

VOCALIZATIONS OF THE TUAMOTU SANDPIPER, *PROSOBONIA CANCELLATA*

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ABSTRACT.—The biology of the endangered Tuamotu Sandpiper (*Prosobonia cancellata*) is essentially unknown. We analyzed vocalizations from presumed adult individuals and pairs, and family groups, recorded in French Polynesia during March 1990 and 2003. We recognized three types of vocalizations. Presumed adults uttered types I and II. These were brief (about 30–40 and 20–120 ms, respectively) and simple in structure (increasing then decreasing in frequency) but harmonically rich, with most energy in the second or third harmonics (peak fundamental frequency was about 775–1,380 Hz), as in some other Scolopacidae. Higher harmonics reached unusually high frequencies for a scolopacid (approaching 14 kHz). Call types I and II were uttered singly or as couplets, triplets, or longer sequences. Type III calls were longer (about 115–470 ms), of narrower bandwidth, and with modulations of a carrier frequency that decreased from about 1,925 to 1,305 Hz; they were given by a presumed family group and may represent calls of dependent young birds. Harmonic richness and variation in frequency and temporal variables within call types are consistent with a short range communication system. Received 14 November 2002, accepted 31 October 2003.

The Tuamotu Sandpiper (*Prosobonia cancellata*) is one of the most highly endangered and least known of the world's shorebird species. It is the only extant member of the genus, the other species becoming extinct by the late 1800s (Zusi and Jehl 1970, Holyoak and Thibault 1984, Sibley and Monroe 1990, Piersma 1996, van Gils and Wiersma 1996). A tropical distribution, atoll habitat, and sedentariness are unique among extant scolopacids, so information about the natural history and behavior of *Prosobonia* likely will be informative about both adaptations and phylogenetic relationships. Avian vocalizations are a traditional source of adaptive and phylogenetic information about nonpasserines and passerines (Irwin 1996, Kroodsmas and Miller 1996, Salzburger et al. 2002). We analyzed available audio recordings and here present the first account of the species' vocalizations, offer provisional behavioral and evolutionary interpretations, and suggest directions for future research.

METHODS

Vocalizations were recorded in French Polynesia by R. and J. Seitre on Anuanu Raro

(20° 17' S, 143° 19' W; 13 March 1990) and Morane (23° 06' S, 137° 04' W; 17 March 1990), and by EV on Morane (8 March 2003). Four sequences of vocalizations were recorded by the Seitres: bird in tree on Anuanu Raro (Seitres' sample 1; $n = 24$ calls), same bird in flight (Seitres' sample 2; $n = 5$), same bird on ground (Seitres' sample 3; $n = 88$), and a group of four to five birds on Morane (Seitres' sample 4; $n = 30$). For Seitres' samples 1–3 the vocalizing bird was alert to the presence of human observers and seemed to be calling as a result. The group on Morane may have been a family and was noted as giving "contact" calls. EV recorded two sequences from a pair (individuals A, B) for a total of 214 calls. Upon analysis, some calls appeared to differ from those that could be ascribed to the two birds (although they may have been different call types from those individuals), so these were included only in overall statistical summaries. The following is an excerpt from EV's notes: "They were clearly aware of my presence, watching me while perched in *Pandanus tectorius* trees and on *Scaevola taccada* shrubs. At times only one of the birds was close by [= sample 1], but during one sequence [= sample 2] the second bird approached more closely and the birds followed each other while moving among the vegetation. Some of the calls seemed to be a response to my presence, but some seemed to be directed at the other pair member, particularly when both birds were close by. Calls

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TABLE 1. Variation between and within call types I and II: descriptive statistics of the vocalizations of the Tuamotu Sandpiper, *Prosobonia cancellata*, recorded in French Polynesia in 1990 (by R. and J. Seitre) and 2003 (by E. VanderWerf). Call type I differed significantly between recordists in duration and peak frequency (*t*-tests, $P < 0.001$ for each comparison), and in Seitres' samples, call types I and II differed significantly from one another in duration and peak frequency (*t*-tests, $P < 0.001$ for each comparison).

