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

EDWARD H. MILLER,1* JUAN IGNACIO ARETA,2 ALVARO JARAMILLO,3 SANTIAGO IMBERTI4 & RICARDO MATUS5

1Biology Department, Memorial University, St. John’s, NL, A1B 3X9, Canada
2Laboratorio de Ecología, Comportamiento y Sonidos Naturales (ECOSON), Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO-CONICET), Rosario de Lerma (4405), Salta, Argentina
3San Francisco Bay Bird Observatory, 524 Valley Way, Milpitas, CA, 95035, USA
4Asociación Ambiente Sur, Carlos Gardel 389, Río Gallegos, Santa Cruz, Argentina
5Kilómetro 7 Sur, Parcela K, Punta Arenas, Chile

We analysed breeding sounds of the two subspecies of South American Snipe Gallinago paraguaiae paraguaiae and Gallinago paraguaiae 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. paraguaiae, 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. paraguaiae 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. paraguaiae 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. paraguaiae. Differences in breeding sounds of G. p. paraguaiae and G. p. magellanica are strong and hold throughout their geographical range. Therefore we suggest that the two taxa be considered different species: G. paraguaiae 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
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 paraguaiae.

Four South American snipe taxa in the G. paraguaiae group have had unstable nomenclatural histories. These forms were originally described as three species (Scolopax paraguaiae Vieillot 1816; Scolopax magellanicus King 1828; and Gallinago andina Taczanowski 1874) plus one subspecies of Gallinago paraguaiae (Capella paraguaiae 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. paraguaiae has been recognized, with subspecies paraguaiae, 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 paraguaiae 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 paraguaiae, 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 paraguaiae, 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 paraguaiae; 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 paraguaiae; the ground colour on the throat and breast of magellanica is reddish-buff, whereas that of paraguaiae is greyish or buffish-grey; the median stripes on the head are profusely flecked with brown in magellanica but mostly black in paraguaiae (Tuck 1972); and magellanica also possesses a less blackish dorsum due to the greater amount of buff markings than in

| Variable          | paraguaiae  | magellanica | andina    |
|-------------------|-------------|-------------|-----------|
| 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 these 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.
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). 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*).

| Element variable | paraguaiae | magellanica | andina |
|------------------|------------|-------------|--------|
|                   |            | Chip        | Long  | Short | Chip |
| Slow Chip Duration (ms) | 31.4 ± 5.18 (29) | 29.1 ± 5.36 (47) | 36.5 ± 5.00 (71) | 64.2 ± 13.83 (44) | 46.8 ± 12.24 (44) | 27.0 ± 2.93 (17) |
| Fast Chip Duration (ms)  | 19.42 | 16.42 | 27.51 | 34.101 | 26.68 | 23.32 |
| Inter-element Interval (ms) | 178 ± 14.3 (29) | 64.1 ± 5.61 (47) | 264 ± 20.2 (71) | 245 ± 43.9 (44) | 216 ± 31.8 (44) | 194 ± 13.4 (17) |
| Duty Cycle (%) | 15.1 ± 2.52 (29) | 31.1 ± 5.15 (47) | 12.2 ± 1.88 (71) | 18.3 ± 4.45 (41) | 12.3 ± 1.37 (17) |
| Repetition Rate (Hz) | 4.79 ± 0.320 (31) | 10.7 ± 0.68 (49) | 3.34 ± 0.205 (75) | 3.23 ± 0.596 (43) | 4.55 ± 0.327 (19) |
| Centre Frequency (Hz) | 2000 ± 324 (30) | 2110 ± 301 (39) | 2340 ± 280 (60) | 2247 ± 393 (38) | 2235 ± 403 (37) | 2468 ± 370 (13) |

Cell entries are grand means across means of individuals ± sd (n) and range. Statistical test results are presented in Table 3. aOne 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). bSee Methods.
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)/(ΣWinnow 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 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. paraguaiae, P; G. p. magellanica, M) and Puna Snipe (G. andina).

