Breeding vocalizations of Baird's Sandpiper *Calidris bairdii* and related species, with remarks on phylogeny and adaptation

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Vocalizations of Baird's Sandpiper were recorded in northeastern Alaska, U.S.A. Males beat the wings continuously in a loose deep flutter during display flights. They utter Rhythmically Repeated Calls (RRCs), Song and Chatter in display flights, and a Laugh when mildly disturbed. RRCs averaged 690 ms long with intervals between them of 280 ms. They have a "buzzy" quality because they comprise a series of rapidly repeated pulses (pulse rate = 77 Hz). Songs are long, complex, multipartite utterances, and usually include Chatter at the end. Laughs are brief, simple trills consisting of a single element type repeated several times. RRCs, Chatter and Laugh are structurally homologous with call types described for other calidridine species. Phylogenetic affinities and signalling distance account for many of the acoustic features of Calidridini.

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Introduction

Research on acoustic communication in songbirds has contributed useful information to systematics, especially below the species level (Payne 1986). Less comparative information on vocalizations in other taxa is available, probably because such species are harder to record and because most do not possess a discrete class of loud, complex vocalizations like "song" as songbirds do. The 24 or 25 species of calidridine sandpipers (Gochfeld et al. 1984, Hayman et al. 1986) offer opportunities for comparative research because they are closely related, exhibit a range of mating and spacing systems, and share certain homologous displays (Pitelka et al. 1974). Earlier work has identified several homologous classes of sounds in calidridines (references in

Miller et al. 1987), and has revealed low intraspecific variation for one type of sound in a representative species (Miller 1986). Thus vocalizations of calidridine sandpipers are potentially valuable in systematic research, and provide a useful contrast to the more widely studied and better-known songbirds.

The present study contributes new information on vocalizations used by breeding calidridines, with special reference to the Baird's Sandpiper *Calidris bairdii*. Our findings support the suggestion that vocal attributes of calidridines are evolutionarily conservative, and suggest that phylogenetic relationships and selective pressures related to transmission distance can explain most features of calidridine nuptial displays (contra Loffredo and Borgia 1986).

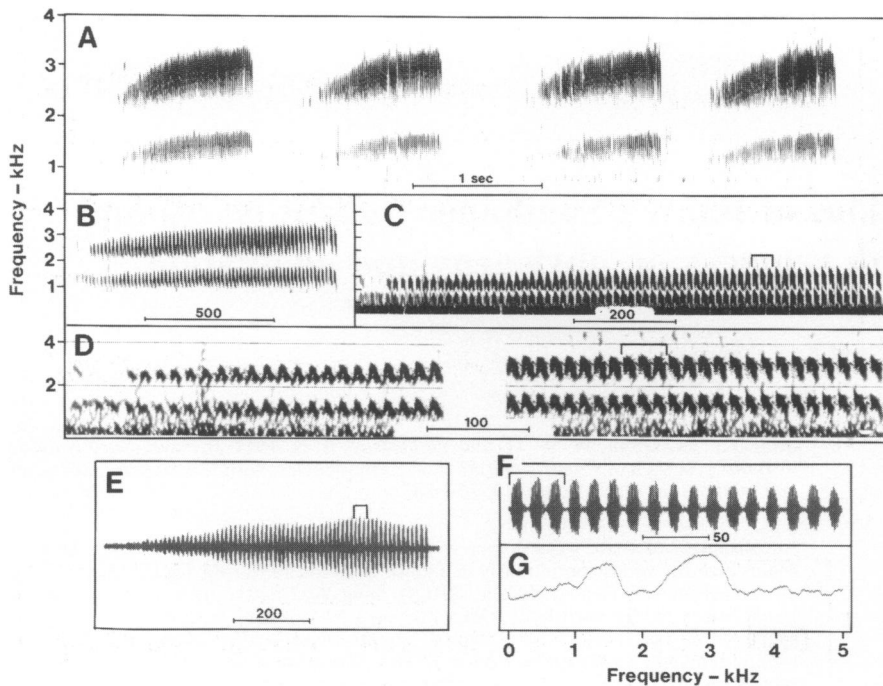Acoustic communication in shorebirds has been re-

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Fig. 1. *Calidris bairdii*, Rhythmically Repeated Calls (RRCs). A – Portion of long sequence of RRCs (analyzing filter bandwidth (afb), 150 Hz). B – Penultimate RRC before Song (afb, 300 Hz). C – Same RRC analyzed at half speed over 0–8000 Hz; three pulses that are analyzed in part G are marked (afb, 600 Hz). D – Beginning and end of same RRC analyzed on logarithmic frequency scale at quarter speed over 0–8000 Hz, with same pulses marked (afb, 180 Hz). E = Oscillogram of same RRC, with same pulses marked. F – Oscillogram of 17 terminal pulses of same RRC, with same pulses marked (signal digitized at 20 kHz). G – Power spectrum of three marked pulses (signal digitized at 20 kHz; FFT based on 1024 points; see Methods). Time markers in ms, except part A.

viewed by Miller (1984). Additional references are summarized in the Appendix to the present paper.

Methods

We recorded *C. bairdii*, Pectoral Sandpipers *Calidris melanotos*, and Buff-breasted Sandpipers *Tryngites subruficollis* near the mouth of the Canning River and on Barter Island, in northeastern Alaska, in June 1979. We used a Nagra IS recorder with a Sennheiser MKH816 ultradirectional ("shotgun") microphone with wind sock. Information on recordings of other species referred to below is summarized in Miller (1983a, b) and Veprintsev (1982). Sound spectrograms were prepared on a Kay Elemetrics Digital Sona-Graph 7800. We used various tape speeds and both linear and logarithmic frequency scales to investigate fine structure. Low tape speed and a logarithmic frequency display were particularly useful in emphasizing fine temporal features while increasing their contrast with background noise. Oscillograms and power spectra were prepared with Micro Speech Lab (MSL, version 2.2[a]), a software package for digitizing and analyzing sound signals. MSL was run on an IBM XT Personal Computer, with a Hewlett-Packard Thinkjet printer. We filtered input signals with a Krohn-Hite model 3750 filter below 500 and above 8000 Hz, at 24 dB per octave. Signals were digitized at 20,000 Hz (it is desirable to digitize at a rate at least 2.5 times a signal's maximum frequency). Spectra discussed below were computed using no pre-emphasis, a Hamming window, and low smoothing (average incorporating four bins on either side of the current bin).