Sample (<i>n</i>) ^a	Call duration (ms)		Peak frequency in F0 (Hz)	
	Mean ± SD	Range	Mean ± SD	Range
Call type I				
Seitre 3 (91)	65.2 ± 10.78	45–122	1,085 ± 43.2	1,005–1,235
VanderWerf 1A (94)	47.1 ± 11.64	22–80	1,194 ± 83.0	1,034–1,378
VanderWerf 1B (6)	73.5 ± 17.42	51–102	1,264 ± 76.0	1,163–1,357
VanderWerf 1 total (101)	48.6 ± 13.44	22–102	1,198 ± 83.5	1,034–1,378
VanderWerf 2A (84)	55.0 ± 12.24	33–86	1,247 ± 61.0	1,077–1,378
VanderWerf 2B (20)	51.6 ± 12.49	33–82	1,177 ± 84.6	991–1,337
VanderWerf 2 total (113)	53.7 ± 12.06	33–86	1,228 ± 72.4	991–1,378
VanderWerf all (214)	51.3 ± 12.96	22–102	1,214 ± 79.1	991–1,378
Call type II				
Seitre 1 (24)	39.3 ± 4.98	31–53	813 ± 28.0	775–861
Seitre 2 (5)	30.6 ± 8.44	21–42	884 ± 51.4	804–919

^a VanderWerf's samples A and B are different individuals.

were given while perched and occasionally in flight.”

Recordings were digitized at 22,050 (Seitres' samples) or 44,100 (EV's samples) Hz from recordings on cassette audiotapes, which were either original recordings made in the field with a dictaphone by the Seitres, or original recordings made on Sony professional 60-min tape by EV using a Marantz PMD222 cassette tape recorder and a Sennheiser ME66 shotgun microphone. We analyzed samples with Raven ver. 1.0 (Cornell Laboratory of Ornithology), or CSL 4100 or Multi-Speech 3700 (Kay Elemetrics Corporation). We measured temporal and frequency variables in Raven on spectrograms produced with (a) filter bandwidth of 141 Hz and grid resolution of 2.90×86 Hz, and (b) filter bandwidth of 35 Hz and grid resolution of 11.6×21.5 Hz, respectively. Maximal frequency of the fundamental frequency (of call types I and II) and initial and terminal frequencies (of call type III) also were measured, using Raven's "Max Frequency" function for a selection of the spectrogram area of interest. We measured intercall intervals between successive calls by individual birds. Not all call variables or intercall intervals could be measured, so reported sample sizes vary.

Spectrograms of type III calls were prepared over a logarithmic scale of 0.5–500

kHz. A logarithmic scale graphically simulates a range of analyzing filter bandwidths, and was best for revealing various acoustical properties of this call type (Marshall 1964, 1977; Marshall and Sugardjito 1986; Miller 1992).

Call type I differed significantly between recordists: calls recorded by EV were significantly briefer and of higher peak frequency (Table 1), perhaps because of EV's superior recording system. However intercall intervals (for intervals < 3 s in duration) did not differ significantly (Kruskal-Wallis test: $Z = 0.33$, $P = 0.56$). Therefore samples from both recordists were combined for the latter variable.

RESULTS

Two broad classes of vocalizations were evident: brief, harmonically rich calls, with most energy in the second or third harmonic (call types I and II), and long, narrow band calls of descending frequency with moderate harmonic structure and most energy in the fundamental frequency (call type III). Call types I and II were either brief (Seitres' samples 1 and 2) or long (Seitres' sample 3 and EV's samples).

Type I calls were the most common in the recordings. They were uttered singly or as couplets, triplets, or longer sequences. Intercall intervals ranged from 64 ms to 8.5 s (mean = 805 ms, median = 555 ms, $n = 250$)

