

NUPTIAL VOCALIZATIONS OF MALE LEAST SEEDSNIPE: STRUCTURE AND EVOLUTIONARY SIGNIFICANCE¹

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Acoustic displays of non-passerines hold promise for understanding how communication is adapted to the physical environment and for resolving systematic relationships. The potential of acoustic characteristics for systematics can be illustrated with shorebirds. Some shorebird displays (e.g., snipe drumming) differ greatly between closely related species, so should be informative about low-level relationships. Other displays (e.g., duetting in stone-curlews, avocets, and oystercatchers; Stepanjan 1970, 1979) are evolutionarily conservative and extremely similar even between shorebird species that diverged from one another millions of years ago; such conservative displays may help to resolve high-order relationships.

A shorebird group whose systematic position may be clarified by acoustic information is the seedsnipe (Thinocoridae). The relationships of the four species of seedsnipe to other shorebirds remain enigmatic despite a wealth of systematic and phylogenetic studies over many years (Strauch 1978, Sibley and Ahlquist 1990, Björklund 1994, Chu 1995). The purpose of this paper is to describe some nuptial vocalizations of seedsnipe and make adaptive and phylogenetic inferences based on acoustic structure.

Vocalizations of seedsnipe have not been analyzed spectrographically (Miller 1984, 1992, 1995), although some behavioral descriptions exist (Maclean 1969, Fjeldsá and Krabbe 1990). In this note, I present spectrographic analyses of long-range vocalizations by male Least Seedsnipe (*Thinocorus rumicivorus*), based on observations during the breeding season in Patagonia. Three kinds of vocalization are described: a complex aerial vocalization and two simpler vocalizations that are uttered when on the ground or a prominence. Variations and other forms of ground and flight display occur (Maclean 1969), but my tape recordings are not adequate for their spectrographic analysis. These vocalizations resemble those of many scolopacids in their rhythmicity, complexity, and syntactical properties, and are notably similar to some vocalizations of Common Snipe (*Gallinago gallinago*). Despite the strong similarities, phylogenetic conclusions cannot be drawn because of the paucity of acoustic data for most species.

METHODS

Least Seedsnipe were recorded opportunistically about 85 km NW of Río Gallegos, Argentina, in November 1977. Recordings of Common Snipe (*G. g. delicata*) from several North American locations including Alaska, Yukon, British Columbia, and Manitoba were analyzed for comparative purposes. Recordings of Common Snipe (*G. g. gallinago*) from Iceland and Russia were also analyzed (Russian recordings were taken from Veprintsev [1982]). All recordings except Veprintsev's were made at 19 cm/sec with a Nagra IS tape recorder and Scotch 208 tape, with a Sennheiser MKH 816 "shotgun" microphone. Analyses were carried out on a microcomputer with the signal-analysis package CSL 4300 (Kay Elemetrics Co., Pine Brook, New Jersey, 07058). Sound samples were digitized at 20,000 Hz. For the sonagrams shown below, analyses were done with a Blackman window, no pre-emphasis, and frame sizes corresponding to an analog analyzing filter bandwidth of 50–60 Hz. Descriptions and measurements given below are based on six to ten examples of each kind of vocalization, from an estimated 10–15 individual birds recorded over four days.

RESULTS

Male seedsnipe commonly perch on prominences such as a knoll, bush, or fencepost and utter two kinds of loud calls in long series. Spectrographically, the two call types are distinguishable from song elements. To the ear, however, there is some similarity, which explains why Maclean (1969) applied the same terms to both. For example, he referred to "a rapid *pu-pu-pu-pu-pu*, derived from the first syllable of . . . *puku*" and (for the Gray-breasted Seedsnipe, *T. orbignyianus*) lengthy "songs" of "as many as 850 *puku* notes" while perched. These descriptions likely refer to the two types of simple calls recognized herein.

One of these call types is a series of rhythmically repeated simple notes (Fig. 1A). The notes have a moderately broad bandwidth (~0.6–1.2 kHz), though no harmonics are present; most energy is at ~0.9–1.1 kHz. The notes are brief (~15–25 msec long), with internote intervals (INIs) of ~200–220 msec, for a call rate of ~4/sec and ~9% coverage by vocalizations during call sequences (i.e., 91% silence).