We made additional measurements on calls used in aerial displays by the White-rumped Sandpiper *Calidris fuscicollis* (see Fig. 8A): total call duration from beginning of pulsed section to beginning of isolated pulse (a–d); duration of pulsed plus terminal section (a–c); duration of terminal tonal section (b–c); interval between terminal tonal section and beginning of isolated pulse (c–d); and interval from beginning of that pulse to the start of pulsing in the next call (d–e). Data are summarized in Tab. 2. The variables (a–d) and (d–e) were taken as estimates of the duration of Rhythmically Repeated Calls (RRCs) and Inter-call Intervals (ICIs), for comparison with other species. Pulse rates were based on the number of pulses per 125 ms for both *C. fuscicollis* and the Broad-billed Sandpiper *Limicola falcinellus*; the samples were taken working backwards from the beginning of the terminal tonal portion of each RRC (see Fig. 8E). For other species with pulsed RRCs, the final 250 ms were used to estimate pulse rate.

The adjusted coefficient of variation (V*) was computed for several variables using the formula of Sokal and Rohlf (1981): $V^* = V(1+(1/4n))$ (see Fig. 9).

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[a]Available from Speech Technology Research Centre, University of Victoria, P.O. Box 1700, Victoria, B.C. Canada V8W 2Y2.

Fig. 2. *Calidris bairdii*, termination of sequence of Rhythmically Repeated Calls (RRCs) followed by Song; the Song ends in Chatter, which is overlain by part of Lapland Longspur *Calcarius lapponicus* song. A – Complete RRC-Song-Chatter sequence; parts 1 and 2 overlap (arrows mark where they meet) (analyzing filter bandwidth, 300 Hz). Part of Chatter is analyzed further in Fig. 4. B – Oscillogram of same sequence (signal digitized at 20 kHz). Time markers, 500 ms.
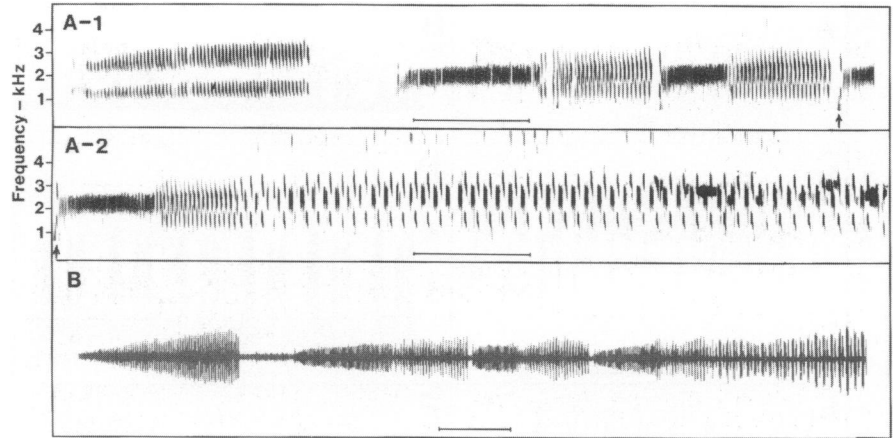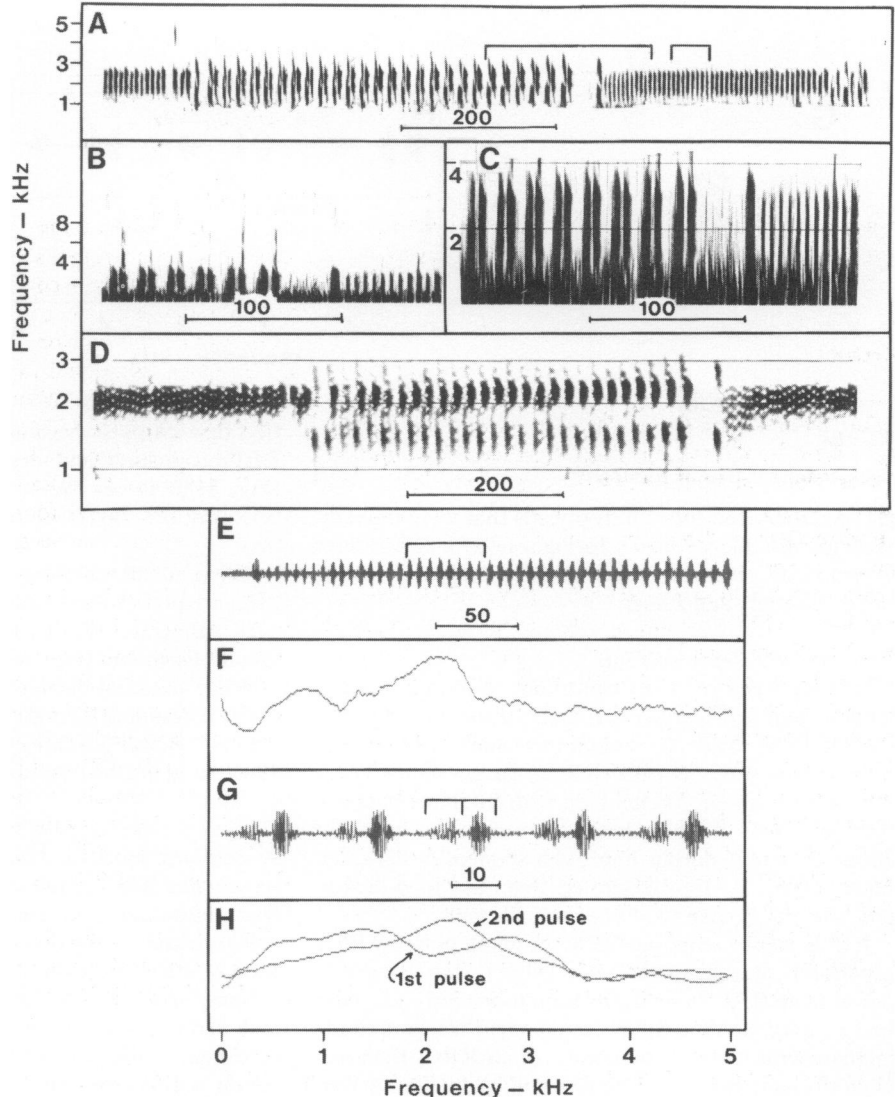