| Comparison of sound elements G. andina Chip and: | ANOVA results | P - estimates from Tukey multiple comparison of means<sup>a</sup> |
|-----------------------------------------------|---------------|---------------------------------------------------------------|
| P Fast Chip, M Chip:                          |               |                                                               |
| Duration                                      | < 0.001, 44.8, (2, 133) | < 0.001                                           |
| Inter-element interval                        | < 0.001, 2287, (2, 133) | < 0.001                                           |
| Centre Frequency                              | < 0.001, 15.3, (2, 109) | < 0.001                                           |
| Duty Cycle                                    | < 0.001, 487, (2, 133) | < 0.001                                           |
| Repetition Rate                                | < 0.001, 4366, (2, 141) | < 0.001                                           |
| P Fast Chip, M Chipper:                       |               |                                                               |
| Duration                                      | < 0.001, 155, (2, 106) | < 0.001                                           |
| Inter-element Interval                        | < 0.001, 770, (2, 105) | < 0.001                                           |
| Centre Frequency                              | < 0.001, 8.12, (2, 86) | 0.034<sup>c</sup>                                      |
| Duty Cycle                                    | < 0.001, 152, (2, 103) | < 0.001                                           |
| Repetition rate                                | < 0.001, 1980, (2, 109) | < 0.001                                           |
| P Slow Chip, M Chip:                          |               |                                                               |
| Duration                                      | < 0.001, 31.5, (2, 115) | < 0.001                                           |
| Inter-element Interval                        | < 0.001, 287, (2, 115) | < 0.001                                           |
| Centre Frequency                              | < 0.001, 14.4, (2, 89) | < 0.001                                           |
| Duty Cycle                                    | < 0.001, 22.6, (2, 115) | < 0.001                                           |
| Repetition rate                                | < 0.001, 3424, (2, 123) | < 0.001                                           |
| P Slow Chip, M Chipper:                       |               |                                                               |
| Duration                                      | < 0.001, 112, (2, 88) | < 0.001                                           |
| Inter-element Interval                        | < 0.001, 45.5, (2, 87) | < 0.001                                           |
| Centre Frequency                              | < 0.001, 7.82, (2, 76) | 0.032<sup>c</sup>                                      |
| Duty Cycle                                    | < 0.001, 20.4, (2, 85) | < 0.001                                           |
| Repetition rate                                | < 0.001, 114, (2, 91) | < 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.
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 *paraguaiae* 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) to prepare the spectrograms.

We screened each variable for normality of residuals, then conducted one-way ANOVAs (using the R function aov) 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: *paraguaiae* Fast Chip – *magellanica* Chip – *andina* Chip; *paraguaiae* 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 the false discovery rate for multiple comparisons, –

| Variable                  | paraguaiae | magellanica | andina  |
|---------------------------|------------|-------------|---------|
| Winnow Duration (sec)     | 2.54 ± 0.531 (92) | 3.39 ± 0.733 (55) | 3.33 ± 0.478 (19) |
| Inter-winnow Interval (sec)| 6.55 ± 1.536 (65) | 7.25 ± 1.21 (22) | 7.20 ± 1.260 (16) |
| Winnow Repetition Rate (per min) | 6.72 ± 1.229 (63) | 5.87 ± 0.687 (21) | 5.78 ± 0.856 (16) |
| Winnow Duty Cycle (%)     | 29.0 ± 7.66 (62) | 29.5 ± 5.99 (21) | 32.2 ± 5.25 (16) |
| Winnow Centre Frequency (Hz) | 1499 ± 206 (57) | 1784 ± 150 (47) | 1534 ± 96.8 (14) |
| Element Duration (msec)   | 161 ± 38.2 (67) | 89.6 ± 22.41 (45) | 76.2 ± 9.70 (15) |
| Element Maximal Duration (msec) | 195 ± 27.9 (69) | 160 ± 50.6 (45) | 89.4 ± 13.6 (15) |
| Inter-element Interval (msec) | 31.0 ± 5.58 (68) | 52.9 ± 10.72 (45) | 31.1 ± 7.80 (15) |
| Pulse Repeation Rate (Hz) | 5.31 ± 0.811 (67) | 7.20 ± 1.203 (45) | 9.40 ± 0.952 (15) |
| Pulse Duty Cycle (%)       | 83.4 ± 3.30 (68) | 62.1 ± 8.35 (42) | 71.0 ± 6.53 (15) |

