



# Snipe taxonomy based on vocal and non-vocal sound displays: the South American Snipe is two species

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We analysed breeding sounds of the two subspecies of South American Snipe *Gallinago paraguayiae paraguayiae* and *Gallinago paraguayiae magellanica* to determine whether they might be different species: loud vocalizations given on the ground, and the tail-generated *Winnow* given in aerial display. Sounds of the two taxa differ qualitatively and quantitatively. Both taxa utter two types of ground call. In *G. p. paraguayiae*, the calls are bouts of identical sound elements repeated rhythmically and slowly (about five elements per second (Hz)) or rapidly (about 11 Hz). One call of *G. p. magellanica* is qualitatively similar to those of *G. p. paraguayiae* but sound elements are repeated more slowly (about 3 Hz). However, its other call type differs strikingly: it is a bout of rhythmically repeated sound couplets, each containing two kinds of sound element. The *Winnow* of *G. p. paraguayiae* is a series of sound elements that gradually increase in duration and energy; by contrast, that of *G. p. magellanica* has two or more kinds of sound element that roughly alternate and are repeated as sets, imparting a stuttering quality. Sounds of the related Puna Snipe (*Gallinago andina*) resemble but differ quantitatively from those of *G. p. paraguayiae*. Differences in breeding sounds of *G. p. paraguayiae* and *G. p. magellanica* are strong and hold throughout their geographical range. Therefore we suggest that the two taxa be considered different species: *G. paraguayiae* east of the Andes in much of South America except Patagonia, and *G. magellanica* in central and southern Chile, Argentina east of the Andes across Patagonia, and Falklands/Malvinas.

**Keywords:** cryptic species, *Gallinago*, geographical variation, mechanical sound, non-vocal sound, snipe, South America, speciation, taxonomy, vocalization.

Nuptial displays often differ between bird species, and display traits commonly are used in descriptions or as a basis for taxonomic recognition of different species (Lanyon 1969, Payne 1986, Alström & Ranft 2003). Visual and vocal displays have been documented most extensively; however, non-vocal acoustic traits of related taxa also have been detailed in several groups, notably manakins, hummingbirds and woodpeckers (Short

1972, Winkler & Short 1978, Prum 1990, 1998, Clark 2014, Clark *et al.* 2018, Miles *et al.* 2018). Distinctive non-vocal sounds were part of the information used to raise a hummingbird subspecies to species level (Feo *et al.* 2015), and differences in a non-vocal sound (produced by the tail during aerial displays) between Common Snipe *Gallinago gallinago* and Wilson's Snipe *Gallinago delicata* were part of the reason for elevating those taxa to species status (Thönen 1969, Miller 1996, Banks *et al.* 2002, Knox *et al.* 2008). To our knowledge, the latter decision is one of only a few instances in which acoustic

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displays have been used in shorebird taxonomy. As in Common and Wilson's Snipes, acoustic (vocal) evidence was used to raise subspecies of plovers to the species level (*Pluvialis*: Connors *et al.* 1993; *Charadrius*: Küpper *et al.* 2009). In the Scolopacidae, vocalizations were used to distinguish a new woodcock (*Scolopax*) species (Kennedy *et al.* 2001) and to clarify woodcock species limits (Mittermeier *et al.* 2014). Finally, vocal differences between western and eastern subspecies of Willet *Tringa semipalmata* suggest that those taxa should be recognized as separate species (Douglas 1998, 1999, Oswald *et al.* 2016, Pieplow 2017).

Phylogenetic placement of snipe (Gallinagini) within the Charadriiformes is clear (Baker *et al.* 2007, Cibois *et al.* 2012) but species relationships within the clade are unresolved and even the number of extant species is an unsettled point. Part of the reason for this situation is that, due to similarity in plumage, there is variable recognition of different taxa as subspecies or species (Hellmayr & Conover 1948, de Schauensee 1966, Tuck 1972, Sutton 1981, Hayman *et al.* 1986, Piersma 1996). To determine whether acoustic traits differ between other closely related snipe taxa apart from Common and Wilson's Snipes, and to extend analyses to both vocal and non-vocal sounds, we analysed breeding displays of the two allopatric subspecies of the South American Snipe *Gallinago paraguaiiae*.

Four South American snipe taxa in the *G. paraguaiiae* group have had unstable nomenclatural histories. These forms were originally described as three species (*Scolopax paraguaiiae* Vieillot 1816; *Scolopax magellanicus* King 1828; and *Gallinago andina* Taczanowski 1874) plus one subspecies of *Gallinago paraguaiiae* (*Capella paraguaiiae innotata* Hellmayr 1932), which is now treated as a subspecies of Puna Snipe *G. andina*. Subsequently, and at one extreme,

some or all of the described species have been treated as subspecies of *Gallinago gallinago* (Tuck 1972, Blake 1977); more commonly, a polytypic species *G. paraguaiiae* has been recognized, with subspecies *paraguaiiae*, *magellanica* and *andina* (and sometimes others; Meinertzhagen 1926, Hellmayr 1932, Hellmayr & Conover 1948, Hayman *et al.* 1986, Piersma 1996). At present, two species are generally recognized in this complex: the widespread South American Snipe with subspecies *paraguaiiae* and *magellanica*, and the more narrowly distributed high-elevation Puna Snipe (Blake 1977, Sibley & Monroe 1990, Jaramillo 2003, Remsen *et al.* 2019). We refer to these taxa as *paraguaiiae*, *magellanica* and *andina* (respectively), hereafter.

Many observers have noted differences in body size among the three taxa: *magellanica* has considerably longer wings and tail than *paraguaiiae*, and *andina* is the smallest form and has a noticeably shorter bill (Table 1). The outer rectrices differ in size across *Gallinago* species (Tuck 1972), presumably in relation to the diverse species-specific tail-generated *Winnow* sounds (names of displays are in title case and italicized; Bahr 1907, Glutz von Blotzheim *et al.* 1977, Reddig 1978, Paulson 2005, O'Brien *et al.* 2006). The outer rectrix of *magellanica* is longer but similar in breadth to that of *paraguaiiae*; by contrast the outer rectrix of *andina* is short and wide (Table 1).

Plumage also differs between the two forms of South American Snipe: that of *magellanica* is overall lighter and more variegated than in *paraguaiiae*; the ground colour on the throat and breast of *magellanica* is reddish-buff, whereas that of *paraguaiiae* is greyish or buffish-grey; the median stripes on the head are profusely flecked with brown in *magellanica* but mostly black in *paraguaiiae* (Tuck 1972); and *magellanica* also possesses a less blackish dorsum due to the greater amount of buff markings than in

**Table 1.** Descriptive statistics on body size in South American Snipe (*Gallinago p. paraguaiiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*).

Variable	<i>paraguaiiae</i>	<i>magellanica</i>	<i>andina</i>
Wing chord (mm)	119 ± 3.5 (102)	130 ± 4.0 (63)	114 ± 1.8 (16)
Culmen (mm)	70.1 ± 3.38 (108)	69.1 ± 4.40 (65)	54.8 ± 3.46 (15)
Outer rectrix length (mm)	42.9 ± 2.50 (62)	46.0 ± 2.85 (46)	40.2 ± 2.14 (16)
Outer rectrix breadth (mm)	4.4 ± 0.52 (103)	4.5 ± 0.88 (11)	5.0 ± 0.50 (9)

Data are shown as mean ± sd (n) (from Tuck 1972: 86).

*paraguaiae* (Hellmayr 1932; Fig. S1). Plumage of *andina* resembles that of *magellanica* more than that of *paraguaiae* (Hellmayr 1932, Tuck 1972; Fig. S1). The original descriptions of *paraguaiae* by Vieillot (1816) and *magellanica* by King (1828), with English translations, are provided in Table S1.

Acoustic differences among *paraguaiae*, *magellanica* and *andina* also have been noted (Blake 1977, Hayman *et al.* 1986, Jaramillo 2003). Piersma (1996: p. 496) mused that *G. p. magellanica* 'may be close to separate species status', and Jaramillo (2003: p. 227) commented that the non-vocal *Winnow* differs greatly between *paraguaiae* and *magellanica* (a 'difference ... as great as in other species pairs of *Gallinago*') and predicted that further study, incorporating acoustic analysis, would confirm that the two forms are different species.

We investigated breeding-season ground vocalizations plus the non-vocal *Winnow* of *paraguaiae* and *magellanica* to determine whether those taxa might be different species. We included *andina* in our analyses, as presumably it is closely related to those forms and its acoustic displays have not been described. We analysed recordings from throughout South America and found: (1) substantial differences in both vocal and non-vocal acoustic displays between the two subspecies and (2) no obvious geographical variation in calls or *Winnows* within each subspecies' range. On that basis, we recommend that *paraguaiae* and *magellanica* be recognized as separate species. The strong acoustic differentiation between these taxa suggests that comparative acoustic analyses may be valuable in resolving species relationships within the *Gallinago/Coenocorypha* clade.

## METHODS

### Species and geographical coverage; sources of recordings

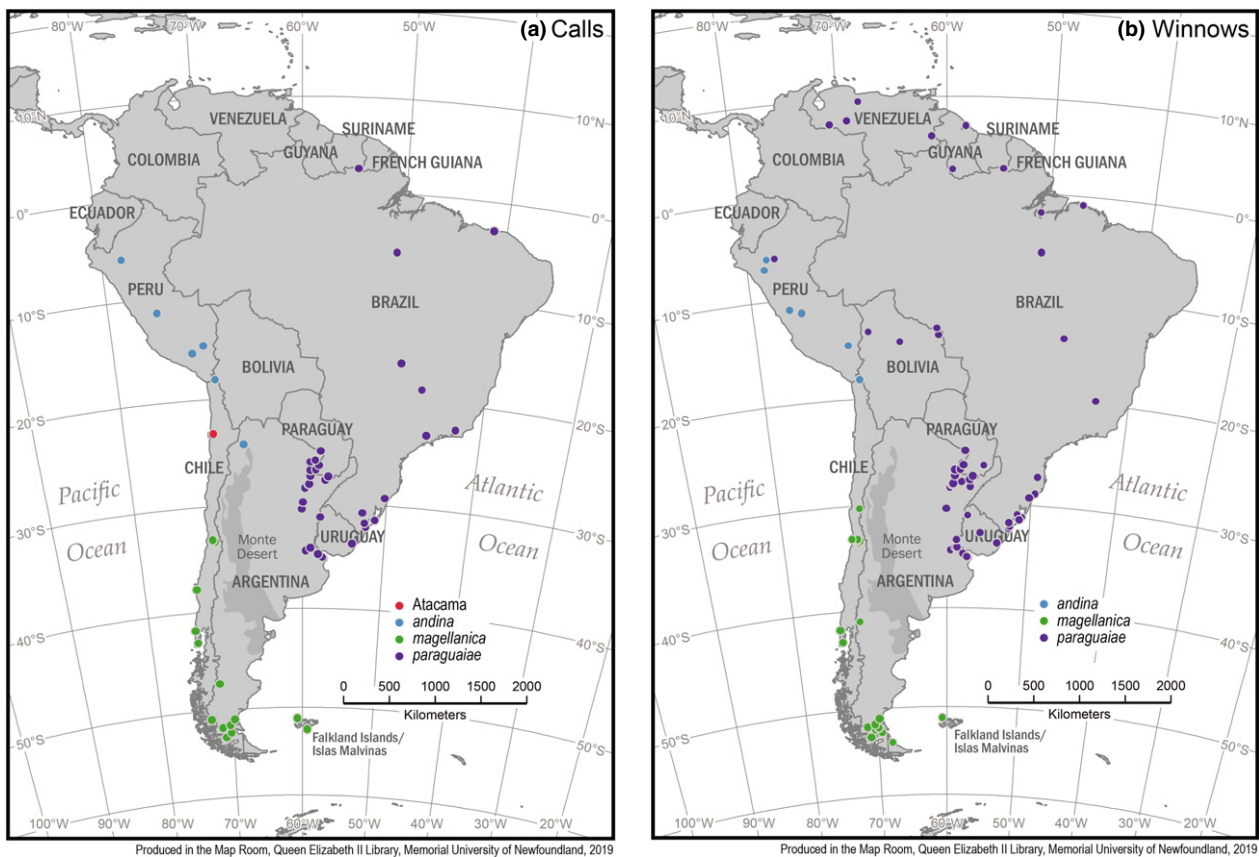
We analysed our own audio recordings, those of several individual recordists (see Acknowledgements) and recordings in sound archives (Table S2). We screened nearly 1300 recordings: *paraguaiae*  $n = 625$ , *magellanica*  $n = 560$  and *andina*  $n = 80$ . We obtained samples of ground calls or *Winnows* from 11 countries: *paraguaiae*  $n = 10$ , *magellanica*  $n = 3$  and *andina*  $n = 3$  (Fig. 1; Table S2). For recordings duplicated across collections (see Table S2), we selected files in wav