Fig. 3. *Calidris bairdii*, further analysis of song. A – End of one pulse train, entire couplet train, and beginning of second pulse train of Song, analyzed at half speed over 0–8000 Hz (analyzing filter bandwith (afb), 300 Hz). Marked portions are analyzed further in other parts of this Fig. B – Last six couplets in train and beginning of second pulse train (first segment marked in part A), analyzed at quarter speed over 0–8000 Hz (afb, 1200 Hz). C – As part B, analyzed on logarithmic frequency scale. D – End of first pulse train, entire couplet train, and beginning of second pulse train in part A, analyzed on logarithmic frequency scale at half speed over 0–8000 Hz (afb, 90 Hz). E – Oscillogram of beginning of second pulse train shown in part A (marked portion corresponds to the second segment marked in part A); F – Power spectrum of eight pulses marked in part E (for E and F, signal digitized at 20 kHz; FFT based on 1024 points). G – Oscillogram of five couplets, from couplet train shown in part A. Marked portions are analyzed further in part H. H – Power spectra of first and second pulses within couplet marked in part G (for G and H, signal digitized at 20 kHz; FFTs were each based on 256 points). Time markers in ms.
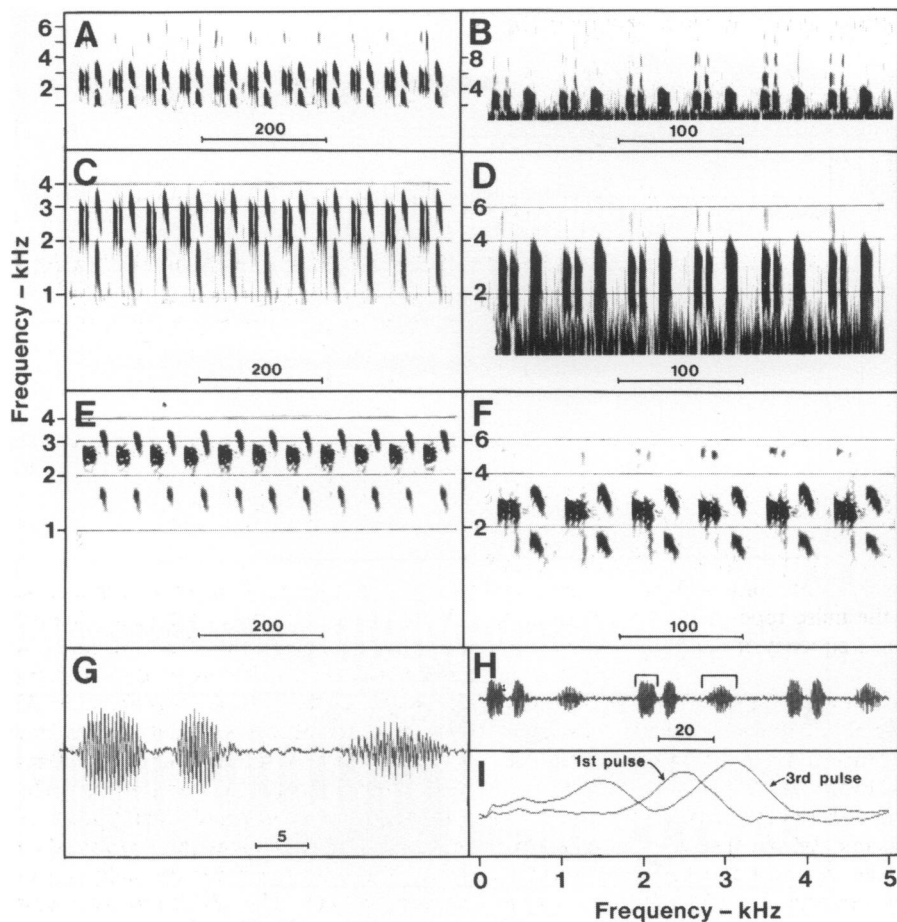
Fig. 4. *Calidris bairdii*, further analysis of Chatter (from Chatter terminating Song shown in Fig. 2). A–F – Portions of Chatter sequence analyzed over 0–8000 Hz using different tape speeds and analyzing filter bandwidths (afb) (A – half speed, afb 600 Hz; B – quarter speed, afb 1200 Hz; C – half speed, logarithmic frequency scale, afb 600 Hz; D – quarter speed, logarithmic frequency scale, afb 1200 Hz; E – half speed, logarithmic frequency scale, afb 90 Hz; F – quarter speed, logarithmic frequency scale, afb 180 Hz). G – Oscillogram of triplet (signal digitized at 20 kHz). H, I – Oscillogram (H) of three triplets and power spectra (I) of the first and third pulses (as marked in part H) of one triplet (signal digitized at 20 kHz; FFTs were each based on 256 points). Time markers in ms.

Results

Vocalizations of Baird's Sandpiper

C. bairdii uttered four kinds of calls that were immediately identifiable as classes distinguished for calidridines in previous research: Rhythmically Repeated Calls, Song, Chatter, and Laugh.

Rhythmically Repeated Calls

Unpaired males of many calidridine species engage in lengthy aerial displays over their future nesting area (Miller 1979). Male *C . bairdii* gave such displays, and uttered long series of calls (RRCs) during them. These RRCs were about 700 ms long with intervals between them of about 300 ms, thus were emitted at a rate of about 60 min^{-1} during unbroken sequences (Tab. 1). Drury (1961, p. 196) described them as "long-drawn-out, slurred, hoarse tooowee-tooowee calls."

RRCs were composed of a series of pulses with a repetition rate of about 77 Hz (Fig. 1, Tab. 1). Early pulses in an RRC were low in amplitude, and each pulse had a rapid rise then fall in frequency. Pulse amplitude increased throughout the course of an RRC, then levelled off near the end. The descending-frequency portion of each pulse became increasingly dominant as an RRC progressed, and was strikingly so by an RRC's end (Fig. 1D). Pulses were about 7–10 ms long (slightly briefer at the start) with intervals between of about 4–5 ms.

The fundamental frequency of RRCs was about 1–1.5 kHz; frequency increased then levelled off throughout each call (Fig. 1A, B, D). Most energy was in the second harmonic (Fig. 1A, G).

While in aerial display, male *C. bairdii* fluttered the wings continuously in a loose deep flutter, in the manner of the Stilt Sandpiper *Calidris himantopus* (Miller 1983b) and Surfbird *Aphriza virgata* (Miller et al. 1987).

Song

A complex kind of calidridine vocalization ("song") punctuates RRC sequences, occurs when a displaying bird's attention is directed towards another bird, and is usually given during descent (Miller 1983a, b). It is also used in other contexts.