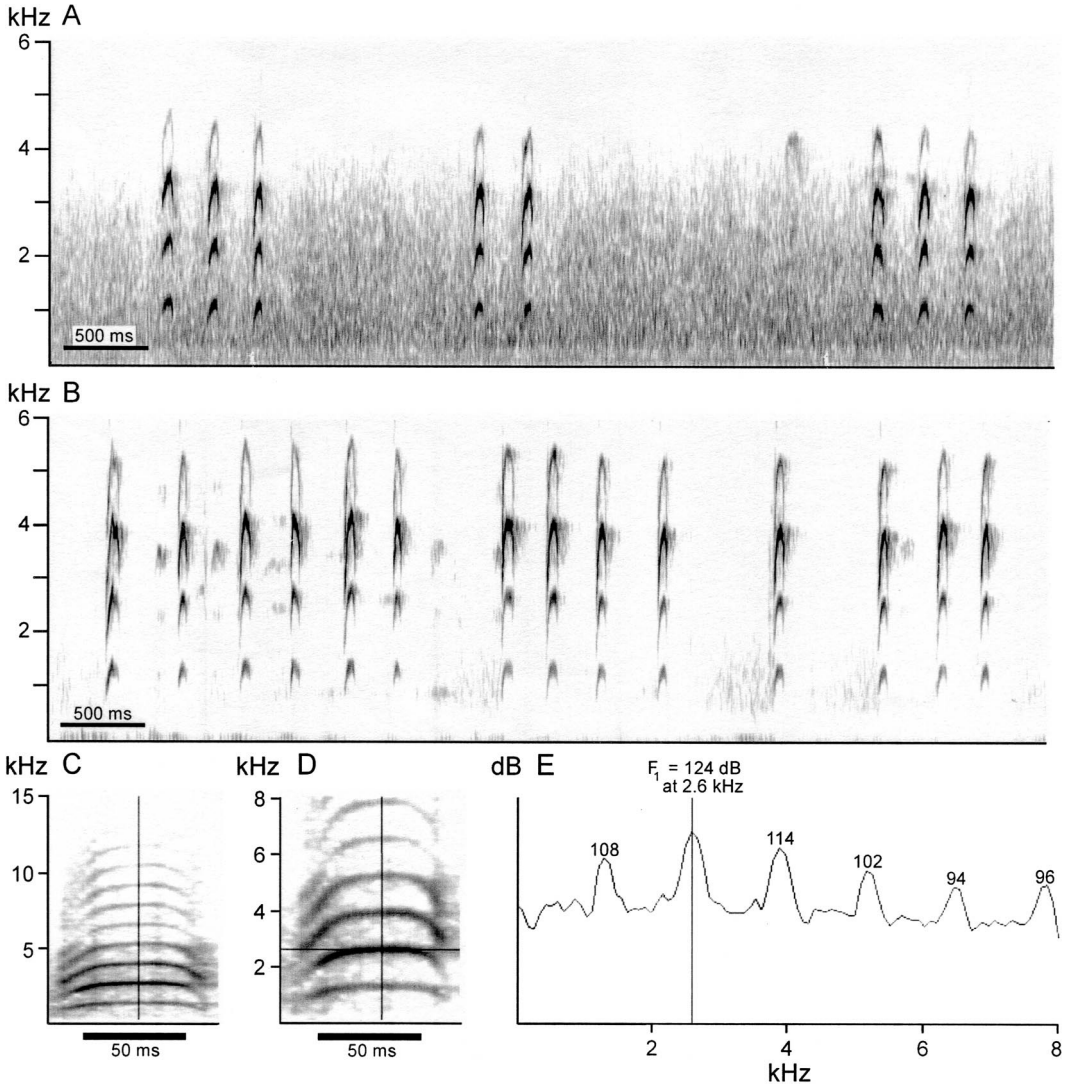


FIG. 1. Rhythmicity is common (A, B) and a broad frequency spectrum with most energy in the second or third harmonics is ubiquitous (C–E) in type I calls of the Tuamotu Sandpiper (*Prosobonia cancellata*). Spectrograms are based on recordings made in French Polynesia in 1990 by R. and J. Seitre (A) and in 2003 by E. VanderWerf (B–E). (A, B) Sequences of calls uttered by single birds (spectrograms produced in CSL 4100; Blackman window, analyzing filter bandwidth = 126 Hz). (C–E) Single call shown as spectrograms with different frequency ranges and (at the point marked by a vertical line in spectrograms C and D) as a power spectrum (spectrograms produced in Raven; Blackman window, filter bandwidth = 141 Hz, grid resolution = 2.9 ms × 86 Hz). (E) Unlabelled values above peaks are in dB.

in the typically skewed manner of interval data (skewness = 4.03). Eight of the intervals were >3 s in duration (five 3–4 s, two 4–5 s, one >8 s). For intervals <3 s long, mean = 687 ms and median = 540 ms ($n = 242$). The presence of rhythmic calling in many sequences is reflected in the predominance of

short intercall intervals: 4.0% for <200 ms; 25.2% for 200–299 ms; 8% for 300–399 ms; and progressively declining values for greater intervals. Examples of rhythmic calling are apparent in Fig. 1A, B.