format from the Macaulay Library, the Sound and Moving Image Catalogue of the British Library, or the Avian Vocalizations Center, in that order. We selected only single samples from multiple recordings of the same bird, as judged by location, date and time of recording, and the similarity of sounds across recordings. Final sample sizes (number of individual birds) for the different sound classes are detailed in the tables.

We lacked recordings of *paraguaiae* from three countries within the known breeding distribution (Colombia, Ecuador, and Trinidad and Tobago) and some countries were poorly represented (notably French Guiana, Guyana and Peru; Fig. 1). Balancing that unevenness, sound samples were recorded by many people over a long period (*paraguaiae* 1964–2018, *magellanica* 1991–2018, *andina* 1983–2018), and one prominent kind of display (*Winnow*) was represented for all countries in the ranges of *andina* and *magellanica*, and for all countries except the three noted for *paraguaiae*.

We deposited our recordings in the Macaulay Library (see Data Statement below). All xenocanto recordings were in mp3 format; all others were in wav format but recording details varied. To standardize sound files for analysis, we converted (as necessary) sound files to wav format, monaural, at a sample rate of 44.1 kHz and 16-bit depth. Sound-file compression can bias measurements on some sound variables (e.g. peak frequency) but most of the variables that we measured were temporal and therefore were little affected by compression (Araya-Salas *et al.* 2017). Furthermore we used only a single 'robust' frequency variable, so mixing results on uncompressed wav files with those that were of lower quality due to conversion from the mp3 format of XC sound files did not affect our results.

The acoustic repertoire of *Gallinago* has been best studied for *G. gallinago* (Glutz von Blotzheim *et al.* 1977, Reddig 1978, 1981, Cramp 1983, Bergmann *et al.* 2008). However, several sound types that are used during the breeding period appear to be nearly universal across *Gallinago* species; we follow Cramp (1983) and Mueller (1999) in referring to them as *Chip* and *Chipper* calls, and the non-vocal *Winnow*, produced by the outer rectrices during dives in aerial displays. *Chip* and *Chipper* calls are given both on the ground and in the air (as described below), but we analysed only those calls that were recorded from birds on the ground.



**Figure 1.** Geographical distribution of samples of ground calls (a) and *Winnow* sounds (b) of South American Snipe (*Gallinago paraguaiae paraguaiae* and *Gallinago paraguaiae magellanica*) and Puna Snipe (*Gallinago andina*) used in the study. One sample of calls from the Atacama region is also shown in (a) (red symbol; see text). The Monte Desert of Argentina separates the distributions of *G. p. paraguaiae* and *G. p. magellanica* in Argentina. Map prepared by D. J. Mercer, Map Room, Memorial University of Newfoundland. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## Descriptions, measurements and analyses

Descriptions and measurements of quantitative variables were based on analyses with RAVEN PRO 64 1.5 ([www.birds.cornell.edu/raven](http://www.birds.cornell.edu/raven)). We used spectrograms for temporal measurements because nearly all sound recordings were too noisy (and many were too weak) for the preferred method of taking such measurements on waveforms (Köhler *et al.* 2018). Settings for measurements were: Window – Blackman window, 200 samples (= 4.54 ms) for temporal measures and 1024 samples (= 23.2 Hz) for the frequency measure (see below), and 3 dB filter bandwidths of 362 Hz and 70.7 Hz, respectively: Time Grid – 90% overlap; and Frequency Grid – DFT size, 256 samples.

We displayed 1 s of each spectrogram on a computer screen about 45 cm wide for measurement and adjusted brightness and contrast as needed before taking measurements. For calls, we selected one good example for each individual bird and measured durations of: (1) five successive elements in *Chip* calls, plus the five Inter-element Intervals (variable names are in title case and are given in the tables) that preceded those call elements, and computed mean values for each individual bird, and (2) all 10 elements in five successive couplets of *magellanica* *Chipper* calls, plus the 10 Inter-element Intervals that preceded those elements, and again computed mean values. As a frequency variable, we used Centre Frequency: 'The frequency that divides the selection into two frequency intervals of equal energy' (Charif *et al.* 2010: 171). Based on trial and error,

**Table 2.** Descriptive statistics on ground vocalizations of South American Snipe (*Gallinago p. paraguaiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*)<sup>a</sup>.

Element variable <sup>b</sup>	<i>paraguaiae</i>			<i>magellanica</i>			<i>andina</i>
	Slow Chip	Fast Chip	Chip	Chipper element			
				Long	Short	Chip	
Duration (ms)	31.4 ± 5.18 (29) 19–42	29.1 ± 5.36 (47) 16–42	36.5 ± 5.00 (71) 27–51	64.2 ± 13.83 (44) 34–101	46.8 ± 12.24 (44) 26–68	27.0 ± 2.93 (17) 23–32	
Inter-element Interval (ms)	178 ± 14.3 (29) 155–206	64.1 ± 5.61 (47) 51–75	264 ± 20.2 (71) 229–315	245 ± 43.9 (44) 165–339	216 ± 31.8 (44) 152–288	194 ± 13.4 (17) 172–209	
Duty Cycle (%)	15.1 ± 2.52 (29) 9–19	31.1 ± 5.15 (47) 19–42	12.2 ± 1.88 (71) 8–17	18.3 ± 4.45 (41) 10–30	12.3 ± 1.37 (17) 10–14	12.3 ± 1.37 (17) 10–14	
Repetition Rate (Hz)	4.79 ± 0.320 (31) 4.3–5.4	10.7 ± 0.68 (49) 10–12	3.34 ± 0.205 (75) 2.8–3.7	3.23 ± 0.596 (43) 1.0–4.6	4.55 ± 0.327 (19) 4.0–5.1	4.55 ± 0.327 (19) 4.0–5.1	
Centre Frequency (Hz)	2000 ± 324 (30) 1292–2672	2110 ± 301 (39) 500–2498	2340 ± 280 (60) 1547–2842	2247 ± 393 (38) 1464–2885	2235 ± 403 (37) 1421–2928	2468 ± 370 (13) 1680–2885	

Cell entries are grand means across means of individuals ± sd (n) and range. Statistical test results are presented in Table 3. <sup>a</sup>One unidentified bird whose *Chip* was recorded in the Atacama Desert had means (for n = 5 calls) on the variables Element Duration to Centre Frequency, respectively, of: 41.2 ± 3.19 (sd) msec, 238 ± 2.28 msec, 14.7%, 3.58 Hz and 1981 Hz (Figs. 1, 3). <sup>b</sup>See Methods.

**Table 3.** Summary of results of 1-way ANOVAs and post-hoc Tukey's honest significance tests on call variables of South American Snipe (*Gallinago p. paraguaiiae*, P; *G. p. magellanica*, M) and Puna Snipe (*G. andina*).

Comparison of sound elements <i>G. andina</i> Chip and:	ANOVA results <i>P</i> , <i>F</i> , (df)	<i>P</i> - estimates from Tukey multiple comparison of means <sup>a</sup>		
		<i>paraguaiiae-magellanica</i>	<i>paraguaiiae-andina</i>	<i>magellanica-andina</i>
P Fast Chip, M Chip:				
Duration	< 0.001, 44.8, (2, 133)	< 0.001	0.38	< 0.001
Inter-element interval	< 0.001, 2287, (2, 133)	< 0.001	< 0.001	< 0.001
Centre Frequency	< 0.001, 15.3, (2, 109)	< 0.001	< 0.001	0.35
Duty Cycle	< 0.001, 487, (2, 133)	< 0.001	< 0.001	0.98
Repetition Rate	< 0.001, 4366, (2, 141)	< 0.001	< 0.001	< 0.001
P Fast Chip, M Chipper:				
Duration	< 0.001, 155, (2, 106)	< 0.001	0.69	< 0.001
Inter-element Interval	< 0.001, 770, (2, 105)	< 0.001	< 0.001	< 0.001
Centre Frequency	< 0.001, 8.12, (2, 86)	< 0.001 <sup>c</sup>	< 0.001	0.12
Duty Cycle	< 0.001, 152, (2, 103)	< 0.001	< 0.001	< 0.001
Repetition rate	< 0.001, 1980, (2, 109)	< 0.001	< 0.001	< 0.001
P Slow Chip, M Chip:				
Duration	< 0.001, 31.5, (2, 115)	< 0.001	0.012 <sup>c</sup>	< 0.001
Inter-element Interval	< 0.001, 287, (2, 115)	< 0.001	0.009 <sup>c</sup>	< 0.001
Centre Frequency	< 0.001, 14.4, (2, 99)	< 0.001	< 0.001	0.35
Duty Cycle	< 0.001, 22.6, (2, 115)	< 0.001	< 0.001	0.95
Repetition rate	< 0.001, 3424 (2, 123)	< 0.001	0.003 <sup>c</sup>	< 0.001
P Slow Chip, M Chipper:				
Duration	< 0.001, 112, (2, 88)	< 0.001	0.22	< 0.001
Inter-element Interval	< 0.001, 45.5, (2, 87)	< 0.001	0.06	< 0.001
Centre Frequency	< 0.001, 7.82, (2, 76)	< 0.001 <sup>c</sup>	< 0.001	0.13
Duty Cycle	< 0.001, 20.4, (2, 85)	< 0.001	0.026 <sup>c</sup>	< 0.001
Repetition rate	< 0.001, 114, (2, 91)	< 0.001	0.16	< 0.001

Descriptive statistics are summarized in Table 2. <sup>a</sup>Computed on means of individual birds with R functions aov and TukeyHSD. <sup>b</sup>Tests within comparison groups are not all independent (see Methods). <sup>c</sup>These *P*-estimates are all > 0.05 after adjusting the false discovery rate for multiple comparisons, using the Benjamini–Hochberg procedure with a false discovery rate of 0.1, and *m* (number of tests) = 15 for each block of tests.

to measure Centre Frequency between low-frequency background noise and higher-frequency biological noise (mainly birds), we measured this variable for a rectangular selection with lower and upper frequencies of 1 and 4 kHz. We measured Centre Frequency on selected high-amplitude elements: single elements in *Chip* calls and each of the two element types in *Chipper* calls; for *Winnows* we positioned the selection around the highest-amplitude portion (typically this was slightly after the temporal mid-point). We selected high-amplitude call elements from long series or near the middle of bouts. Measures on Centre Frequency varied substantially, presumably due mainly to variation in recording distance, background noise, and whether recordings were originals or copies, among other factors.