The second kind of simple call is also uttered rhythmically, but is organized as two alternating note types (Fig. 1B). One type spans ~0.8–1.3 kHz, with most energy over ~1.0–1.3 kHz. These notes are ~50–55 msec long. Briefer notes (~20–25 msec long) alternate

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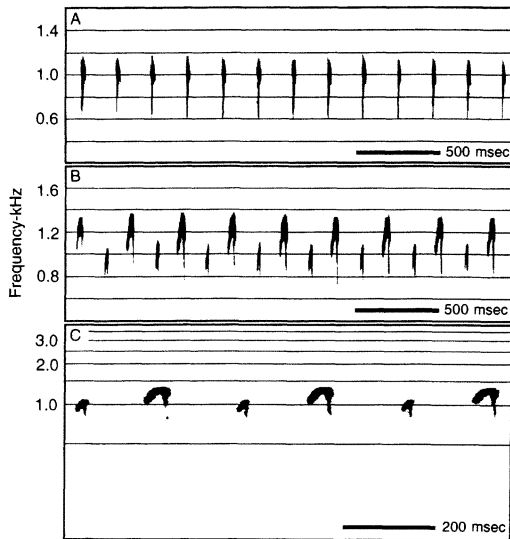


FIGURE 1. Sonograms of ground/perch advertisement calls by male Least Seedsnipe. A—Part of long calling sequence of single notes. B—Part of long calling sequence of double notes. C—Part of (B), on logarithmic frequency scale and different time scale. Analyses were done over the frequency ranges 100–2000 Hz (A–B) and 100–5000 Hz (C).

with them, and are ~ 0.8 – 1.1 kHz in frequency. Intervals are ~ 140 – 145 msec long following long notes and ~ 115 – 130 msec long following brief notes. No harmonics are present in either note type. Call rate is ~ 5 – 6 /sec, with vocalizations accounting for 22% of calling time (=78% silence within calls).

Common Snipe have two well known vocal forms similar to those just described for the Least Seedsnipe. As in the latter species, Common Snipe also give them from the ground or prominences, including mounds, fenceposts, houses, power lines, and trees. Both call types are uttered during parts of aerial displays as well (Miller, unpubl.). The first of the two loud call types is the *Chip* (often termed *yak*). The second is the *Chipper* (often termed *jick-jack*). The names *Chip* and *Chipper* follow Cramp (1983). Sonograms of these call types are in Grudzien (1976) for *delicata*, and in Glutz et al. (1977), Reddig (1978, 1981), Bergmann and Helb (1982), and Cramp (1983) for *gallinago*.

The *Chip* is uttered rhythmically in long monotonous series at a rate of ~ 2 – 4 /sec. It has two variants that may represent distinct call types, one shaped as an inverted chevron on sonagrams (Fig. 2A), the other as a chevron (Fig. 2B). They are ~ 50 – 80 msec long, separated by intervals of ~ 190 – 330 msec (yielding $\sim 21\%$ vocal coverage = 79% silence). The *Chipper* likewise is uttered in long monotonous series, but at a higher rate (~ 5 – 6 /sec; Fig. 2C–E). It consists of two alternating note types that differ in frequency attributes (see Fig. 1E) but are similar in temporal features to those of the Least Seedsnipe: brief notes are ~ 20 – 40 msec, long notes are ~ 45 – 50 msec and INIs are ~ 140 – 180 msec long (vocal coverage ~ 17 – 21% of time =

$\sim 80\%$ silence). The main differences from seedsnipe are frequency modulation and harmonic structure, the latter being responsible for the broad bandwidth and high frequencies reached.

The most complex vocalization of male Least Seedsnipe is aerial “song.” In the early morning, when it is still very dark, male seedsnipe rise silently in aerial displays to a height of ~ 10 m then, just after maximal height is reached, start to glide gradually downward while uttering a long complex vocalization; toward the end of the glide they may dive before landing (Maclean [1969] observed heights up to 15–20 m). Males seemed to give these aerial displays only a few times each morning, and sporadically during the daylight hours.