Other distinctive attributes of type I calls are the large frequency range (to nearly 14

kHz in some of EV's recordings; the frequency range was smaller in Seitres' samples, likely due to the poor recording equipment used), rich harmonic structure, and peak energy in second or third harmonics (Fig. 1C–E). Type I calls were brief, with means of 59–65 ms in Seitres' samples and 47–51 ms in EV's samples (Table 1). They were structurally simple, with most showing a gradual increase in frequency to a peak around the midpoint of the call, then a gradual decrease, and with few elaborations except position of the peak frequency and quasi-rhythmic frequency modulation. The transition point in frequency in brief calls was little more than a sharp inflection point, but in longer calls frequency increased then decreased slowly, and sometimes frequency changed little over much of the call (Fig. 2p, q). The mean peak frequency of the fundamentals were 813–1,023 Hz (Seitres' samples) and 1,194–1,214 Hz (EV's samples).

Peak frequency occurred at or just past the midpoint in most type I calls, but preceded the midpoint in some (Fig. 2f–i). The frequency contour was usually simple but modulations of the carrier frequency sometimes occurred at the beginning (Fig. 2l, second call), middle (Fig. 2g–i), or throughout (Fig. 2m). Other variations occurred in duration and (between some individuals) in whether peak frequency occurred in the second or third harmonic (e.g., the calls of birds A and B in Fig. 3l).

Within Seitres' samples, call type II was significantly shorter than and of lower peak frequency than call type I (Table 1). The two call types were similar in being harmonically rich and consequently in covering a broad frequency range (Figs. 2, 3a–f). The lower frequency range evident in Seitres' sample of type II calls likely resulted from the poor recording equipment used, as noted. Patterns of frequency change and frequency variations were similar to those noted for call type I (Fig. 3a–f). However, recordings of this call type were of poor quality and some details of acoustic structure may not have been apparent.

Temporal and frequency variation in call types I and II were substantial (Table 1). For example, durations varied nearly three-fold within Seitres' sample of type I calls, and more than two-fold within Seitres' samples of type II calls; peak frequency varied by about

10–20% within Seitres' samples. Even greater variation characterized EV's samples (overall, five-fold differences in duration and about 40% variation in peak frequency). Nonrandom variation within samples also was apparent. In the long sequence of calls in Seitres' sample of type I calls, the first five calls were 101, 125, 112, 94, and 74 ms long, the eighth was 80 ms long, and the other 82 calls ranged from 43–70 ms in duration. In the same sample, the second and third calls had the highest peak frequency.

Type III calls ($n = 30$) were distinctive (Fig. 3). They were longer, higher in frequency, and harmonically less rich than call types I or II. In addition, most energy was in the fundamental frequency, not in higher harmonics. Mean values were 280 ms \pm 67.7 SD duration (range 113–471 ms) with initial frequency of the fundamental at 1,926 Hz \pm 402.2 SD (range 1,467–3,027 Hz), terminal frequency of the fundamental at 1,305 Hz \pm 262.1 SD (range 947–2,360 Hz), and frequency range of the fundamental at 623 Hz \pm 279.5 SD (range 253–1,440 Hz). In the sample, 27 calls began at frequencies $< 2,100$ Hz, three calls began at $> 2,700$ Hz, and no intermediate values were recorded.

Some type III calls began with complex modulations (Fig. 3g, m) or sharp decreases in frequency (Fig. 3h, k, l). The carrier frequency often declined monotonically but exceptions were numerous (e.g., frequency reversals and shifts). Quasi-rhythmic modulations of the carrier frequency were common over the course of each call. Calls ended variably in the rate and pattern of frequency decrease, and some ended with pronounced downward frequency sweeps (Fig. 3h, j). The second harmonic usually was evident but higher harmonics were only variably apparent throughout part or all of the calls.