Cell entries are grand means across individuals ± sd (no. birds) and range. Statistical test results are presented in Table 5. aSee Methods. bFor regular temporal parts of Winnows only; parts with irregular timing (e.g. Fig. 8I, J) were excluded for this measure.
Figure 2. The South American Snipe Gallinago paraguaiae paraguaiae 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.

© 2019 British Ornithologists’ Union
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

![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.

![Figure 3](image-url)
from the ground, slight prominence or elevation (e.g. fence post). The sounds are harmonically rich and, as in *paraguaiae*, the harmonic of highest amplitude is always above the fundamental (Figs 4 and 5). As in *paraguaiae*, 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 *paraguaiae* in also being composed of rhythmically repeated sound elements of a single kind (Fig. 4). Chip elements are longer in *magellanica* than in *paraguaiae* (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
elements are lower in magellanica than in paraguaiae (Fig. 3; Tables 2 and 3). Finally, Chip calls of magellanica are higher in frequency than either kind of Chip call of paraguaiae (2360 vs. 2000–2030 Hz, respectively).

The second type of ground call of magellanica (Chipper) is completely different from calls of paraguaiae, 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 audible quality to Chipper calls.

© 2019 British Ornithologists' Union
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 paraguaiae (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 paraguaiae: 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 paraguaiae (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 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 paraguaiae (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 paraguaiae: 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 paraguaiae (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 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.

© 2019 British Ornithologists’ Union

**Figure 6.** The Chipper of breeding South American Snipe Gallinago paraguaiae 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.

Species distinctiveness of snipe sounds 979
Temporal irregularities in inter-element intervals are common. See panel i.
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 paraguaiae paraguaiae or Gallinago paraguaiae 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 171886; (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 paraguaiae, 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: paraguaiae – The Winnow of paraguaiae 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 paraguaiae 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 paraguaiae, 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 paraguaiae. In magellanica the Winnow is composed of repeated n-tuplets (usually couplets) of one longer and one to several
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 paraguaiae, Winnow sound elements of magellanica typically increase in amplitude and duration as the sound progresses, with one to several brief soft
terminal elements. Most energy in the high-amplitude penultimate sound elements is at 1800 kHz, about 300 Hz higher than in *paraguaiae* (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 *paraguaiae*, resulting in a nearly identical Duty Cycle (27%; Fig. 10; Tables 4 and 5).

*Winnow* sounds vary across individuals of *magellanica*, as in *paraguaiae*, 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 *paraguaiae* 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 *paraguaiae* 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 *paraguaiae* 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. paraguaiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*).

| Variable                      | ANOVA results | *P* – estimates from Tukey multiple comparison of means<sup>a</sup> |
|-------------------------------|---------------|-----------------------------------------------------------------|
|                               |               | *paraguaiae-magellanica* | *paraguaiae-andina* | *magellanica-andina* |
| *Winnow* 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 |
| *Winnow* Repetition Rate      | < 0.001, 7.81, (2, 97) | 0.007<sup>bc</sup> | 0.007<sup>bc</sup> | ~ 1 |
| *Winnow* Duty Cycle           | 0.27, 1.34, (2, 96) | 0.95 | 0.23 | 0.49 |
| *Winnow* 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 |

<sup>a</sup>Descriptive statistics are summarized in Table 4. <sup>bc</sup>Computed on means of individual birds with the R functions aov and TukeyHSD. Tests within comparison groups: n = m independent (see Methods). 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.

© 2019 British Ornithologists’ Union
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.