Calls often start with a low-amplitude section, but this was audible only at close range in the field, and was apparent only in high-quality sound recordings.

Therefore, we excluded that portion from our measurements on calls for which it was expressed (an example for *magellanica* is given below).

*Winnows* start gradually with low-amplitude elements and end with one to several low-amplitude elements. Thus, *Winnow* Durations were slightly underestimated and Inter-winnow Intervals were slightly overestimated. We derived the Duty Cycle (DC) and Repetition Rate (RR) of *Winnows* from means of those measures: DC = 100 (*Winnow* duration / (*Winnow* duration + Inter-winnow Interval)); and RR = (number of *Winnows* / (Σ*Winnow* durations + Σdurations of Inter-*Winnow* Intervals that followed those *Winnows*)).

*Winnows* of the taxa differed greatly in the kinds of elements they contained and in how elements changed over the course of each *Winnow*, so we used the following procedure to derive measures that were roughly comparable across species. First, for all taxa we ignored the one-to-several soft

**Table 4.** Descriptive statistics on *Winnows* of South American Snipe (*Gallinago p. paraguaiiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*).

Variable <sup>a</sup>	<i>paraguaiiae</i>	<i>magellanica</i>	<i>andina</i>
<i>Winnow</i> Duration (sec)	2.54 ± 0.531 (92) 1.4–4.5	3.39 ± 0.733 (55) .8–5.5	3.33 ± 0.478 (19) 2.8–4.2
Inter- <i>winnow</i> Interval (sec)	6.55 ± 1.536 (65) 2.3–9.8	7.25 ± 1.21 (22) 4.3–9.3	7.20 ± 1.260 (16) 4.5–8.8
<i>Winnow</i> Repetition Rate (per min)	6.72 ± 1.229 (63) 4.8–12	5.87 ± 0.687 (21) 4.8–8.1	5.78 ± 0.856 (16) 4.7–7.7
<i>Winnow</i> Duty Cycle (%)	29.0 ± 7.66 (62) 16–55	29.5 ± 5.99 (21) 18–42	32.2 ± 5.25 (16) 23–45
<i>Winnow</i> Centre Frequency (Hz)	1499 ± 206 (57) 1163–2282	1784 ± 150 (47) 1464–2067	1534 ± 96.8 (14) 1406–1766
Element Duration (msec)	161 ± 38.2 (67) 99–218	89.6 ± 22.41 (45) 44–162	76.2 ± 9.70 (15) 58–90
Element Maximal Duration (msec)	195 ± 27.9 (69) 123–261	160 ± 50.6 (45) 57–302	89.4 ± 13.6 (15) 69–115
Inter-element Interval (msec) <sup>b</sup>	31.0 ± 5.58 (68) 19–45	52.9 ± 10.72 (45) 31–79	31.1 ± 7.80 (15) 20–50
Pulse Repetition Rate (Hz)	5.31 ± 0.811 (67) 3.9–7.8	7.20 ± 1.203 (45) 5.0–11	9.40 ± 0.952 (15) 8–12
Pulse Duty Cycle (%)	83.4 ± 3.90 (68) 73–89	62.1 ± 8.35 (42) 42–81	71.0 ± 6.53 (15) 59–81

Cell entries are grand means across individuals ± sd (nof birds) and range. Statistical test results are presented in Table 5. <sup>a</sup>See Methods. <sup>b</sup>For regular temporal parts of *Winnows* only; parts with irregular timing (e.g. Fig. 8I, J) were excluded for this measure.

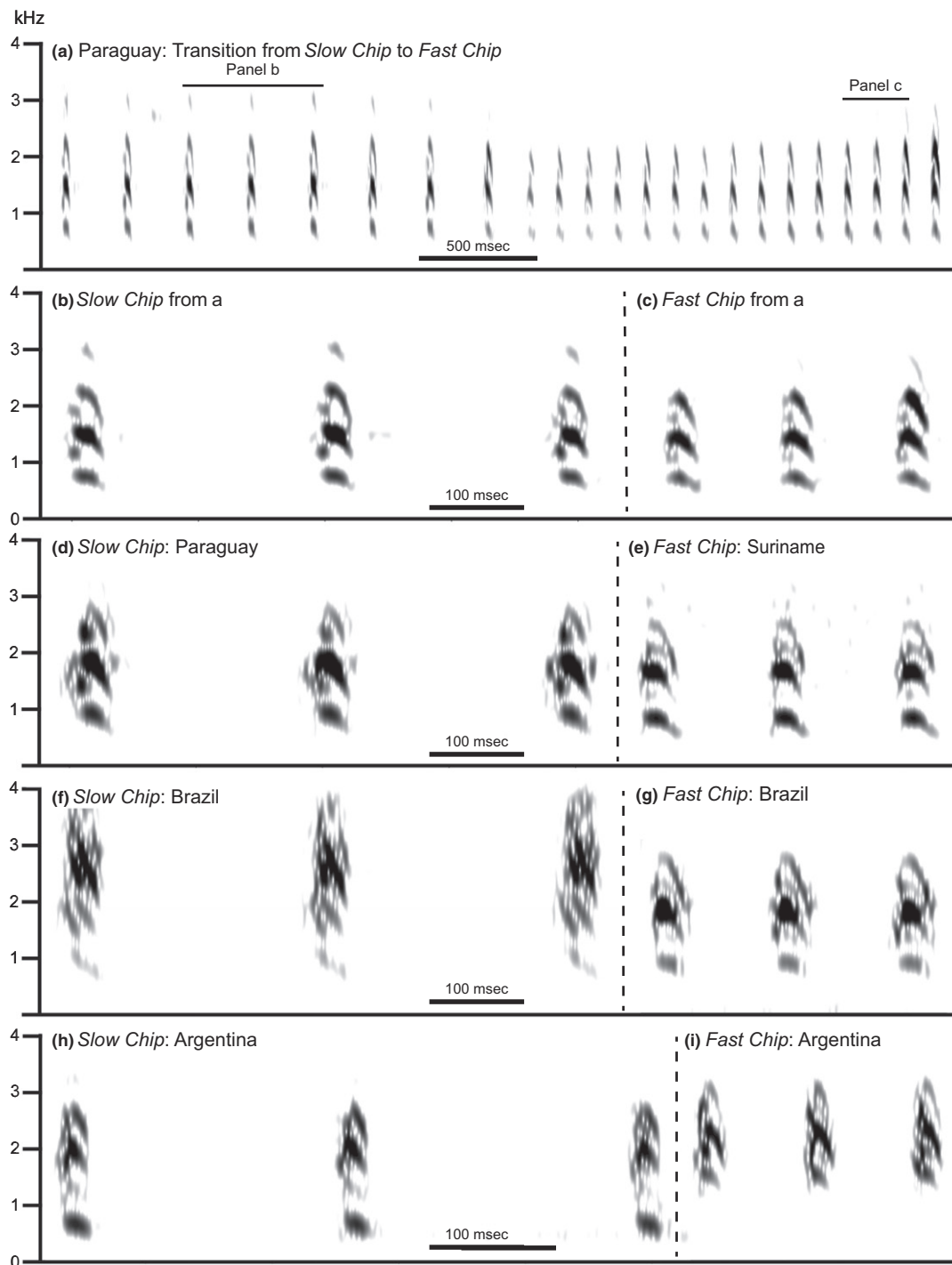
terminal elements and measured high-amplitude longer elements in the body of the *Winnow*. We measured one good *Winnow* recording from each individual bird. For *paraguaiiae* and *andina*, we selected the longest *Winnow* element as a reference point, and measured the duration of that element, the two elements that preceded it, and the two elements that succeeded it; the mean of those measurements was Element Duration. We also measured the five silent intervals that preceded those elements, and computed the mean of those measures (= Inter-element Interval). We derived Duty Cycle and Repetition Rate of sound elements as for *Winnows*. We used the same procedures for *magellanica*, but measured 10 sound elements where possible, as they varied more in that form.

Elements within *Winnows* of *magellanica* commonly show coupled modulation of frequency and amplitude (see below). In some individual birds and in some weak recordings, such low-frequency/amplitude portions of elements appeared as silences on spectrograms. This contributed to variation in estimates of Element Duration and Inter-element Interval.

We used PRAAT (praat6043\_win64; [http://www.fon.hum.uva.nl/praat/download\\_win.html](http://www.fon.hum.uva.nl/praat/download_win.html)) to prepare the spectrograms.

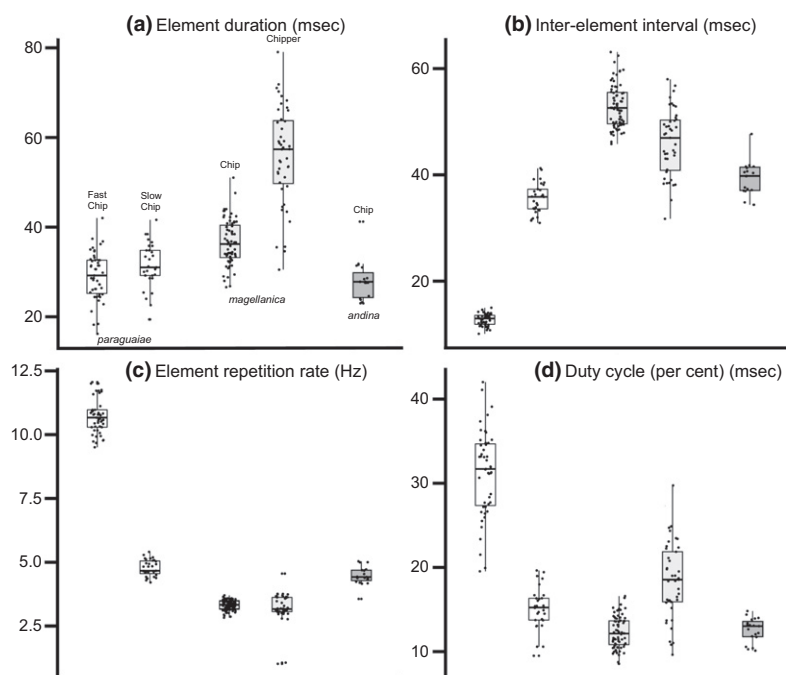
We screened each variable for normality of residuals, then conducted one-way ANOVAs (using the R function `avov`) on each of the five call variables for each combination of calls across species, followed by the *post-hoc* Tukey's honest significance test (using the R function `TukeyHSD`) for each combination: *paraguaiiae* Fast Chip – *magellanica* Chip – *andina* Chip; *paraguaiiae* Slow Chip – *magellanica* Chip – *andina* Chip; etc. We then adjusted the false discovery rate for multiple comparisons, using the Benjamini–Hochberg procedure with a false discovery rate of 0.1, and  $m$  (number of tests) = 15 for each combination of tests (McDonald 2014). Not all the tests were independent, for two reasons. First, estimates of Duty Cycle and Repetition Rate of sound elements were derived from measurement variables and so are positively correlated with one another and with the variables from which they were derived (Duty Cycle and Element Duration were positively correlated with one another, for example). Second, some measurement variables were correlated with one another: for example, in *Chip* and *Chipper* of *magellanica*, Element Duration and Inter-element Interval were negatively correlated with one another.