Song of *C. bairdii* lasted several seconds long and included two alternating types of elements plus Chatter (see below; Fig. 2). The first type of element was a simple sequence of pulses of about 250–650 ms duration

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Fig. 5. *Calidris bairdii*, Laugh. A – One-element laugh (analyzing filter bandwidth (afb), 300 Hz). Sections marked "1" and "2" were 50 and 40 ms long, respectively; their power spectra are shown in part E. B – Two-element Laugh (afb, 300 Hz). C – Same Laugh as in part A, shown on logarithmic frequency scale (afb, 45 Hz). D – Oscillogram of laugh shown in parts A and C. E – Power spectra of marked segments in part A; fundamental frequency and second harmonic are marked for each (signal digitized at 20 kHz; FFTs were each based on 1,024 points). Time markers in ms.
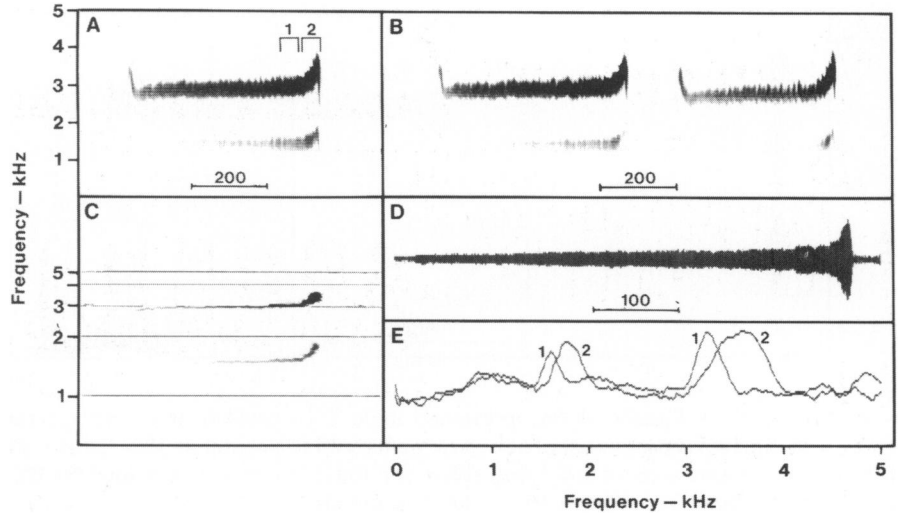
(Figs 2 and 3). Each pulse was 3–4 ms long with intervening intervals of 3–4 ms; the pulse repetition rate was about 160 Hz. The dominant frequency of this pulse train was 2–2.3 kHz (Fig. 3).

The second type of Song element was a rapid series of pulse pairs. Each pulse pair was about 10 ms long with intervals between of 7 ms; the first and second pulses were each 4 ms long, separated by about 2 ms (Fig. 3). The first pulse of each pair had a distinctive harmonic structure with a strong fundamental frequency of around 1.4 kHz. In contrast, the second pulse had a higher fundamental frequency (around 2.2–2.3 kHz) and no detectable higher harmonics (Fig. 3H).

Songs typically ended (and sometimes began) with Chatter.

Chatter

Chatter is a prominent kind of call in several calidridine species (Miller 1983a, b). It is frequently associated with Song but also occurs by itself, so is treated as a distinct class of vocalization.

In *C. bairdii* we only heard Chatter in association with Song: Chatter always terminated Songs. Chatter exhibited sequential grading in amplitude, repetition rate, and frequency (Fig. 2). It consisted of rapidly repeated triplets of pulses. Each triplet was about 30–35 ms long, separated from adjacent triplets by 15 ms. Pulse durations were about (in sequence) 5, 4 and 10 ms long, with intervening intervals of 3 and 10 ms. The fundamental frequency of the first and second pulses in each triplet was about 2.5 Hz, and the pulses showed no higher harmonics. The third pulse was distinctly different, with a fundamental around 1.5 kHz but with most energy in the second harmonic (Fig. 4).

Laugh

Laughs were uttered by birds early in the breeding cycle when mildly disturbed by our presence. They sounded similar to the Laugh of *Aphriza* though the elements were longer, and closely resembled the Laugh of Red Knot *Calidris canutus* (see Cramp 1983).

Fig. 6. *Calidris melanotos*, hoot sequence of displaying male. A – Logarithmic frequency scale, analyzing filter bandwidth (afb) 11.3 Hz. B – Linear frequency scale, afb 75 Hz. C – Logarithmic frequency scale, afb 22.5 Hz. D – Linear frequency scale, afb 150 Hz. Time marker, 1 s.
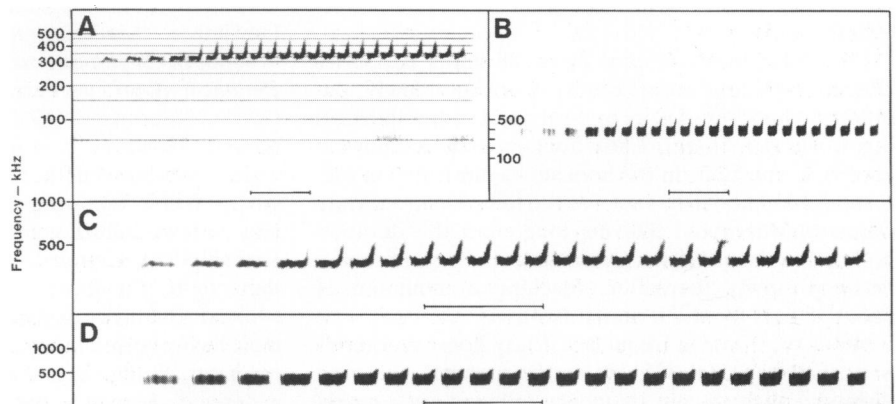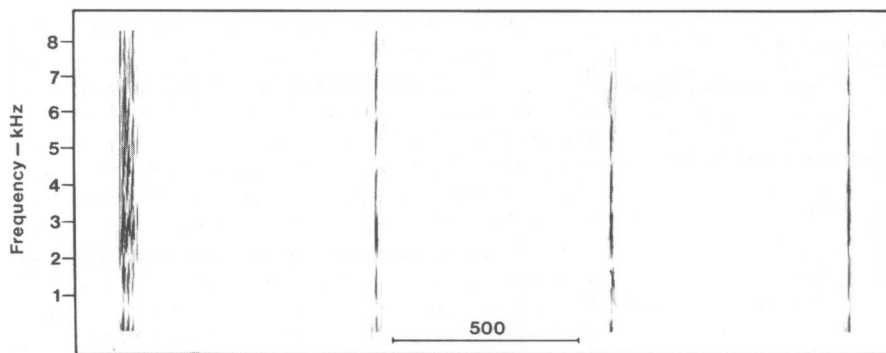
Fig. 7. *Tryngites subrufi-collis,* call sequence of displaying male ("gulp" followed by three "ticks") (analyzing filter bandwidth, 300 Hz). Time marker in ms.

We analyzed 18 Laughs of one presumed male *C. bairdii.* Thirteen of these consisted of two elements, and the other five consisted of only one. First (or lone) elements averaged 531 ms long (S.D. = 44.1), intervals between elements averaged 145 ± 13.1 ms, and second elements averaged 425 ± 24.4 ms. Each element began at around 1.5 kHz, dropped quickly by about 500 Hz, then rose gently in frequency and amplitude until near the end when frequency increased rapidly to 1.5–2 kHz (Fig. 5). The second harmonic contained much more energy than the fundamental.