DISCUSSION

We provisionally identified three call types of *Prosobonia* based on our limited recordings. The species' repertoire almost certainly is larger, as in other scolopacids (Miller 1984, 1992). However, repertoires of species that communicate mainly over short distances may show much structural intergradation and few distinct structurally defined classes (Green 1975, Marler 1976, Green and Marler 1979).

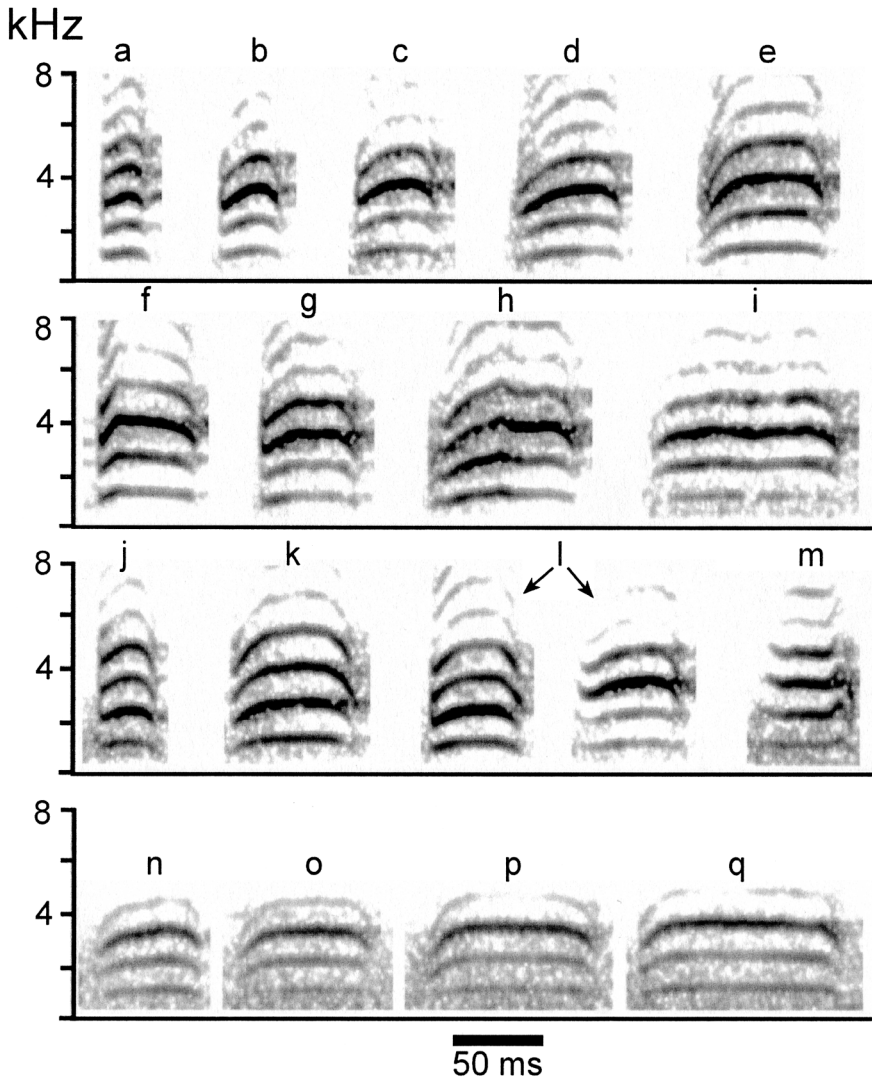


FIG. 2. Much fine scale variation is present in temporal and spectral features of type I calls of the Tuamotu Sandpiper (*Prosobonia cancellata*). Spectrograms are based on recordings made in French Polynesia in 1990 by R. and J. Seitre (n–q) and in 2003 by E. VanderWerf (a–m; successive calls by birds A and B are shown in spectrogram l). Spectrograms were produced in Raven (Blackman window, filter bandwidth = 223–226 Hz, grid resolution = 1.45–1.47 ms \times 86 Hz).

Among shorebirds, the Northern Jacana (*Jacana spinosa*) provides an example of structural integration (Jenni et al. 1974, Mace 1981, Jenni and Mace 1999); *Prosobonia* may be another example, judging by its type I and II calls.