We thank the following recordists for allowing us to use their original tape recordings: P. W. Boesman, R. Fraga, D. E. Kroodsma, I. Roessler, R. W. Woods and K. Zyskowski. We also acknowledge the many other recordists who have contributed snipe recordings to publicly accessible archives or as commercial recordings. E.H.M. thanks H. F. del Castillo for organizing and participating in the 2008 Paraguayan research. P.-P. Bitton, A. Hurford, R. W. Rogers, E. Salogni and D. R. Wilson advised on graphics and data analysis. Finally, we thank P.-P. Bitton for translating Vieillot (1816), and B. Levett for translating the Latin summary in King (1828).

**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/); when catalogued, they can be found by filtering for the authors’ names within each species.

**REFERENCES**

Alström, P. & Ranft, R. 2003. The use of sounds in avian systematics and the importance of bird sound archives. *Bull. Br. Orn. Club* 123A: 114–135.

Andersson, M. 1994. *Sexual Selection*. Princeton: Princeton University Press.

Araya-Salas, M., Smith-Vidaurre, G. & Webster, M. 2017. Assessing the effect of sound file compression and background noise on measures of acoustic signal structure. *Bioacoustics* 28: 57–73.

Bahr, P.H. 1907. On the ‘bleating’ or ‘drumming’ of the Snipe (Gallinago coelestis). Proc. Zool. Soc. Lond. 1907: 12–35.

Baker, A.J., Pereira, S.L. & Paton, T.A. 2007. Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. *Biol. Lett.* 3: 205–209.

Baker, A.J., Tavares, E.S. & Elbourne, R.F. 2009. Countering criticisms of single mitochondrial DNA gene barcoding in birds. *Mol. Ecol. Resour.* 9(Suppl. 1): 257–268.
Banks, R.C., Cicero, C., Dunn, J.L., Kratter, A.W., Rasmussen, P.C., Remsen, J.V., Jr., Rising, J.D. & Stotz, D.F. 2002. Forty-third supplement to the American Ornithologists’ Union Check-List of North American Birds. Auk 119: 897–906.

Bergmann, H.-H., Helb, H.-W. & Baumann, S. 2008. Die Stimmen der Vögel Europas. 474 Vogelporträts mit 914 Runden und Gesängen auf 2200 Sonogrammen. Wiesbaden: Aula-Verlag, GmbH.

Blake, E.R. 1977. Manual of Neotropical Birds: Speniscidae (Penguins) to Laridae (Gulls and Allies), Vol. 1. Chicago: University of Chicago Press.

Charif, R.A., Waack, A.M. & Strickman, L.M. 2010. Raven Pro 1.4 User’s Manual. Ithaca: Cornell Lab of Ornithology.

Cibois, A., Dekker, R.W.R.J., Pasquet, E. & Thibault, J.-C. 2012. New insights into the systematics of the enigmatic Polynesian Sandpipers Aechmorhynchus parvirostris and Prosobonia leucoptera. Ibis 154: 756–767.

Clark, C.J. 2014. Harmonic hopping, and both punctuated and gradual evolution of acoustic characters in Selasphorus hummingbird tail-feathers. PLoS One 9: e93829.

Clark, C.J., McGuire, J.A., Bonaccorso, E., Berv, J.S. & Prum, R.O. 2018. Complex coevolution of wing, tail, and vocal sounds of courting male bee hummingbirds. Evolution 72: 630–646.

Collar, N. 2013. The Bernard Tucker Memorial Lecture: a species is whatever I say it is. Br. Birds 106: 130–142.

Collar, N.J., Fishpool, L.D.C., del Hoyo, J., Pilgrim, J.D., Seddon, N., Spottiswoode, C.N. & Tobias, J.A. 2016. Toward a scoring system for species delimitation: a response to Remsen. J. Field Ornithol. 87: 104–115.

Connors, P.G., McCaffery, B.J. & Maron, J.L. 1993. Speciation in golden-plovers, Pluvialis dominica and P. fulva: evidence from the breeding grounds. Auk 110: 9–20.

Coyne, J.A. & Orr, H.A. 2004. Speciation. Sunderland: Sinauer.