Song is a vocalization up to 15 sec long consisting of four to five note types (Fig. 3A). It begins with several soft notes that increase successively in frequency. They are followed by a long sequence of alternating loud note types in short series (*wikiti* of Maclean [1969]). One note type spans ~ 0.6 – 1.2 kHz and is very brief. Harmonic structure is absent. These brief notes (pulses) occur in triplets in Figures 3A–B, with a decline in frequency and increase in duration occurring progressively over each triplet (note durations increase from ~ 20 to ~ 40 msec within triplets). The pulse triplets alternate with one or two longer (~ 55 – 95 msec) notes at lower frequency (~ 0.6 – 0.9 kHz). The longer notes characteristically rise, sometimes in step-fashion, to a constant-frequency portion, then drop off quickly at

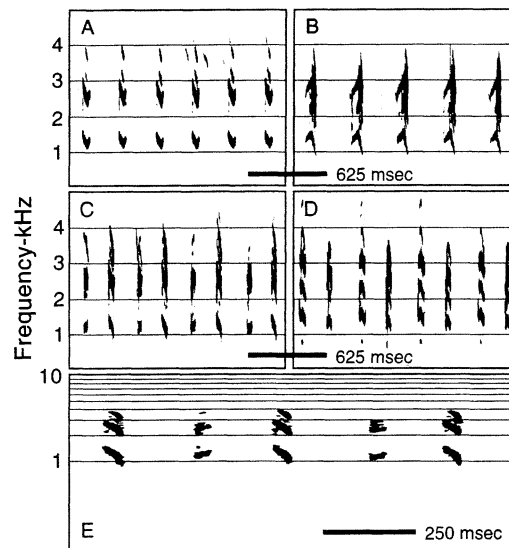


FIGURE 2. Sonograms of ground/perch advertisement calls by male Common Snipe, illustrating single- and double-call forms resembling those of Least Seedsnipe. A—Part of long calling sequence of single notes (*G. g. delicata*). B—Ditto, for *G. g. gallinago*. C—Part of long calling sequence of double notes (*G. g. delicata*). D—Ditto, for *G. g. gallinago*. E—Part of C, on logarithmic frequency scale and different time scale. Analyses were done over the frequency ranges 100–2000 Hz (A–D) and 100–5000 Hz (E).

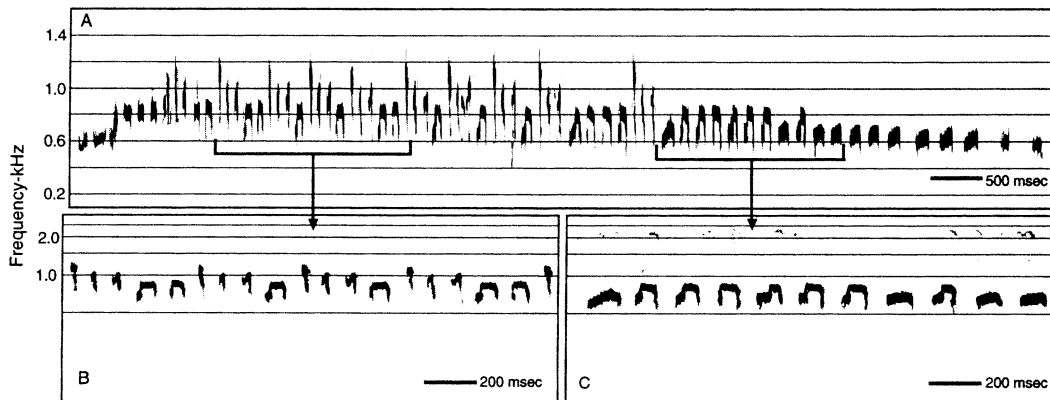


FIGURE 3. Sonograms of song in display flight by male Least Seedsnipe. A—Complete song (marked parts are shown in B and C, on logarithmic frequency scale and different time scale). Analyses were done over the frequency range 100–2000 Hz.

the end. During this portion of song, notes are uttered at a rate of ~9–10/sec, and occupy ~40% of a song's duration.