We analysed *Winnow* variables as for calls. As for calls, not all tests were independent. Only



**Figure 2.** The South American Snipe *Gallinago paraguaiiae paraguaiiae* utters two kinds of loud ground calls during the breeding period, the *Slow Chip* and *Fast Chip*. Each kind of call consists of a single type of sound element that is repeated rhythmically. (a) *Slow Chip* followed immediately by *Fast Chip*, illustrating that no intermediates occur in the transition between the two call types. Recording data: (a–c) Paraguay (26.5°S, 58.0°W), 11 November 2008, E. H. Miller; (d) Paraguay (26.5°S, 58.0°W), 13 November 2008, E. H. Miller; (e) Suriname (2.3°N, 54.6°W), 17 June 2017, K. Zyskowski; (f) (xeno-canto 22080), Brazil (32.1°S, 52.2°W), 1 August 2008, N. Athanas; (g) (Macaulay Library 18872), Brazil (30.8°S, 52.8°W), 25 October 1972, W. Belton; (h) Argentina (26.2°S, 58.9°W), 13 December 2006, J. I. Areta; (i) Argentina (33.0°S 58.5°W), 15 May 2015, J. I. Areta.





**Figure 3.** Graphical summary of trends in temporal characters measured on sound elements of ground calls of the South American Snipe *Gallinago paraguaiae paraguaiae* and *Gallinago paraguaiae magellanica*, and Puna Snipe *Gallinago andina*. *Chipper* sound elements and the intervals between sound elements in both *Chip* and *Chipper* are notably longer in *G. p. magellanica* than in the other taxa (a,b), and *G. p. magellanica* calls are uttered more slowly (c). The duty cycle also is higher in *G. p. magellanica*, especially in the *Chipper* (d). The top and bottom of each box on the boxplot mark the 75th and 25th percentiles, respectively, and the horizontal black line is at the 50th percentile. The top of the line extending above each box is at the largest value within 1.5 times the interquartile range above the 75th percentile; the bottom of the line extending above each box is at the smallest value within 1.5 times the interquartile range below the 25th percentile. The same shades of grey for the taxa are used in other graphs. On the non-independence of some comparisons, see Methods.

Winnow Duration and Inter-winnow Interval were significantly (but moderately) negatively correlated in each species.

## RESULTS

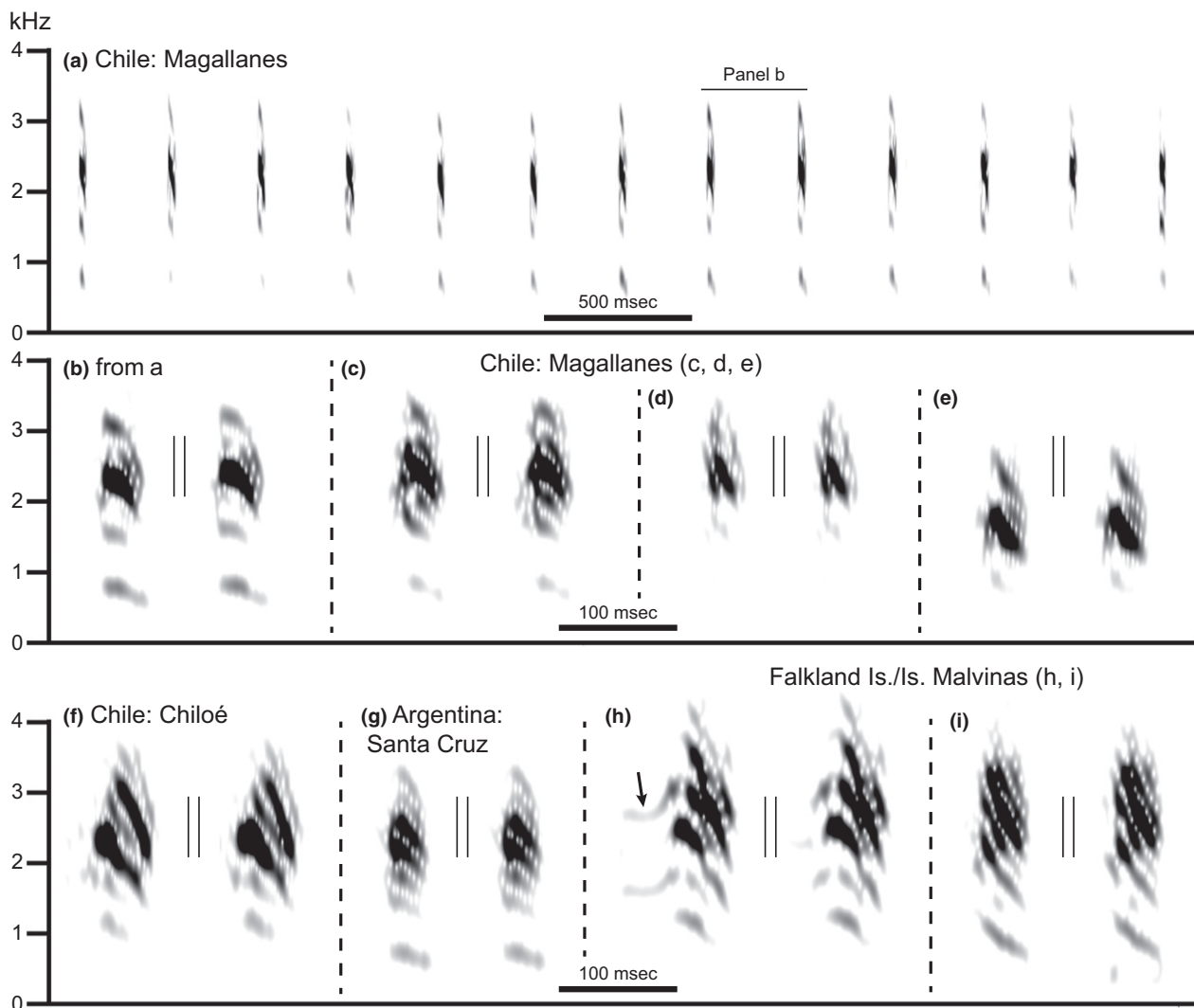
Ground calls: *paraguaiae* — Loud calls, comprising rhythmically repeated elements, were uttered in long series or in bouts from the ground, slight prominence, or elevation (e.g. fence post). The sounds are harmonically rich, and the harmonic of highest amplitude is invariably well above the fundamental. Acoustic structure varies substantially across birds, but within individuals is uniform and similar between call types (Fig. 2).

Two kinds of calls occur, which we named *Slow Chip* and *Fast Chip* based on the difference in how rapidly the sound elements are uttered (Figs 2 and 3). Element Duration is similar between the two call types (about 30 ms; figures given in the text

are approximate), but intervals between successive elements average 2.8 times as long in *Slow Chips* (180 vs. 65 ms) so Repetition Rate and Duty Cycle of sound elements are much lower than in *Fast Chips*: 5 vs. 11 Hz and 15 vs. 30%, respectively (Fig. 3; Tables 2 and 3).

Aerially displaying birds uttered *Chip* and *Chipper* calls frequently, separately from or overlapping with the beginning or end of *Winnows*, and utter *Fast Chip–Slow Chip* (or the reverse) sequences (or sequences of just one of the call types) in descent from displays. They also give these calls in aerial chases of, or aerial displays with, other birds ('arched-wing display', 'wing-arch flight', etc.; Tuck 1972, Reddig 1981, Sutton 1981, Cramp 1983).

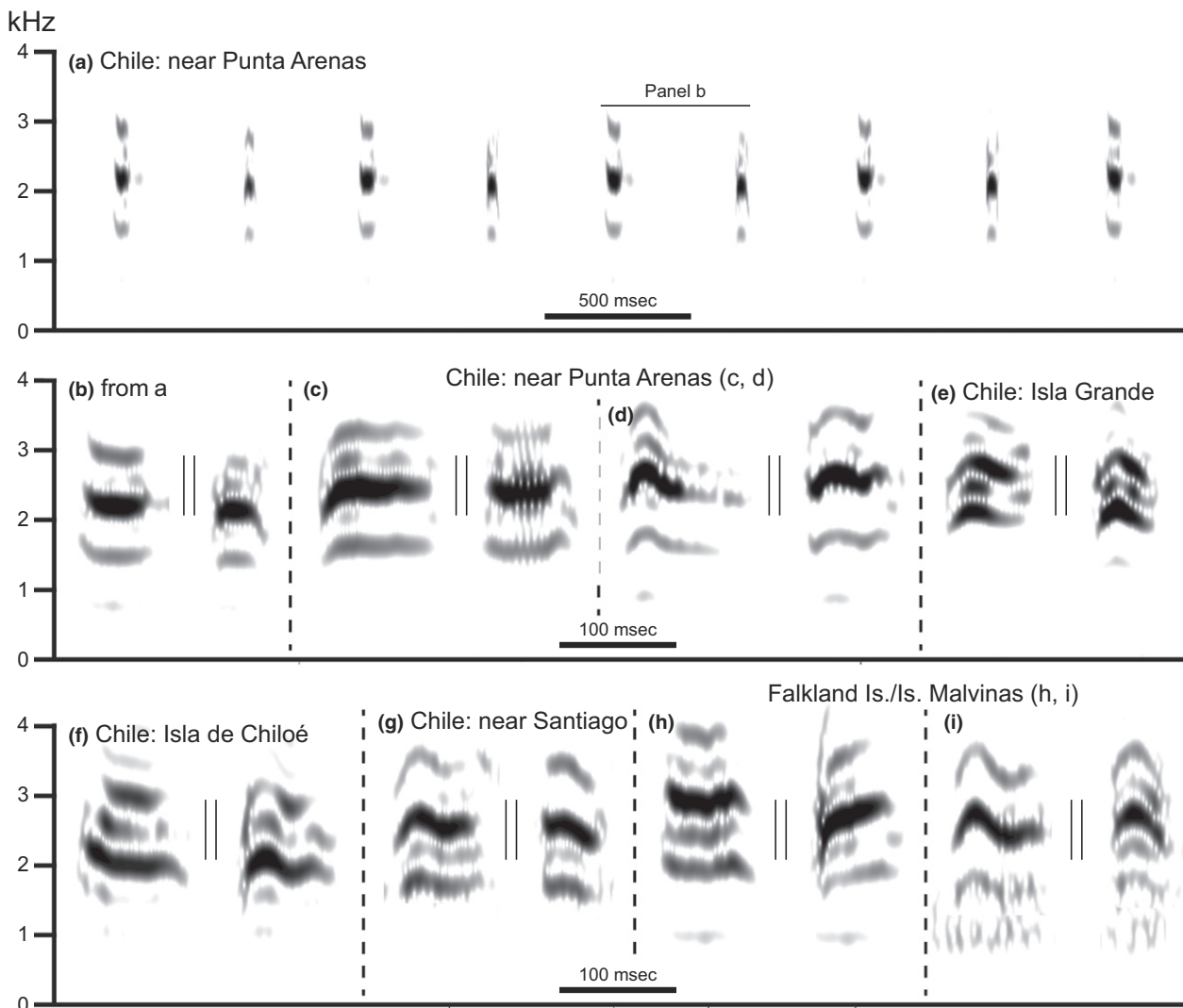
Ground calls: *magellanica* — As for *paraguaiae*, two kinds of call occur comprising either rhythmically repeated sound elements or repeated couplets, uttered in bouts or long series