Call type I (and perhaps type II) presumably is the one described by most authors. Hayman et al. (1986:337) stated that “a soft high-pitched whistle is the only call de-

scribed.” Holyoak and Thibault (1984:77) remarked that “the most common and characteristic call is a series of high-pitched whistled sounds, often repeated for a long time when the bird is perched or in flight” (EHM translation). Other descriptions include “a high pitched piping sound that [the bird] keeps up practically all day” (Bruner 1972:58), “a soft ‘pew’ ‘pew’ squeaking call [given] almost continually” (Holyoak 1973:28), and “a high-

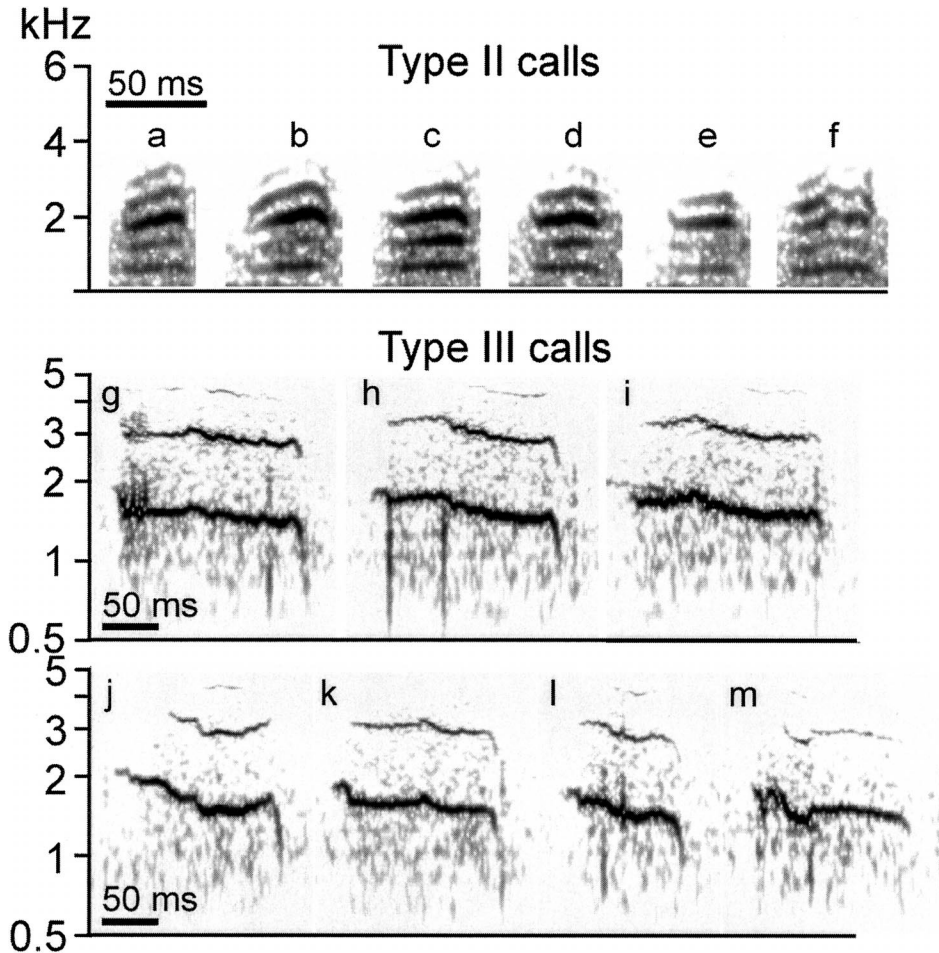


FIG. 3. Small to large differences in temporal or spectral attributes distinguish type II and type III calls of the Tuamotu Sandpiper (*Prosobonia cancellata*). Spectrograms are based on recordings made in French Polynesia in 1990 by R. and J. Seitre. Spectrograms a–f were produced in Raven (Blackman window, filter bandwidth = 141 Hz, grid resolution = 2.9 ms × 86 Hz); spectrograms g–m were produced in CSL 4100 (Blackman window, filter bandwidth = 63 Hz).

pitched piping or squeaky whistle uttered continuously when the bird forages” (Pratt et al. 1987:147). The apparently incessant use of this call type during foraging suggests that birds often are close to conspecifics (possibly mates, parents, or offspring), hence the call functions proximately to maintain proximity, spacing, or contact, or to inform about movement or ongoing behavior (Maier 1982, Conner et al. 2001), with ultimate functions in mate guarding or maintenance of family integrity.