A transition occurs about halfway through each song, with a switch to lower-frequency and longer notes resembling the long notes just described (Fig. 3C). These notes decline in frequency overall (to <600 Hz at the end), are longer (~90–130 msec), narrower in bandwidth, and have simpler frequency modulation than earlier notes in the song. The later notes are the “far-carrying *puku puku puku*” sounds described by Maclean (1969). The brief pulsed notes drop out, so the rate of calling declines (5–6/sec), and vocalization occupies more of the time (~56% = 44% silence).

Song of Common Snipe is a long complex utterance that is given at various times during Drumming display flights, particularly during the terminal dive. It comprises alternating sequences of note types similar to those illustrated in Figure 2 (Miller, unpubl.).

ADAPTATIONS IN VOCAL BEHAVIOR AND ACOUSTIC STRUCTURE

Vocal behavior of Least Seedsnipe shows general agreement with predictions about adaptations for signal transmission in open environments (Wiley and Richards 1982). The use of bushes and other prominences as calling posts reduces acoustic degradation caused by interference with the ground surface and vegetation. Vocalizing in aerial display reduces degradation similarly, and also increases broadcast range. As well, Least Seedsnipe song is most common in the very early morning, when the high atmospheric turbulence that characterizes open environments is minimal.

Some frequency characteristics of Least Sandpiper vocalizations likewise seem interpretable as adaptations for long-distance transmission in open environments. Unlike many open-country species, Least Seedsnipe vocalizations are not especially narrow in bandwidth, but the absence of harmonic structure nevertheless results in the integrity of spectral information over relatively long distances. Low-frequency sounds attenuate least over distance, and all vocalizations of

this species are low in frequency (e.g., song is only ~500Hz–1.3 kHz) considering its small size: 14 males in the Royal Ontario Museum averaged 68 g in fresh weight (Dunning [1993] gives estimates of 40–45 g). In this respect, the Least Seedsnipe is similar to another small (~60 g; Dunning 1993) open-country species that advertises on the ground, the Plains-wanderer (*Pedionomus torquatus*), which has long-distance advertising calls at ~15–570 Hz (mainly 300–350 Hz) (Pettigrew and Larsen 1990).

The simple structure and rhythmic repetition of ground/perch vocalizations enhance the ability of listeners to accurately perceive the sounds over long distances (Schleidt 1973). More subtle information can be conveyed over long distances by gradual changes in frequency, loudness, and duration that take place throughout calling sequences, as listeners can detect the trends even if some notes are degraded or parts of a call sequence cannot be heard. Such sequential grading is simplest in one-note calls; in two-note calls, grading occurs at several levels—as individual notes, note pairs, and associated INIs are affected. Effective long-distance communication through multi-level sequential grading is also likely for song, despite its high structural complexity and hierarchical organization. For example, at a coarse level, the song in Figure 3 exhibits a general decline in frequency after the first ~5 notes; at finer levels, the brief notes organized as triplets in Figure 3B show sequential grading, and the note groupings which include the triplets themselves commonly exhibit sequential grading, although this is not apparent in Figure 3.

PHYLOGENY

Least Seedsnipe vocalizations show strong similarities to vocalizations of Common Snipe and some calidridine sandpipers. Some similarities are in high-order attributes of vocalizations such as repertoire characteristics, note-group structure, and sequencing. As noted above, high-order attributes are predicted to evolve most slowly, hence to be most useful for investigating affinities between distantly related groups.