**Figure 4.** The South American Snipe *Gallinago paraguaiiae magellanica* utters two kinds of loud ground call during the breeding period, one of which is the *Chip*. This consists of a single type of sound element that is repeated rhythmically. Two successive elements from eight different birds are shown in (b–i); the natural intervals between them are reduced for graphical purposes. The arrow in panel h marks the introductory part of the call, as described in the text. Recording data: (a,b) Chile (53.2°S, 70.9°W), 16 October 2004, E. H. Miller; (c) Chile (51.7°S, 70.1°W), 6 November 2004, S. Imberti; (d) Chile (52.7°S, 69.4°W), 9 November 2005, E. H. Miller; (e) Falkland Is./I. Malvinas (51.3°S, 60.7°W), 10 November 1995, D. E. Kroodsma; (f) Chile (41.9°S, 74.0°W), 2 September 2006, E. H. Miller; (g) Argentina (51.7°S, 70.1°W), 6 November 2004, S. Imberti; (h) Falkland Is./I. Malvinas (51.3°S, 60.6°W), 10 November 1995, D. E. Kroodsma; (i) Falkland Is./I. Malvinas (51.3°S, 60.6°W), 1 January 1999, A. Jaramillo.

from the ground, slight prominence or elevation (e.g. fence post). The sounds are harmonically rich and, as in *paraguaiiae*, the harmonic of highest amplitude is always above the fundamental (Figs 4 and 5). As in *paraguaiiae*, acoustic structure varies substantially among birds, but within birds it is uniform and similar between call types (Figs 4 and 5).

One kind of *magellanica* call (*Chip*) is similar to the *Fast Chip* and *Slow Chip* of *paraguaiiae* in also being composed of rhythmically repeated sound elements of a single kind (Fig. 4). *Chip* elements are longer in *magellanica* than in *paraguaiiae* (37 vs. 30 ms) and are separated by silent intervals of more than 0.25 s in *magellanica*; therefore both the Duty Cycle and Repetition Rate of sound

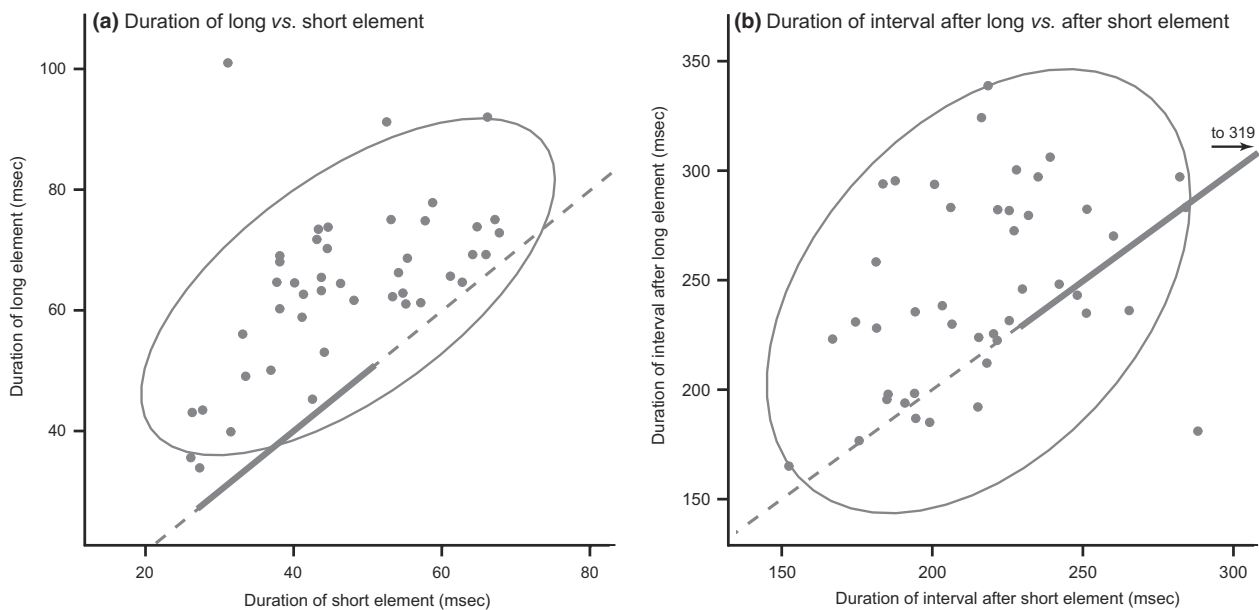


**Figure 5.** A second type of loud ground call given by breeding South American Snipe *Gallinago paraguayiae magellanica* is the *Chipper*. This call type is composed of a train of rhythmically repeated sound couplets, the members of which differ in duration and frequency, and in the interval between them. Successive long and brief elements (respectively) from eight different birds are shown in (b–i); the natural intervals between them are reduced for graphical purposes. Recording data: (a,b) Chile (53.0°S, 70.8°W), 16 October 2004, E. H. Miller; (c,d) Chile (53.0°S, 70.8°W), 16 October 2004, E. H. Miller; (e) Chile (52.9°S, 70.0°W), 8 November 2005, E. H. Miller; (f) Chile (41.9°S, 73.9°W), 2 September 2006, E. H. Miller; (g) (xeno-canto 19484), Chile (33.3°S, 70.8°W), 6 September 2006, F. Schmitt; (h) (Internet Bird Collection 1185185), Falkland Is./I. Malvinas (51.3°S, 60.6°W), 15 December 2010, L. Demongin; (i) Falkland Is./I. Malvinas (51.3°S, 60.6°W), 1 January 1999, A. Jaramillo.

elements are lower in *magellanica* than in *paraguayiae* (Fig. 3; Tables 2 and 3). Finally, *Chipper* calls of *magellanica* are higher in frequency than either kind of *Chipper* call of *paraguayiae* (2360 vs. 2000–2030 Hz, respectively).

The second type of ground call of *magellanica* (*Chipper*) is completely different from calls of *paraguayiae*, as it consists of alternating couplets that are repeated slowly and rhythmically. Within

each couplet, the sound elements differ from one another both acoustically and in the duration of the intervening silent intervals. One of the element types is higher in amplitude and frequency, is longer, and is usually followed by a longer silent interval (Figs 5 and 6; Tables 2 and 3). These different attributes of the rhythmically repeated couplets impart the disyllabic audile quality to *Chipper* calls.



**Figure 6.** The *Chipper* of breeding South American Snipe *Gallinago paraguaiiae magellanica* is characterized by rhythmically repeated couplets of sound elements, one of which is always longer than the other (a). Usually the interval following the long element also is longer than that following the brief element within each couplet (b). In contrast, the sound elements in the *Chip* calls of *G. p. magellanica* are uniform in duration and in the periods of silence that separate them (solid segments on lines of equality); the ranges of values for *Chip* Element Duration (a) and Inter-element Interval (b) are shown as solid segments on the line of equality. The 95% confidence ellipse is shown in each panel. The same shade of grey for *G. p. magellanica* is used in other graphs.

The longer and briefer of the two element types in *Chipper* calls average 63 and 48 ms in duration, respectively, longer than the *Chip* of this taxon or the *Slow Chip* or *Fast Chip* of *paraguaiiae* (Fig. 3; Tables 2 and 3). Brief elements of the *Chipper* average about 75% of the duration of long elements within individual birds (ratio mean = 0.74, sd = 0.143, range = 0.31–0.74,  $n = 44$ ). Intervals following brief elements are ~90% of the duration of intervals that follow long elements (ratio mean = 0.90, sd = 0.173, range = 0.62–1.59,  $n = 44$ ). Durations of long and brief elements, and intervals between them, are significantly related within individual birds ( $r = 0.76$ ,  $P < 0.001$ ,  $n = 44$ ; and 0.35,  $P < 0.02$ ,  $n = 44$ ).

In combination with the Inter-element Intervals, the repetition rate of *Chipper* elements is low (3.3 Hz). As for the *Chip* of *magellanica*, the Centre Frequency of *Chipper* is higher than in *paraguaiiae*: 2250–2270 Hz (Fig. 3; Tables 2 and 3).

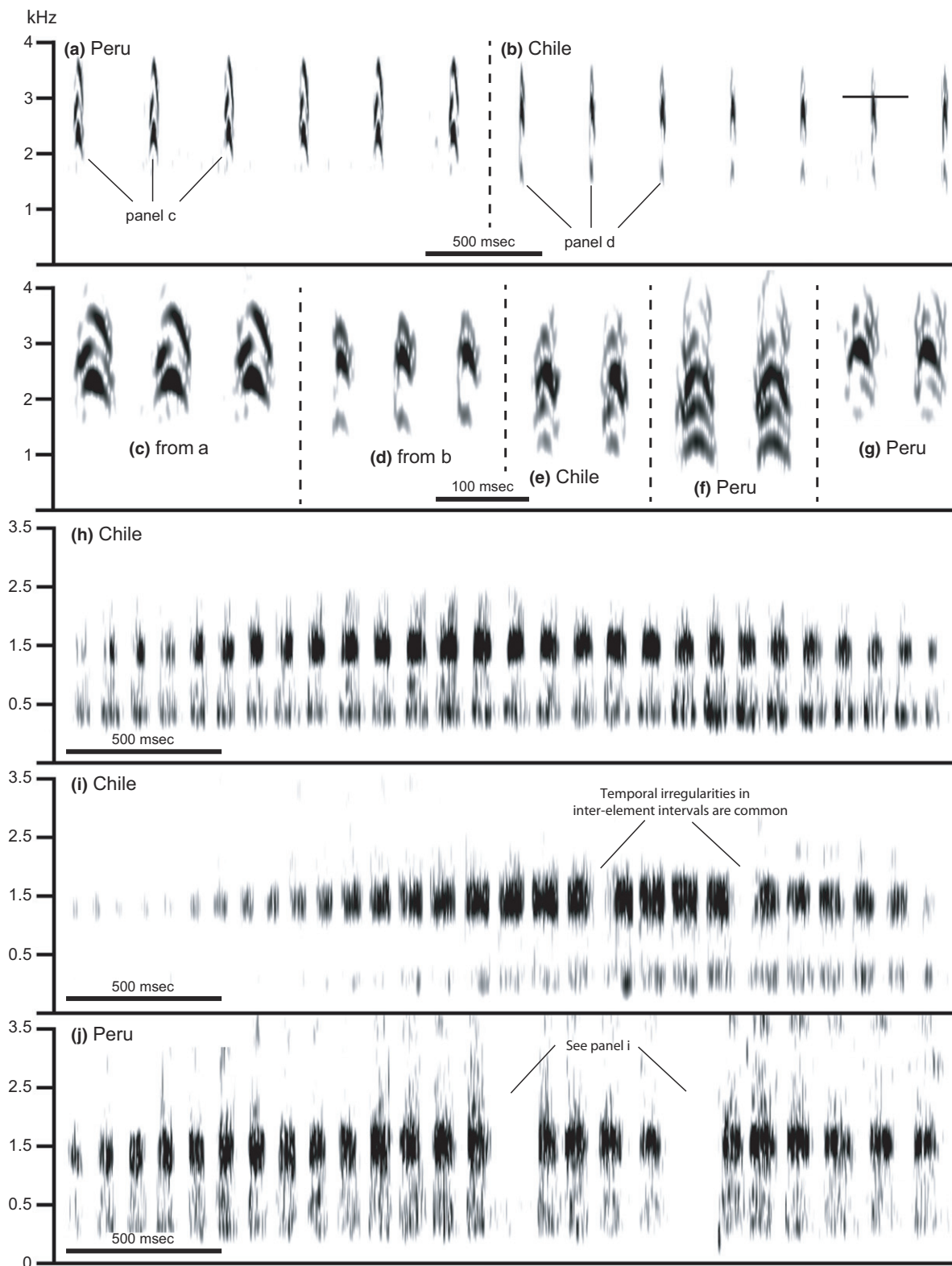
*Chip* and *Chipper* calls are given in similar aerial contexts (and upon landing) as for the *Chip* calls of *paraguaiiae* (see above).