Vocalizations of Pectoral Sandpiper

We describe here only the well known "hooting" of male *C. melanotos;* the species utters many other kinds of vocalizations that deserve specific study.

Aerial displays of male *C. melanotos* are different from those of most calidridines in being low to the ground (only a meter or two high), in involving directed flight with continuous wingbeats, and in having distinct bouts of calls (hoots). Males began such displays silently and, through a curious "pumping" action involving the wings, somehow expanded the lower throat and upper chest. The expansion appeared as a pendulant laterally compressed "dewlap". When the expansion was complete, a hoot series was initiated with one to several soft calls. The hoots then became louder. Hoots were not uttered in synchrony with the slow deep wingbeats used during the display (contra Pitelka 1959 and Myers 1982).

Displaying males uttered up to 28 hoots per series (Pitelka 1959, our observations). Correspondingly, durations of hoot series were up to about 8 s (that shown in Fig. 6 was 6.5 s long). Early hoots in each series were longest in duration. In the hoot series illustrated in Fig. 6, the second hoot (the first was too faint for an accurate estimate) was about 320 ms long, and the duration declined to about 190 ms for the seventh hoot. Duration declined slowly thereafter, reaching a minimum of about 160 ms for the terminal hoot.

Hoots were low in frequency. Early hoots in a series were between 300–325 Hz in frequency, and each showed a slight rise in frequency followed by a nearly

constant-frequency portion. Later hoots had an initial portion at 325–350 Hz, then showed a sharp frequency rise to just below 450 Hz (Fig. 6).

Vocalizations of Buff-breasted Sandpiper

Displays of male *Tryngites* have been described by Parmelee et al. (1967) and Myers (1979). During these displays males uttered two kinds of wide-band sounds: a brief "tick" sound and a slightly longer frequency-modulated sound (Fig. 7). The latter was uttered when males engaged in a vertical pumping action of the head and neck ("gulping" of Parmelee et al. 1967, p. 32). The sounds could only be heard over short distances. Males were silent when they jumped in their low flutter display (a ritualized form of flutter-fighting; Miller 1984).

Discussion

Phylogenetic considerations

RRCs are homologous as a rhythmically repeated, structurally simple type of call. A dichotomy into pulsed and non-pulsed RRCs seems to be distinct, though several species (e.g., *C. himantopus,* Long-toed Stint *C. subminuta*) show strong rhythmic modulation of the carrier frequency (Fig. 8). Repeated, loud pulsed calls are also used in long-distance advertisement by other species (e.g., Common Nighthawk *Chordeiles minor;* Davis 1962), including other Scolopacidae (e.g., Asiatic Dowitcher *Limnodromus semipalmatus,* Eurasian Woodcock *Scolopax rusticola,* American Woodcock *Philohela minor;* see Ferrand (1983), Fiebig and Jander (1985), Veprintsev (1982), and references in Miller (1984)). However, non-pulsed RRCs are much more widely distributed in the Scolopacidae, occurring in tringines, Willet *Catoptrophorus semipalmatus,* godwits, and curlews (Glutz von Blotzheim et al. 1975, 1977, Sordahl 1979, Cramp 1983, Miller 1984), so we judge them to be the form from which pulsed RRCs have evolved. By this reasoning, pulsed RRCs in calidridines must have evolved independently from those of *L. semipalmatus, Scolopax,* and *Philohela.* If pulsed RRCs are a derived character, then one phylogenetic grouping

Tab. 1. Descriptive statistics for temporal attributes of Rhythmically Repeated Calls (RRCs) in display flights of Calidridini[a].

	Duration of RRC (ms)	Duration of ICI[b] (ms)	Terminal buzz rate (Hz)
Group I			
1. *Aphriza virgata*[c]	326±31.0 (107)	109±7.8 (95)	–
2. *Calidris canutus*	1113±85.5 (91)	153±21.6 (78)	–
3. *C. ferruginea*	903±42.9 (7)	121±378 (6)	–
4. *C. himantopus*	726±86.0 (140)	446±97.9 (104)	–
5. *C. minutilla*[d]	367	103	–
6. *C. ruficollis*	516±12.2 (43)	352±40.1 (42)	–
7. *C. subminuta*	627±19.5 (3)	235 (1)	–
Group II			
8. *Calidris alba*	458±36.4 (94)	864±193.6 (92)	44±1.3 (99)
9. *C. alpina*	609±90.8 (491)	159±44.8 (422)	79±3.4 (500)
10. *C. bairdii*	690±99.3 (28)	280±138.9 (22)	77±6.8 (37)
11. *C. fuscicollis*	186±12.5 (60)	305[e]	74±3.2 (61)
12. *C. ptilocnemis*	522±79.4 (26)	596±164.6 (23)	42±2.0 (25)
13. *Eurynorhynchus pygmeus*	492±29.6 (4)	79±4.1 (4)	165±5.2 (5)
14. *Limicola falcinellus*	324±28.3 (53)	48±3.6 (38)	48±0.0 (53)

a. Each entry is Ȳ ± S.D. (N).
b. ICI = Inter-call Interval (interval between successive RRCs).
c. Data from Miller et al. (1987).
d. Data from Miller (1986). N was > 2,000. See Tab. 1 of Miller (1986) for detailed statistical summary.
e. For *C. fuscicollis*, this estimate was computed as the sum of the mean intervals (c–d) and (d–e) (see Fig. 8 and Tab. 2).

includes Sanderling *Calidris alba*, Dunlin *C. alpina*, *C. bairdii*, *C. fuscicollis*, Rock Sandpiper *C. ptilocnemis*, Spoon-billed Sandpiper *Eurynorhynchus pygmeus*, and *Limicola* (the Purple Sandpiper *C. maritima* will presumably also fall here, when its RRCs are analysed). The only obvious candidate for a group nested within this one includes *C. fuscicollis* and *Limicola*, which have differentiated RRCs with "tonal" (non-pulsed) termination (see Fig. 8).

RRCs occur in discrete bouts or trains in various species of scolopacids including Wandering Tattler *Heteroscelus incanus* and Lesser Yellowlegs *Tringa flavipes* (Miller 1984). The evolutionary transition between trains and ill defined long calling sequences seems, a priori, to be an easy one, so the possession of one or the other state may carry little useful phylogenetic informa-

tion. Several calidridine species that lack pulsed RRCs have strongly ritualized bouts of RRCs, notably the Western Sandpiper *Calidris mauri* and *C. melanotos* (and presumably also the Sharp-tailed Sandpiper *C. acuminata*); their bouts are similar in showing sequential grading from long to brief calls, which also successively increase slightly in frequency (Holmes 1973, Myers 1982, Veprintsev 1982). *Aphriza* (and presumably also the Great Knot *Calidris tenuirostris*) also utters RRC bouts, each followed by Song (Miller et al. 1987). It is not clear to us whether the Little Stint *Calidris minuta* also utters RRCs in bouts (see Fig. 1 of Cramp 1983, p. 308). Only *C. mauri* and *C. melanotos* seem similar enough in this attribute to be placed together phylogenetically.