A repertoire characteristic shared by Least Seedsnipe and Common Snipe is the presence of similar one- and two-part ground/perch calls. The calls are structurally similar in the brevity and simplicity of their constituent elements and in other features: percent of time covered by calls; rhythmic repetition in long series resulting in "tonic" displaying; and, for the two-note calls, a syntactical arrangement of alternating note types and associated INI durations. The calls are also functionally similar, in being long-distance displays used by breeding males from the ground or perches. Considering the great phylogenetic distance between the Thinocoridae and other shorebird taxa (Sibley and Ahlquist 1991, Björklund 1994, Chu 1995), I hesitate to suggest that the two vocal types are homologous between Least Seedsnipe and Common Snipe; however, it is noteworthy that very similar organization to the two-part call occurs in other scolopacids such as the Chatter call of Least and Baird's Sandpipers (*C. bairdii*) and Motorboat Sound of Semipalmated Sandpiper (*C. pusilla*) (Miller 1983a, 1983b, Miller et al. 1988). The rapid, lengthy, and rhythmic repetition of a set of brief notes that differ from one another and sometimes differ also in associated INIs (e.g., Figs 1B-C, 2) may therefore be a very old feature of vocal organization in the Scolopacida (= Jacanidae, Rostratulidae, Pedionomidae, Scolopacidae, and Thinocoridae; Sibley and Ahlquist 1990).

Some simple syntactical properties are progressive changes in loudness, frequency, and call rate over the course of a song (Lemon 1977). More complex syntax is the organization of notes into groups, nonrandom sequencing of both attributes and note types within and across note groups, and characteristics of multi-level sequential grading. At this level of description, these syntactical properties all occur in Least Seedsnipe song, and hold promise for use in phylogenetic studies. At present, however, neither these nor any other vocal characters of Least Seedsnipe shed light on the family's systematic position. To make progress in this area, more detailed behavioral and spectrographic information about nuptial vocalizations is needed from other shorebird species, beginning with *T. orbignyianus* and *Attagis*. At present, even available analyses of *G. gallinago* vocalizations are inadequate for phylogenetic studies (Miller 1996).

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FLORIDA SCRUB-JAY FORAGES ON BACK OF WHITE-TAILED DEER¹

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The propensity of Florida Scrub-Jays (*Aphelocoma coerulescens*) to become extremely tame around humans, willingly to perch and even to rest on the hand, shoulder, or head, has been commented upon by naturalists for over a century. We hypothesized (Woolfenden and Fitzpatrick 1984) that the behavior stems from an ancestral willingness to perch and forage on the backs of native mammals, in a low-growing habitat that lacks large, diurnal, terrestrial predators. Records exist for Florida Scrub-Jays perching and apparently removing ticks from domestic cattle (Bent 1946) and feral hogs (Baber and Morris 1980). Dixon (1944) and Isenhardt and DeSante (1985) observed Western Scrub-Jays (*Aphelocoma californica*) doing the same on mule and black-tailed deer (*Odocoileus hemionus*), and the latter authors even speculated that a "cleaning station" relationship existed between bird and deer. Here we describe an encounter between a Florida Scrub-Jay and an adult white-tailed deer (*Odocoileus virginianus*), and summarize evidence that the behavior is not unusual. The encounter was video-taped by a deer hunter while he sat in a tree overlooking the scene. Our description

is based on careful study of his video, a copy of which is deposited in the archives at Archbold Biological Station.

On 25 September 1994, Mr. Andrew Reiner was video-recording scenery and deer movements from a deer-stand outside of, but immediately adjacent to, the western boundary of Archbold Biological Station, near Lake Placid, Highlands County, Florida. At approximately 07:00 EDT a large buck deer with full antlers slowly walked along the margin of a wide, sand firelane bordering dense oak scrub and scrubby flatwoods. The deer stopped several times to browse. During one such stop, a Florida Scrub-Jay (band combination ARZ = 3-year old resident male breeder) flew into view and perched on a pine snag several meters from the deer. As the deer moved on, the jay made an aborted flight toward it, left the video frame momentarily, then reappeared and alighted on the back of the deer near its shoulders. The deer showed no indication of surprise, but continued to browse, head down.

Upon landing the jay immediately picked at the back of the deer as if to take food, then hopped posteriorly to the haunches. There the jay first picked at, then sharply pecked at and nibbled, a spot on the deer's right rear buttock. The sharp peck prompted the deer to lower its haunches slightly, head still down. The deer remained frozen in this posture for several seconds before picking up its head and casually looking back toward the jay. The jay then hopped forward again to the shoulder region, making a few additional gentle picks. At this point the deer easily could have brushed away the jay with its muzzle or antlers, but instead remained seemingly unperturbed while watching the

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