Cramp, S. (ed.) 1983. Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Vol. 3: Waders to Gulls. Oxford: Oxford University Press.

Dominguez, M.C., Agrain, F.A., Flores, G.E. & Roig-Junent, S.A. 2016. Vicariance events shaping southern South American insect distributions. Zoolog. Scripta 45: 504–511.

Douglas, H.D. 1998. Response of Eastern Willets (Catoptrophorus s. semipalmatus) to vocalizations of Eastern and Western (C. s. inomatus) willets. Auk 115: 514–518.

Douglas, H.D. 1999. Is there a sound reception window in coastal environments? Evidence from shorebird communication systems. Naturwissenschaften 86: 228–230.

Feo, T.J., Musser, J.M., Berv, J. & Clark, C.J. 2015. Divergence in morphology, calls, song, mechanical sounds, and genetics supports species status for the Inaguan hummingbird (Trochilidae: Calliphlox ‘evelynae’ ‘lyrae’). Auk 132: 248–264.

Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. (eds) 1977. Handbuch der Vögel Mitteleuropas, Band 7: Charadriformes (2. Teil). Wiesbaden: Akademische Verlagsgesellschaft.

Hayman, P., Marchant, J. & Prater, T. 1986. Shorebirds. An Identification Guide to the Waders of the World. London: Croom Helm.

Helbig, A.J., Knox, A.G., Parkin, D.T., Sangster, G. & Collinson, M. 2002. Guidelines for assigning species rank. Ibis 144: 518–525.

Hellmayr, C.E. 1932. The birds of Chile. Field Museum of Natural History Publication 308, Zoological Series 19.

Hellmayr, C.E. & Conover, B. 1948. Catalogue of birds of the Americas and the adjacent islands in Field Museum of Natural History including all species and subspecies. Field Museum of Natural History, Zoological Series vol. 13, part 1, no: 3.

Jaramillo, A. 2003. Birds of Chile. Princeton: Princeton University Press.

Johnsen, A., Rindal, E., Ericson, P.G.P., Zuccon, D., Kerr, K.C.R., Stoeckle, M.Y. & Lifjeld, J.T. 2010. DNA barcoding of Scandinavian birds reveals divergent lineages in trans-Atlantic species. J. Ornithol. 151: 565–578.

Kennedy, R.S., Fisher, T.H., Harrap, S.C.B., Diesmos, A.C. & Manamantam, A.S. 2001. A new species of woodcock (Aves: Scolopacidae) from the Philippines and a re-evaluation of other Asian/Papuanasian woodcocks. Forktail 17: 1–12.

King, P.P. 1828. Extracts from a letter addressed by Capt. Phillip Parker King, R.N., F.R.S. and L.S., to N.A. Vigors, Esq., on the animals of the Straits of Magellan. Zool. J. 4: 91–105.

Knox, A.G., Collinson, J.M., Parkin, D.T., Sangster, G. & Svensson, L. 2008. Taxonomic recommendations for British birds: fifth report. Ibis 150: 833–835.

Köhler, J., Jansen, M., Rodríguez, A., Kok, P.J.R., Toledo, L.F., Emmrich, M., Graw, F., Haddad, C.F.B., Rodel, M.-O. & Vences, M. 2018. The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. Zootaxa 4251: 1–124.

Küpper, C., Augustin, J., Kosztolányi, A., Figuerola, J., Burke, T. & Székely, T. 2009. Kentish versus Snowy Plover: phenotypic and genetic analyses of Charadrius alexandrinus reveal divergence of Eurasian and American subspecies. Auk 126: 839–852.

Lanyon, W.E. 1969. Vocal characters and avian systematics. In Hinde, R.A. (ed.) Bird Vocalizations: Their Relation to Current Problems in Biology and Psychology: 291–310. Cambridge: Cambridge University Press.

McCloskey, J.T. & Thompson, J.E. 2000. Aging and sexing Common Snipe using discriminant analysis. J. Wildl. Manage. 64: 960–969.