RRCs comprise one to several parts. In species with non-pulsed RRCs, differentiation has occurred at the beginning of RRCs, with the derivation of several brief introductory elements there (*Aphriza, C. mauri*, Least Sandpiper *C. minutilla*). Rhythmic frequency modulation occurs at the beginning of RRCs in other species (e.g., Rufous-necked Stint *Calidris ruficollis*), and this has probably provided the raw material for such derivations. *C. canutus* has a unique kind of complex non-pulsed RRC, with its two portions distinguished by fundamental frequency and harmonic structure (Fig. 8K). We are not comfortable with proposing any phylogenetic groupings using these attributes.

Several species do not have RRCs: Semipalmated Sandpiper *Calidris pusilla*, Temminck's Stint *C. temminckii*, Ruff *Philomachus pugnax*, and *Tryngites*. The latter two species have highly divergent signalling systems because of their lek social organization, so the absence of RRCs for them may just reflect convergence. The absence of RRCs in *Calidris pusilla* and *C. temminckii* may be a shared derived homology, however.

Punctuated Fluttering (PF) is a distinctive flight mode used by several species during DFs, including *C. alpina*, *C. minutilla*, *C. ptilocnemis* (and presumably *C. maritima*), and *C. pusilla*. Species known to lack PF, based on our observations, all share a deep loose flutter in DFs: *Aphriza, C. bairdii*, and *C. himantopus*. We are surprised at the incongruence between distributions of one of these flight modes and pulsing of RRCs.

In summary, derived states of RRCs include rhythmic

Tab. 2. Descriptive statistics for temporal attributes of Rhythmically Repeated Calls in display flights of *C. fuscicollis*.

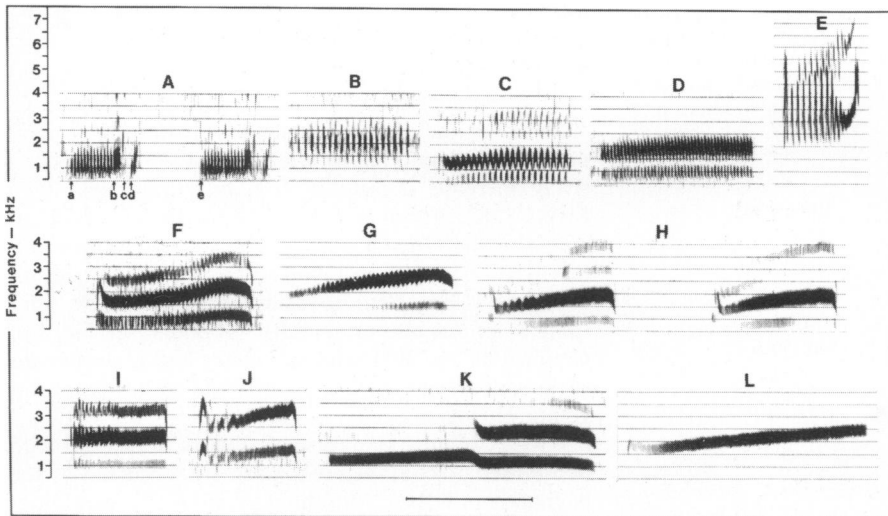| Variable*	Ȳ	S.D.	N
Duration (a–d)	252 ms	12.0	60
Duration (a–c)	186 ms	12.5	60
Duration (b–c)	23.5 ms	4.64	61
Interval (c–d)	54 ms	8.8	62
Interval (d–e)	251 ms	21.9	52
Pulse rate	74 Hz	3.2	61

*For explanation see Fig. 8 and Methods.

Fig. 8. Calidridine species, Rhythmically Repeated Calls (RRCs). A – *Calidris fuscicollis* (two RRCs separated by natural interval; letters indicate points for measurements (see Methods)). B – *C. alba.* C – *C. ptilocnemis.* D – *C. alpina.* E – *Limicola falcinellus.* F – *C. subminuta.* G – *C. himantopus.* H – *C. ruficollis* (two RRCs separated by natural interval). I – *Aphriza virgata.* J – *C. minutilla.* K – *C. canutus.* L – *C. ferruginea.* Analyzing filter bandwidth, 300 Hz. Time marker 500 ms.

FM, pulsing, organization into bouts, and differentiation into parts. The latter (plus bout organization?) has probably evolved several times. PF is probably derived relative to continuous deep loose fluttering in DFs (*Aphriza* glides when vocalizing in DFs). To refine phylogenetic analysis of this group, it will be necessary to analyze more call types in other species, such as Laugh, Chatter, and brooding calls. These are more difficult to record, but are far more evolutionarily conservative than Song (especially) or RRCs, and will permit inclusion of deviant species like *Philomachus* and *Tryngites,* and of species that have lost certain call types (e.g., *C. pusilla, C. temminckii*). The fine structure of calls should also be revealing. In *C. bairdii* both Song and Chatter show fine details of frequency and timing that are at or below the limits of avian perceptual resolution. For example, pulse duration and inter-pulse intervals are only a few ms long, and in Chatter adjacent pulses differ strikingly in fundamental frequency and harmonic structure. Presumably the characteristics of pulse structure in these two call types are perceived in an integrated manner; this would tend to conserve such features as couplet or triplet organization through evolutionary time. Certainly the structure of Chatter in *C. bairdii* is strikingly similar to that in *C. pusilla* ("motorboat sound"; Miller 1983b) and *C. minutilla* (Miller 1983a). Further fine analyses of calls for other species is therefore likely to be revealing.

Finally, further research should be directed towards comparative analysis of character variation in sounds. In an earlier study, the interval between RRCs of *C. minutilla* was found to be more variable than RRC duration, and frequency characteristics of RRCs were even less variable; the latter is in keeping with a broad trend in birds. Analysis of the limited material available to us extends this analysis and reveals that RRC duration is less variable than the interval between RRCs, while the pulse rate in pulsed RRCs is even less variable

(Fig. 9). Such a trend may signify that there are general constraints to evolution, and may reveal that characters of low variability contain most phylogenetic information.