Ground calls: *G. andina* – Only one kind of call (*Chip*) is present in recordings of this form (Fig. 7).

In most elements, the increase to and decrease from the peak frequency are approximately equal in duration; in contrast, the descending frequency portion is more prominent in sound elements of the *Chip* of *paraguaiiae* and *magellanica* (compare Figs 2, 4 and 7). In temporal variables, *andina* is closer to *paraguaiiae* than to *magellanica*, but the Centre Frequency of *andina* is the highest of all the taxa (2470 Hz; Fig. 3; Tables 2 and 3).

Ground calls: Summary – Homologies of ground calls across the three taxa are unknown, but some generalizations are possible based on the trends and statistical analyses (Tables 2 and 3). First, durations of and intervals between sound elements are longer in *magellanica* than in *paraguaiiae* or *andina*. Repetition Rate and Duty Cycle of sound elements are very high in the *Fast Chip* of *paraguaiiae*: 11 Hz and < 30%, respectively, vs. 3–5 Hz and 12–18% for other calls/taxa. Calls of *andina* are higher in frequency than calls of the other taxa. Finally, the single recording of a *Chip* call from the Atacama region resembles the *Chip* of *magellanica* (Fig. 8).

Flight Displays: General remarks – The ‘winnowing flight’ (Mueller 1999; also termed



**Figure 7.** The Puna Snipe *Gallinago andina* utters one kind of loud ground call during the breeding period, the *Chip*, which consists of a single type of sound element that is repeated rhythmically (a,b); it probably also has a second call type that has not been recorded (see text). The *Winnow* of this species is unlike that of *Gallinago paraguaiiae paraguaiiae* or *Gallinago paraguaiiae magellanica* in consisting of brief rhythmically repeated sound elements that increase gradually in duration and amplitude to the centre of or to near the end of the sound. Like the other taxa, sound elements decline in amplitude and duration at the end. Temporal irregularities in the rhythm of delivery of sound elements are present in several sound recordings (e.g. i,j); we did not measure inter-element intervals in such parts. Recording data: (a,c) (Macaulay Library 171896), Peru (11.5°S, 74.9°W), 3 October 2008, P. A. Hosner; (b,d) Chile (18.2°S, 69.3°W), 25 October 2010, J. I. Areta; (e) Chile (18.2°S, 69.3°W), 21 October 2006, E. H. Miller; (f) (British Library 25078 = Macaulay Library 240620 = xeno-canto 16199), Peru (15.0°S, 70.4°W), 18 December 1983, N. Krabbe; (g) (Macaulay Library 86903741), Peru (15.6°S, 71.6°W), 18 February 2018, P. E. A. Condo; (h) Chile (18.2°S, 69.3°W), 20 November 2011, E. H. Miller; (i) Chile (18.2°S, 69.3°W), 21 November 2011, J. I. Areta; (j) (xeno-canto 8502), Peru (7.0°S, 78.3°W), 3 October 2006, H. van Oosten.

'bleating' (Tuck 1972), 'drumming-flight' (Cramp 1983), etc.) is the main flight display of *paraguaiiae*, *magellanica* and *andina*, and is similar in form to that of *G. gallinago*, *G. delicata* and other snipe species (Tuck 1972, Reddig 1978, 1981, Cramp 1983). We had few visual observations of display flights of *andina* because we only recorded them in darkness, so the following is based primarily on data for the other two taxa.

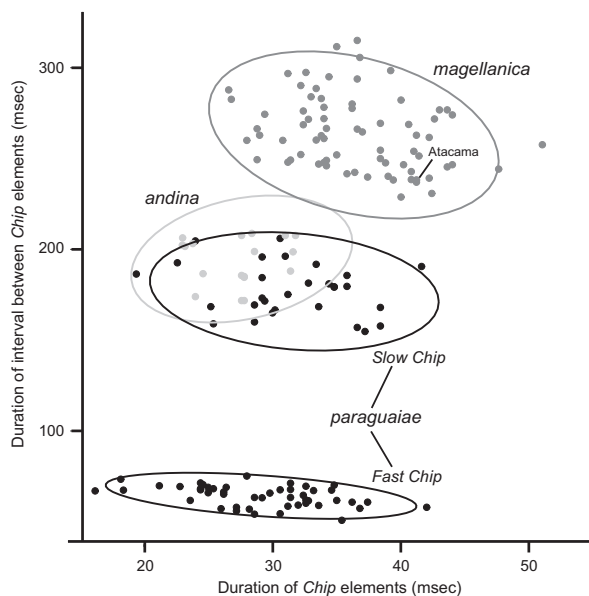
Displaying birds cover areas of up to several hundred metres in extent, interrupting otherwise

continuous flight with repeated dives when *Winnow* sounds are produced. Flight tracks sometimes are approximately repeated, or displaying birds reverse direction or slowly shift the area over which they display. Winnowing flights are highly contagious, and once we saw five birds (*magellanica*) lift and display concurrently over an area only a few hundred metres across, in response to a sixth bird that had started to display. In such circumstances, flight displays overlap both spatially and acoustically. Winnowing displays can be long (some > 1 h in duration in *magellanica*) and are punctuated by dives at roughly regular intervals unless the birds travel to another area or interact with other birds.

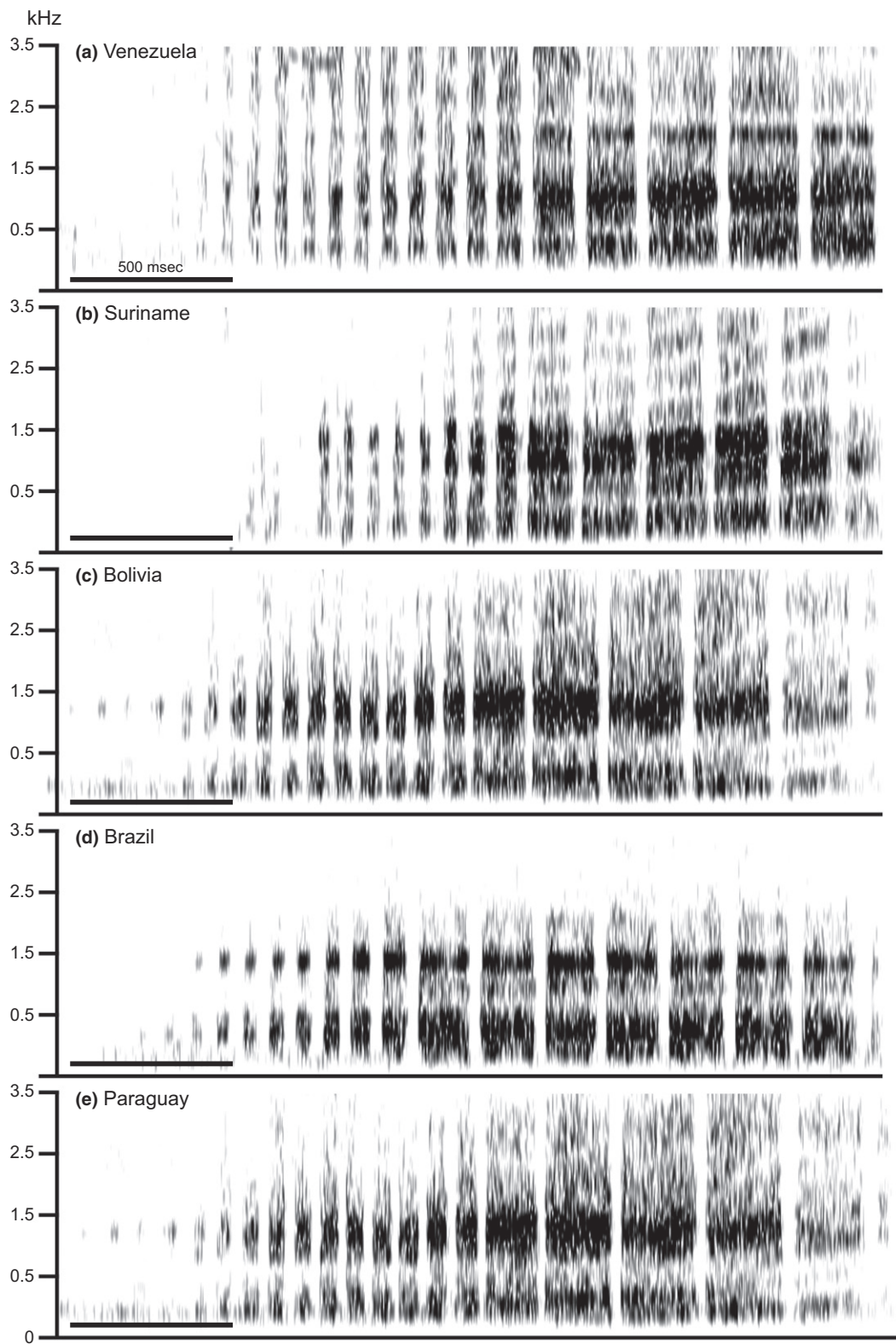
*Winnow: paraguaiiae* – The *Winnow* of *paraguaiiae* comprises a series of roughly constant-frequency broadband sounds that increase progressively in amplitude and duration (to a maximum of 170 ms on average) from the beginning to near the end of the *Winnow*; one to several brief low-amplitude sound elements terminate the *Winnow* (Fig. 9). Weak modulations in amplitude appear within long sound elements (e.g. Fig. 9d). Most energy in the high-amplitude penultimate sound elements is at ~ 1500 Hz (Fig. 10; Tables 4 and 5). *Winnows* of *paraguaiiae* are 2.6 s long, separated by intervals of 7.0 s, for a repetition rate of 6.5 Hz and duty cycle of 28% (Fig. 10; Tables 4 and 5).

The basic structure of the *Winnow* sounds is uniform over the distribution of *paraguaiiae*, from the northern coast of South America (Venezuela; Guyana; Suriname) south to Bolivia, Paraguay, southeastern Brazil, Uruguay and northeastern Argentina (Fig. 9).

