. V., & S. YU. FOKIN. 1981. [Lek and calls of shorebirds.] Ornitologia 16: 64-72.
- USPENSKI, S. M. 1969. Die Strandläufer Eurasiens (Gattung *Calidris*). Wittenberg, West Germany, A. Ziemsen.