A comprehensive discussion of relationships based on acoustic and anatomical characters would be inappropriate at this stage of our knowledge. Some of our findings are not consistent with generally accepted relationships within the Calidridini, for example. Information on more call types and more species, and on other
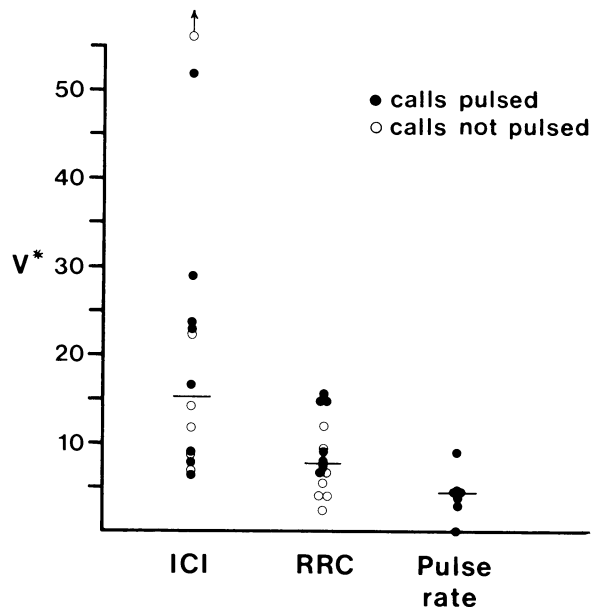

Fig. 9. Calidridine species, relationship of coefficient of variation to variable type. Data for *Calidris minutilla* are for totals on variables T1 and T3 in Tab. 1 of Miller (1986). Short horizontal bars represent median values for each variable. V* = adjusted coefficient of variation (see Methods); RRC = duration of Rhythmically Repeated Call; ICI = inter-call interval (between successive RRCs).
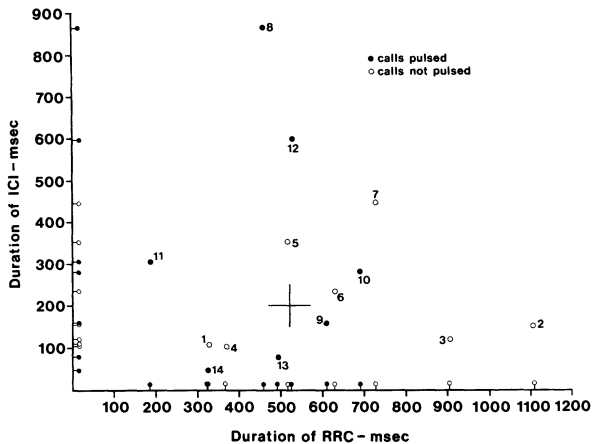
Fig. 10. Calidridine species, bivariate plot of mean duration of the interval between Rhythmically Repeated Calls (RRCs) (ICI = inter-call interval) against mean duration of RRC. Numbers refer to species listed in Tab. 1. Sticks show dispersion of species along each axis. Joint median is shown as a cross.

kinds of characters, is needed to resolve and clarify relationships in the group.

Adaptive considerations

In the preceding section we summarized information which shows that a range of vocal attributes, from entire classes of vocalization to the fine structure of acoustic organization, have been retained in different calidridine species over evolutionary time.

RRCs are the most important kind of long-distance, undirected, broadcast sound signal in most calidridines. Their brevity and stereotypy, and their rhythmic repeated utterance, enable listeners to integrate information over successive calls and thus to accurately receive information about a caller's location and attributes (e.g., individuality, size). The rapid rhythmic repetition of RRCs probably permits reception of details, though the importance of details in complex RRCs (e.g., in *C. fuscicollis* and *C. minutilla*) may be to nearby listeners rather than distant ones. Stereotypy of RRCs is equivalent to high *correlational redundancy* (e.g., frequency characteristics of RRCs in *C. minutilla* are highly intercorrelated; Miller 1986); rhythmic repetition of stereotyped calls leads to high temporal predictability or *sequential redundancy*. Both aspects of redundancy should promote accurate reception over long distances in a noisy environment.

RRCs in some species (e.g., *C. canutus,* Curlew Sandpiper *Calidris ferruginea*) are narrow and fairly constant in bandwidth, attributes that may be adaptations to minimize frequency-dependent attenuation over distance (Miller and Baker 1980, Wiley and Richards 1982, Miller 1983a,b). If this correlation is

strong, species such as *Limicola,* whose RRCs have a broad bandwidth, would be predicted to have shorter average signalling distances.

RRCs have a median duration of 519 ms for species listed in Tab. 1, with a range of about 200–1100 ms; ICIs have a median duration of 197 ms within a range of 50–900 ms. Durations of RRCs are thus slightly positively skewed, and of ICIs strongly so (Fig. 10). Considered together, these estimates reveal that RRCs account for a median percentage of 77% of total time during calling sequences (this figure includes estimates of 80% for bouts of *C. melanotos* and 92% for *C. mauri*). The distribution is negatively skewed, with only 3/18 species below 50%, and 13/18 above 70% (Fig. 11). There are no differences between species with pulsed and non-pulsed RRCs on these measures. It appears that most species use a strategy of densely "packing" their sound transmissions, regardless of RRC duration.

Calidridine Song and Chatter cannot be analyzed as simply as RRCs. In some species (e.g., *Aphriza, C. alpina, C. ptilocnemis*) the loud Song is transmitted effectively over long distances and exhibits high sequential redundancy based on brief, rhythmically repeated subunits (these show sequential grading in *C. alpina* and *C. ptilocnemis*) (Miller 1983b, Miller et al. 1987, E. H. Miller, unpubl. data). In most other species Song has much less internal repetition, has longer subunits, and generally is more structurally complex (e.g., *C. himantopus, C. minutilla*; Miller 1983a,b). Chatter, like Song, has been well described for very few species, but it is organized consistently as long series of rapidly repeated couplets, triplets, quadruplets, etc. (Miller 1983a,b). In *C. pusilla,* RRCs are lacking and Chatter ("motorboat sound") has replaced them as the major long-distance
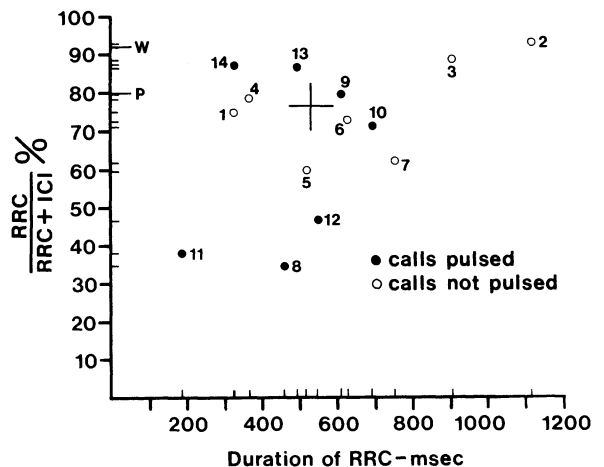

Fig. 11. Calidridine species, relationship of the percentage of time occupied by Rhythmically Repeated Calls (RRCs) during display flights, to call duration (ICI = inter-call interval). Numbers refer to species listed in Tab. 1. Sticks show dispersion of species along each axis. *Calidris mauri* (W) and *C. melanotos* (P) are shown on vertical axis (at 92.1% and 79.6%, respectively; see text). Joint median, for 16 values on the vertical axis and 14 on the horizontal, is shown as a cross.

sound signal (Miller 1983b). The comments made earlier about high sequential redundancy being an effective way to transmit RRCs can also be applied to Chatter (and to some species' Song), with a much briefer integration time required. However, Song and Chatter appear to have more diverse uses in calidridine communication than do RRCs, so the relationships of structure to function cannot be adequately discussed until more detailed behavioral observations are available.