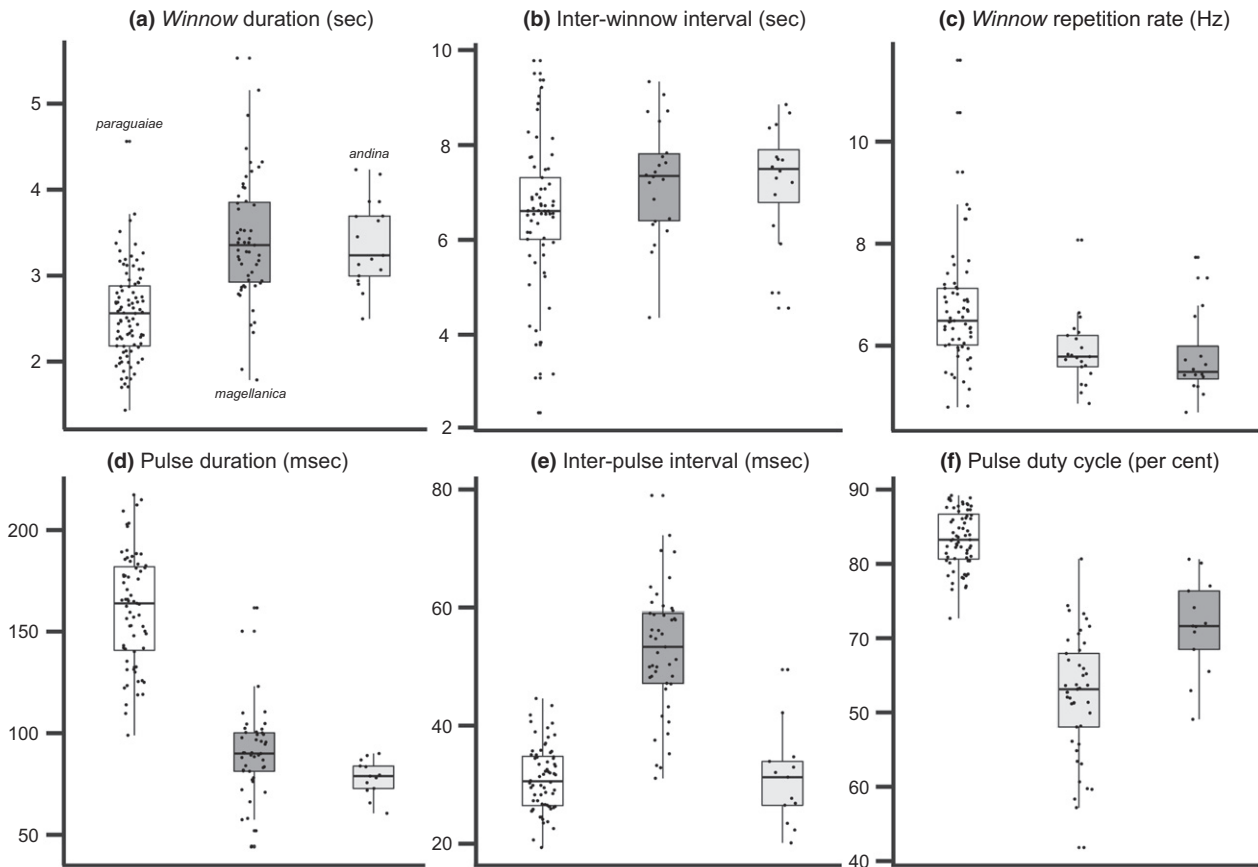
*Winnow: magellanica* – This differs greatly from the *Winnow* of *paraguaiiae*. In *magellanica* the *Winnow* is composed of repeated *n*-tuplets (usually couplets) of one longer and one to several



**Figure 8.** *Chip* calls of the South American Snipe *Gallinago paraguaiiae paraguaiiae* and *Gallinago paraguaiiae magellanica*, and Puna Snipe *Gallinago andina*, differ strongly even in two simple temporal measurements of sound elements: Element Duration and Inter-element Interval. A single recording of *Gallinago* from the Atacama region (marked) suggests that it can be attributed to *G. p. magellanica* (see text). The 95% confidence ellipses are shown. The same shades of grey for the taxa are used in other graphs.



**Figure 9.** The *Winnow* of the South American Snipe *Gallinago paraguaiiae paraguaiiae* consists of sound elements that increase gradually in duration and amplitude until near the end, when one to several soft, brief elements typically occur. Recording data: (a) (Macaulay Library 67992), Venezuela (9.6°N, 68.0°W), 26 August 1964, P. A. Schwartz; (b) Suriname (2.3°N, 54.6°W), 17 June 2017, K. Zyskowski; (c) (Macaulay Library 52421), Bolivia (13.8°S, 68.2°W), 3 June 1990, T. Parker; (d) (Macaulay Library 68409), Brazil (31.0°S, 51.5°W), 19 August 1993, D. W. Finch; (e) Paraguay (26.5°S 58.0°W), 11 November 2008, E. H. Miller.

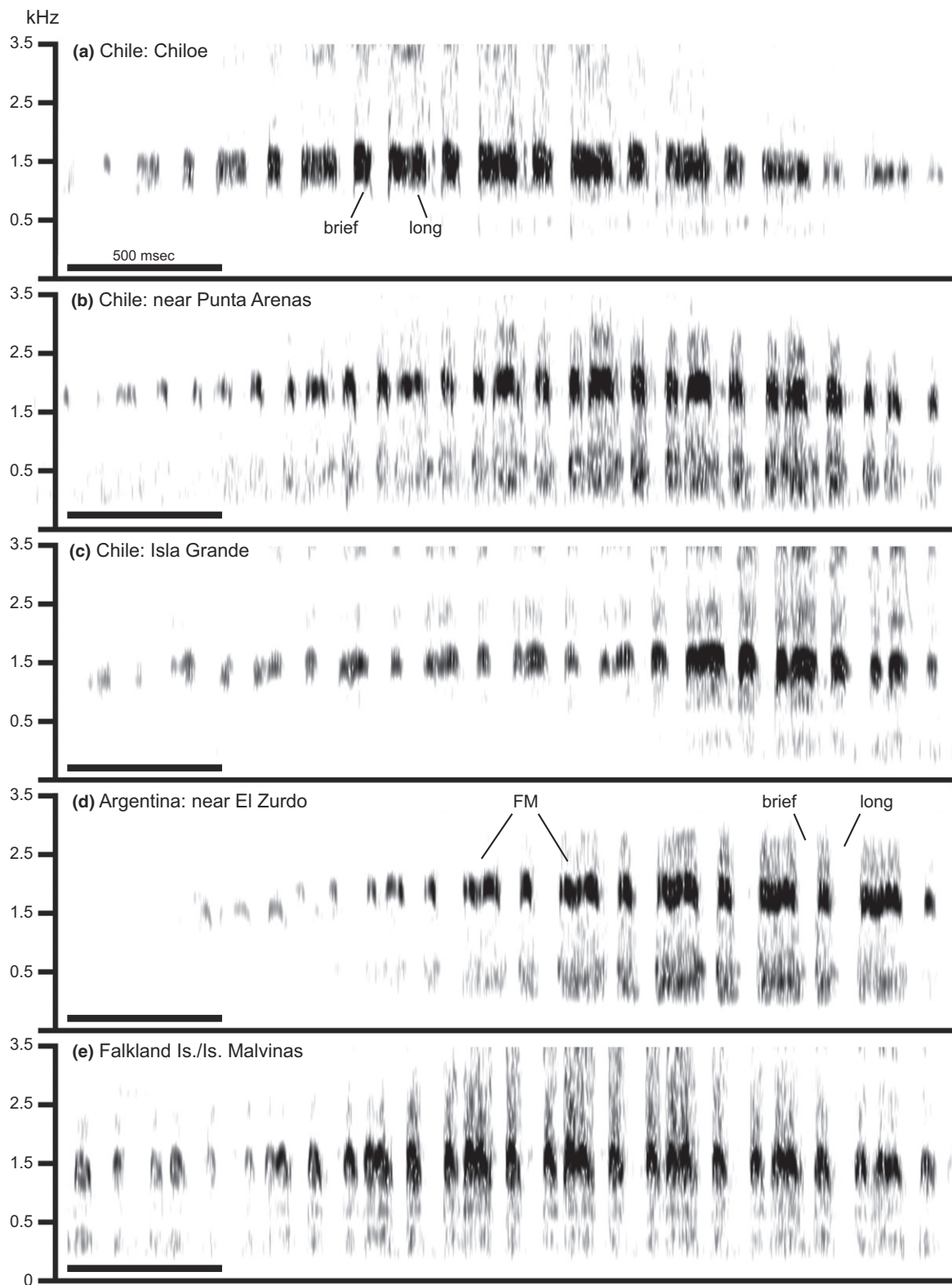


**Figure 10.** Graphical summary of trends in temporal characters measured on *Winnow* sounds of the South American Snipe *Gallinago paraguaiiae paraguaiiae* and *Gallinago paraguaiiae magellanica*, and Puna Snipe *Gallinago andina*. *Winnow* sounds and inter-*Winnow* intervals were on average briefest in *G. p. paraguaiiae* among the three taxa (a,b), so *Winnow* sounds were given at the highest rate (c; the duty cycle was similar across the taxa). Duration of pulses (as defined operationally; see Methods) was greatest in *G. p. paraguaiiae* (d), and the interval between pulses was brief (e), so the pulse duty cycle was very high (f; pulse-repetition rate across the taxa was ~ 5, ~7 and ~ 9, respectively). The inter-pulse interval in *Winnow* sounds was substantially higher in *G. p. magellanica* than in the other taxa (e). The top and bottom of each box on the boxplot mark the 75th and 25th percentiles, respectively, and the horizontal black line is at the 50th percentile. The top of the line extending above each box is at the largest value within 1.5 times the interquartile range above the 75th percentile; the bottom of the line extending above each box is at the smallest value within 1.5 times the interquartile range below the 25th percentile. The same shades of grey for the taxa are used in other graphs. On the non-independence of some comparisons, see Methods.

brief elements, separated by differing silent intervals; together these impart a stuttering quality to the sound (Fig. 11). Pronounced frequency and amplitude modulation occur in many elements, especially longer ones, and sometimes

points of low frequency/amplitude appear as silences in spectrograms (Fig. 11). As in *paraguaiiae*, *Winnow* sound elements of *magellanica* typically increase in amplitude and duration as the sound progresses, with one to several brief soft





**Figure 11.** The *Winnow* of the South American Snipe *Gallinago paraguaiiae magellanica* consists of sound elements that are briefer than in *Gallinago paraguaiiae paraguaiiae* and often appear as repeated couplets (e.g. c,d) or triplets (e.g. b,e) of elements that differ in duration; elements between sound elements also vary. The sound elements (especially longer ones) often show frequency modulation (d). As in *G. p. paraguaiiae*, and *G. andina*, elements increase gradually in duration and amplitude until near the end of the sound, when one to several soft, brief elements typically occur (all panels). Recording data: (a) Chile (41.9°S, 73.9°W), 2 September 2006, E. H. Miller; (b) Chile (53.0°S, 70.9°W), 22 October 2004, E. H. Miller; (c) Chile (52.7°S, 69.5°W), 7 November 2005, E. H. Miller; (d) (Internet Bird Collection 1127919), Argentina (52.0°S, 71.2°W), 2 November 2001, S. Imberti; (e) Falkland Is./I. Malvinas (51.3°S, 60.6°W), 10 November 1995, D. E. Kroodmsma.

terminal elements. Most energy in the high-amplitude penultimate sound elements is at 1800 kHz, about 300 Hz higher than in *paraguaiiae* (Tables 4 and 5). *Winnow* sounds of *magellanica* are 3.4 s long, separated by intervals of 8.9 s; thus the durations of both *Winnow* and Inter-winnow Interval are slightly longer than in *paraguaiiae*, resulting in a nearly identical Duty Cycle (27%; Fig. 10; Tables 4 and 5).