Notably lacking from our sample were nuptial vocalizations that might be expected to be

long, loud, repetitive, or acoustically complex, and given aerially or from a prominent display post. However, such a call type may be that described as a “joyous trill” in flight by Quayle (cited by Holyoak and Thibault 1984:77). Also, one undisturbed Tuamotu Sandpiper was observed flying slowly low (<3 m) above short vegetation, while repeating a call resembling the flight call (“tsee-wee-wee”; Hayman et al. 1986:333) of the Common Sandpiper (*Actitis hypoleucos*; Wijkema and Wijkema 1997, J. T. Wijkema pers. comm.). These descriptions may refer to the same call type, which was not represented in our samples.

Quayle (cited by Holyoak and Thibault 1984:77) also described other call types, one resembling the call of a young chicken (but slightly softer) and the other a low "mih." Neither of these descriptions resembles calls we analyzed.

Prosobonia call types I and II had some syntactical organization, expressed as (1) successive grading (similarities across calls uttered in succession; e.g., initial calls in Seitre's sample 3) or (2) short trills (e.g., couplets, triplets). Successive grading is ubiquitous in trill-like calls of animals, including shorebirds (e.g., piping of *Haematopus* oystercatchers; alarm trills of calidridines; Cramp 1983; Glutz et al. 1975, 1977; Higgins 1993; Higgins and Davies 1996; Miller 1984), and intergradation from single to multi-element calls has been noted in some species (Miller 1979, Miller and Baker 1980, Conner et al. 2001). Call types I and II of *Prosobonia* resemble the latter situation, with brief, simple calls occurring individually at variable intervals or as couplets or more repetitions.

We have referred to call types I and II as being simple in structure, but simplicity and complexity are relative terms. Brief calls cannot be as structurally complex as long calls because they are temporally constrained so cannot achieve higher order temporal structure, such as complex syntax (Miller 1982). Considering their brevity, call types I and II were complex both as individual utterances and as vocal classes. First, these calls spanned an unusually large frequency range and showed strong structuring across this range (emphasized second or third harmonics also are widespread in calidridines; e.g., Cramp 1983; Glutz et al. 1975, 1977; Higgins 1993; Higgins and Davies 1996; Miller 1979, 1984). Complexity as a vocal class was increased through variation across call repetitions; frequency modulations were variably present in all parts of the call, fundamental frequency and duration varied across repetitions, and syntactical organization was expressed via sequential grading (see above).

Acoustical attributes of *Prosobonia* vocalizations suggest that they function mainly in short distance communication. Broadband complex spectra suffer attenuation and other changes over distance, so are most suitable as short distance signals (Bradbury and Vehren-

camp 1998). Similarly, high acoustic variation (grading) is common in avian communication over short distances (Bradbury and Vehrencamp 1998; Marler 1976; Miller 1984, 1991). The latter relationship is due jointly to lack of physical degradation in sound signals over short distances, plus the great importance of extrasignal (contextual) sources of information in short distance signaling (Smith 1977, 1997). Subtle variations within vocal classes, such as variable frequency modulations in call types I and II, may be important short range communication signals (Hailman and Ficken 1996).

Call type III was recorded only from an apparent family group, so may have been uttered by young birds. In structure it resembles calls of chicks of other scolopacid species in being long, narrow in bandwidth, and (in many cases) of descending frequency when communicating "distress" (Douglas 1996; Nethersole-Thompson and Nethersole-Thompson 1979; Tikhonov and Fokin 1979; 1980). In some scolopacids, juveniles retain their chick calls until after fledging (Payne and Pierce 2002).

In our view, future research on vocal communication in *Prosobonia* should document the complete vocal repertoire and investigate functions of vocal classes and organization (e.g., in the Common Greenshank, *Tringa nebularia*, tempo of calling by itself is communicatively significant; Nethersole-Thompson and Nethersole-Thompson 1979, 1986). Knowledge of nuptial vocalizations and communication will be important for understanding the mating system. Finally, chick vocalizations and vocal development are poorly known in shorebirds but are likely to be informative about both behavioral function and phylogenetic relationships.

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