Loffredo and Borgia (1986) recently surveyed acoustic characteristics and mating systems of birds and concluded that sound signals of polygynous species tend to be noisier, broader in bandwidth, and less melodic than in monogamous species. Our findings disagree with theirs: we believe that phylogenetic relationships and transmission distance are the main determinants of acoustic characteristics. For example, in the phylogenetic grouping we proposed based on the harsh-sounding, pulsed RRCs, are a polygynous species (*C. fuscicollis*), a polyandrous species (*C. alba*), and monogamous species (remaining species listed in Tab. 1; Pitelka et al. 1974). RRC bandwidth is greatest for *Limicola* in this group, and the remaining species differ little from one another. Among these species with the ancestral non-pulsed form of RRC are the polygynous *C. ferruginea* and *C. melanotos*; most of the other species are monogamous, and all have similar RRCs.

The preceding contrasts were made for RRCs, a type of sound used for long-distance transmission, so signalling distance was "held constant" for the comparisons. Fewer comparisons are possible for short transmission distances. The latter permit a variety of sound characteristics to be used because no effective degradation or attenuation occurs. Broad-band sounds are used by the polygynous *Tryngites* and Great Snipe *Gallinago media* (Loffredo and Borgia 1986), and graded acoustic systems occur in the polyandrous jacanas and phalaropes (Miller 1984), in keeping with the permissive role played by short distances in the evolution of sound characteristics.

A relationship between mating system and acoustic characteristics in Scolopacidae may exist, but it is confounded by phylogenetic relationships and demands of long-distance signalling. Furthermore, the nature and intensity of competition for mates, and the kinds of information encoded in different sound classes must be crucial to the functioning of any such relationship; relevant detailed behavioral studies have simply not been done. We are pessimistic that any meaningful pattern would emerge, in any case. It is hard to imagine sound classes of scolopacids that are harsher-sounding or broader in bandwidth than Song of *Aphriza* or *C. himantopus*, more complex than in *C. bairdii*, *C. himantopus*, *C. pusilla*, or dowitchers *Limnodromus*, or more melodic than in *C. minutilla* – all monogamous species (Miller 1983a,b, Miller et al. 1983, 1984, 1987).

In our view, to explore the relationships of mating system to acoustic signalling, attention should be focussed on the behavior of communicating, rather than on the physical nature of the sounds used.

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Appendix: Recent literature on shorebird acoustics

A review of published sound analyses (mainly sound spectrograms) for shorebirds is in Miller (1984) (76 references). Additional references follow, and are indicated by the reference number in parentheses after each species. Taxa for which analyses did not previously exist are denoted by an asterisk. My earlier reference to *Calidris minuta* song in the paper by Tikhonov and Fokin (1981, their Fig. 1E) is incorrect; it should be *C. temminckii* (their figure legend is incorrect; P. Tomkovich in litt.). This is corrected as ref. 15 below.

Burhinidae
Burhinus capensis (6), **B. vermiculatus* (6)
Charadriidae
Charadrius hiaticula (6), **Ch. mongolus* (6), **Ch. pecuarius* (6), **Ch. tricollaris* (6), **Ch. wilsonia* (2), *Pluvialis apricaria* (12), *P. dominica* (6), *P. squatarola* (6), **Vanellus albiceps* (6), **V. armatus* (6), **V. coronatus* (6), **V. crassirostris* (6), **V. melanopterus* (6), **V. senegallus* (6), *V. vanellus* (12).
Glareolidae
**Cursorius rufus* (6), *Glareola nordmanni* (6), **G. nuchalis* (6), *G. pratincola* (6), *Rhinoptilus cinctus* (6).
Haematopodidae
**Haematopus moquini* (6), *H. ostralegus* (6, 12).
Jacanidae
**Actophilornis africanus* (6)
Recurvirostridae
Himantopus himantopus (6), *H. mexicanus* (13), *Recurvirostra americana* (13), *R. avosetta* (6)
*Rostratulidae
**Rostratula benghalensis* (6)
Scolopacidae
**Aphriza virgata* (9, 10), *Arenaria interpres* (6), *Calidris alba* (6, 9), *C. alpina* (6, 9, 12), **C. bairdii* (6, 9), *C. canutus* (6, 9), *C. ferruginea* (6, 9), *C. fuscicollis* (9), *C. himantopus* (9), *C. melanotos* (6, 9), *C. minuta* (6), *C. minutilla* (7, 8, 9), **C. ptilocnemis* (9), **C. ruficollis* (6, 9), **C. subminuta* (6, 9), *C. temminckii* (6, 12, 15, 16), *Coenocorypha aucklandica* (11), *Gallinago gallinago* (12, 17), *G. media* (6), **G. nigripennis* (6), *Limicola falcinellus* (9, 14), **Limnodromus semipalmatus* (5), *Limosa limosa* (6), *Numenius arquata* (6, 12), *N. minutus* (3), *N. phaeopus* (6, 12), *Phalaropus lobatus* (6), *Ph. tricolor* (6), *Scolopax rusticola* (4), *Tringa erythropus* (6), *T. glareola* (6, 12), *T. hypoleucos* (6), *T. melanoleuca* (12), *T. nebularia* (6, 12), *T. ochropus* (6, 12), *T. stagnatilis* (6), *T. totanus* (6, 12), **Tryngites subruficollis* (6, 9), *Xenus cinereus* (6)

References: 1 – Baker and Hockey (1984); 2 – Bergstrom (1988); 3 – Boswall and Veprintsev (1985); 4 – Ferrand (1983); 5 – Fiebig and Jander (1985); 6 – Maclean (1985); 7 – Miller (1985); 8 – Miller (1986); 9 – Miller et al. (the current paper); 10 – Miller et al. (1987); 11 – Miskelly (1987); 12 – Nethersole-Thompson and Nethersole-Thompson (1986); 13 – Sordahl (1986); 14 – Svensson (1987); 15 – Tikhonov and Fokin (1981); 16 – Tomkovich and Fokin (1984); 17 – Thielcke (1976).