*Winnow* sounds vary across individuals of *magellanica*, as in *paraguaiiae*, but basic organization is uniform across the range, from north-central Chile south to southern Patagonia (Chile and Argentina), the Falklands/Malvinas, and north to Rio Negro, Argentina (Fig. 11).

*Winnow: andina* – At its simplest, the *Winnow* of *andina* consists of a rhythmic series of brief elements that increase gradually in duration to a maximum that is reached sometimes before the *Winnow* temporal midpoint and sometimes around or much later (Fig. 7). The silent intervals between sound elements sometimes are irregular in duration, causing audible breaks in rhythm (e.g. Fig. 7i,j).

The *Winnow* of this species differed strikingly from the other taxa in the brevity of its sound elements (only 75 ms; Tables 4 and 5), but resembles the *Winnow* of *paraguaiiae* more than that of *magellanica*.

*Winnow: Summary* – *Winnow* sounds differ greatly in temporal properties across the three taxa, most strikingly in the differentiation of long and short sound elements in *magellanica*. Among the three taxa studied, the non-vocal *Winnow* of *magellanica* stands out for its distinctive stuttering quality, which results from the presence of two or more kinds of sound elements that alternate and are repeated as sets. In addition, the sound elements in *magellanica* show pronounced (coupled) amplitude and frequency modulation. In the *Winnow* sounds of *paraguaiiae* and *andina*, sound elements simply exhibit sequential (successive) grading: they change gradually and successively in duration, frequency and amplitude over the sound and are not differentiated otherwise. Lastly, the sound elements of *paraguaiiae* and *andina* lack pronounced amplitude/frequency modulation.

**Table 5.** Summary of results of 1-way ANOVAs and post-hoc Tukey's honest significance tests on *Winnow* variables of South American Snipe (*Gallinago p. paraguaiiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*).

Variable	ANOVA results <i>P</i> , <i>F</i> , (df)	<i>P</i> – estimates from Tukey multiple comparison of means <sup>a</sup>		
		<i>paraguaiiae-magellanica</i>	<i>paraguaiiae-andina</i>	<i>magellanica-andina</i>
<i>Winnow</i> Duration	< 0.001, 39.8, (2, 161)	< 0.001	< 0.001	0.97
Inter-winnow Interval	0.07, 2.68, (2, 100)	0.12	0.24	0.99
<i>Winnow</i> Repetition Rate	< 0.001, 7.81, (2, 97)	0.007 <sup>c</sup>	0.007 <sup>c</sup>	~ 1
<i>Winnow</i> Duty Cycle	0.27, 1.34, (2, 96)	0.95	0.23	0.49
<i>Winnow</i> Centre Frequency	< 0.001, 15.9, (2, 131)	< 0.001	0.025 <sup>c</sup>	0.25
Element Duration	< 0.001, 140, (2, 122)	< 0.001	< 0.001	0.30
Inter-element Interval	< 0.001, 107, (2, 123)	< 0.001	~1	< 0.001
Element Duty Cycle	< 0.001, 166, (2, 123)	< 0.001	< 0.001	< 0.001

Descriptive statistics are summarized in Table 4. <sup>a</sup>Computed on means of individual birds with the R functions aov and TukeyHSD. <sup>b</sup>Tests within comparison groups are not all independent (see Methods). <sup>c</sup>These *P*-estimates are 0.03, 0.04, and < 0.05, respectively, after adjusting the false discovery rate for multiple comparisons, using the Benjamini–Hochberg procedure with a false discovery rate of 0.1, and *m* = 15 (for *Winnows*) or *m* = 9 (for *Winnow* elements) for the number of tests.

## DISCUSSION

We found substantial acoustic differences between the allopatric South American Snipe subspecies *paraguaiae* and *magellanica* in both vocal and non-vocal acoustic displays. The differences are both qualitative and quantitative, and differ sufficiently that one can identify the taxa unequivocally based on only brief recordings. Below we comment on the differences that we found, and conclude that *paraguaiae* and *magellanica* should be recognized as separate species. We also make recommendations for further research on snipe acoustic displays and systematics.

### Acoustic differences between *paraguaiae* and *magellanica*

Breeding *paraguaiae* and *magellanica* both utter two kinds of ground call, but these differ in many ways. The disyllabic *Chipper* call of *magellanica* is made up of rhythmically repeated sound couplets, each composed of two different kinds of sound elements; this kind of call is nearly universal in the *Gallinago/Coenocorypha* clade (Miller & Baker 2009, E. H. Miller & J. I. Areta unpubl. data), so we interpret the absence of a disyllabic call in *paraguaiae* as a derived condition.

It is not clear which type of *Chip* call of *paraguaiae* corresponds to the *Chipper* call of *magellanica*, but the *Slow Chip* was the less common call of *paraguaiae* in our samples (about 40%) and *Chipper* the less common of *magellanica* (about 35%), which may suggest that they are homologues. Behavioural studies of *paraguaiae* and *magellanica* that detail contextual uses of the call types would shed light on this matter. We found only one kind of ground call for *andina* (*Chip*), presumably because only a small number of recordings were available; it seems likely that this species also has a *Chipper* call. Parenthetically, Sick (1993) mentioned that *paraguaiae* in Brazil produces a disyllabic ground call. No other worker has reported this or recorded such a sound, to our knowledge.

As for vocalizations, *Winnow* sounds also differ quantitatively across the three taxa (e.g. sound elements are much longer in *paraguaiae* than in *andina*). In addition, the *Winnow* of *magellanica* differs qualitatively from both *paraguaiae* and *andina*. In the latter two taxa, sound elements exhibit simple successive grading in duration, amplitude

and frequency over the course of each *Winnow*. In contrast, sound elements in *Winnow* sounds of *magellanica* form repeated sets (usually couplets); the sound elements differ in duration, as do the silent intervals between sound elements. These characteristics impart a distinctive stuttering quality to the *Winnow* of *magellanica*.

In summary, acoustic displays of *paraguaiae* and *magellanica* differ in multiple quantitative and qualitative traits, over several structural scales (e.g. sound-element durations and the temporal pattern of organization of sound elements within *Winnow* sounds). In the absence of phylogenetic information, genetic differences or the potential for interbreeding, the decision about whether to recognize these allopatric taxa as separate species can only be based on observable traits such as display traits (Peterson 1998, Helbig *et al.* 2002, Sangster 2014, Collar *et al.* 2016). Indeed, even if genetic information were available, 'there is no fixed threshold of genetic divergence which can be used to determine whether two taxa are species or not' (Collar 2013: p. 139) and substantial phenotypic differences between species can be present with little to no genetic differentiation (Rheindt *et al.* 2011).

Multiple lines of evidence support recognition of *paraguaiae* and *magellanica* as separate species:

- 1 The three different kinds of long-distance breeding-season displays that we studied, all differ;
- 2 Some of the differing acoustic traits do not even overlap between *paraguaiae* and *magellanica*;
- 3 The acoustic structure of the displays is uniform throughout the geographical distribution of each form (West-Eberhard 1983, Wilkins *et al.* 2013);
- 4 Acoustic differences between *paraguaiae* and *magellanica* are substantial and much greater than those used to elevate another genetically little-differentiated pair of subspecies to species status (i.e. *G. gallinago* and *G. delicata*; Zink *et al.* 1995, Baker *et al.* 2009, Johnsen *et al.* 2010), and are also much greater than differences between *paraguaiae* and *andina*;
- 5 The three taxa differ in morphology of outer rectrices, which is related to sound production (see Introduction);
- 6 The displays are breeding-season displays that presumably have been shaped by sexual selection, and such displays commonly evolve

rapidly and differ substantially between closely related species (Andersson 1994, Coyne & Orr 2004, Price 2007).

East of the Andes, the Monte Desert separates the southern limit of the breeding range of *paraguaiae* and the northern limit of the breeding range of *magellanica*, as is the case with other taxa (Fig. 1; Domínguez *et al.* 2016). Without a time-dated molecular phylogeny or basic knowledge about whether *paraguaiae* and *magellanica* are even sister taxa, it is not possible to speculate about historical factors that led to or maintain this allopatric distribution.

### Recommendations for future research

It is easy to record and analyse snipe sounds, but there is a dearth of basic information about patterns, uses and meaning of the sounds: sexual, individual and contextual differences in sound structure; social functions; relation of displays to stage of the breeding cycle; and diel and seasonal patterns of display (e.g. do *Winnow* properties change over the season as rectrices become worn?; Miskelly 1987, Miskelly *et al.* 2006).

More audio recordings of snipe are needed to improve coverage of the geographical ranges of even well-known species. In the *paraguaiae*–*magellanica*–*andina* group, recordings are desirable from the possible northern range limit (Atacama) to central Chile for *magellanica*, and recordings are especially desirable for *Gallinago andina innotata*, a distinctively marked subspecies of *andina* known only from three specimens collected along Rio Loa (Antofagasta) in northern Chile in 1923 (Hellmayr 1932: pp. 389–390).

Acoustic differences in the *Winnow* between different species presumably are related to how the rectrices are spread and controlled to produce sound, the morphology of rectrices, and gross motor patterns used in dives. The use of outer rectrices in sound production by male snipe presumably led to longer rectrices in males, even though the male is the smaller sex (Tuck 1972, Glutz von Blotzheim *et al.* 1977, Cramp 1983, McCloskey & Thompson 2000, Ura *et al.* 2005, Włodarczyk *et al.* 2011). To elucidate this apparently allometric relationship comparatively, information on other snipe species is needed.

The greatest impediment to documenting evolutionary patterns in speciation and breeding

displays is the absence of a dated species-level phylogeny of extant species of *Gallinago* and *Coenocorypha*. Knowledge of evolutionary patterns in and relationships of tail morphology and size to phylogeny and social system likewise requires more information than exists on multiple topics, such as the anatomy of tail muscles, anatomical specializations of rectrices for sound production or to minimize damage from aerodynamic forces, and behaviour in dives.

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### Data Availability Statement

Some recordings of the authors have been deposited in sound archives (see Table S2). We contributed all others vocalizations that we analysed in this study to the Macaulay Library (<https://www.macaulaylibrary.org/>; ML); when catalogued, they can be found by filtering for the authors' names within each species.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** General plumage differences among South American Snipe (*Gallinago paraguayiae* and *Gallinago paraguayiae magellanica*) and Puna Snipe (*Gallinago andina*) are visible in these photographs

(see descriptions in text and Table S1): (A) Uruguay (A. Jaramillo); (B) Santa Cruz, Argentina (S. Imberti); and (C) Salta, Argentina (J. I. Areta).

**Table S1.** Original descriptions of *Gallinago paraguaiiae paraguaiiae*<sup>a</sup> and *Gallinago paraguaiiae magellanica*.<sup>b</sup>

**Table S2.** Summary of publicly accessible archived recordings of *Winnows* and ground calls of South American Snipe (*Gallinago paraguaiiae*

*paraguaiiae*, *Gallinago paraguaiiae magellanica*) and Puna Snipe (*Gallinago andina*) analysed in this study (recordings of only snipe calls upon and after being flushed, and in parental ‘alarm’, are excluded). Archives used were: AV, AVoCet<sup>a</sup>; BL, British Library<sup>b</sup>; FM, Florida Museum<sup>c</sup>; IBC, The Internet Bird Collection<sup>d</sup>; ML, Macaulay Library<sup>e</sup>; and XC, xeno-canto<sup>f</sup>. Some catalogue errors in taxonomic designation are noted in “Remarks”.