McDonald, J.H. 2014. Handbook of Biological Statistics, Vol. 3. Baltimore: Sparky House.

Meinertzhagen, A.C. 1926. A review of the subfamily Scolopacinae. Part I. The snipes and semi-woodcocks. Ibis 68: 477–521.

Miles, M.C., Schuppe, E.R., Ligon, R.M. & Fuxjager, M.J. 2018. Macroevolutionary patterning of woodpecker drums reveals how sexual selection elaborates signals under constraint. Proc. R. Soc. B 285: 20172628.

Miller, E.H. 1996. Acoustic differentiation and speciation in shorebirds. In Kroodsma, D.E. & Miller, E.H. (eds) Ecology and Evolution of Acoustic Communication in Birds: 241–257. Ithaca: Cornell University Press.
Miller, E.H. & Baker, A.J. 2009. Antiquity of shorebird acoustic displays. Auk 126: 454–459.

Miskelly, C.M. 1987. The identity of the Hakawai. Notornis 34: 95–116.

Miskelly, C.M., Bell, E.A., Elliott, G.P. & Walker, K.J. 2006. ‘Hakawai’ aerial display by three populations of subantarctic snipe (genus Coenocorypha). Notornis 53: 375–381.

Mittermeier, J.C., Burner, R.C., Oliveros, C.H., Praviradiaga, D.M., Irham, M., Haryoko, T. & Moyle, R.G. 2014. Vocalisations and display behaviour of Javan woodcock Scolopax saturata support its status as a distinct species. Forktail 30: 130–131.

Mueller, H. (1999). Wilson’s Snipe (Gallinago delicata), version 2.0. In Poole, A.F. & Gill, F.B. (eds) The Birds of North America. Ithaca: Cornell Lab of Ornithology.

O’Brien, M., Crossley, R. & Karlson, K. 2006. The Shorebird Guide. Boston: Houghton Mifflin.

Oswald, J.A., Harvey, M.G., Remsen, R.C., Foxworth, D.U., Cardiff, S.W., Dittman, D.L., Megna, L.C., Carling, M.D. & Brumfield, R.T. 2016. Willet be one species or two? A genomic view of the evolutionary history of Tringa semipalmata. Auk 133: 593-614.

Paulson, D.R. 2006. Shorebirds of North America: The Photographic Guide. Princeton: Princeton University Press.

Payne, R.B. 1986. Bird songs and avian systematics. In Johnston, R.F. (ed.) Current Ornithology, 3 edn: 87–126. New York: Plenum.

Peterson, A.T. 1998. New species and species limits in birds. Auk 115: 555–558.

Pieplow, N. 2017. Peterson Field Guide to Bird Sounds of Eastern North America. Boston: Houghton Mifflin Harcourt.

Piersma, T. 1996. Family Scolopacidae (sandpipers, snipes and phalaropes). In del Hoyo, J., Elliott, A. & Sargatal, J. (eds) Handbook of the Birds of the World. Hoatzin to Auks, Vol. 3: 444–487. Barcelona: Lynx Edicions.

Price, T. 2007. Speciation in Birds. Greenwood Village: Roberts & Company.

Prum, R.O. 1990. Phylogenetic analysis of the evolution of display behavior in the Neotropical manakins (Aves: Pipridae). Ethology 84: 202-231.

Prum, R.O. 1998. Sexual selection and the evolution of mechanical sound production in manakins (Aves: Pipridae). Anim. Behav. 55: 977–994.

Reddig, E. 1978. Der Ausdrucksflug der Bekassine (Capella gallinago gallinago). J. Ornithol. 119: 357–387.

Reddig, E. 1981. Die Bekassine Capella gallinago. Wittenberg Lutherstadt: Die Neue Brehm-Bucherei, A. Ziemsen Verlag.

Remsen, J.V., Jr, Areta, J.I., Cadena, C.D., Claramunt, S., Jaramillo, A., Pacheco, J.F., Robbins, M.B., Stiles, F.G., Stotz, D.F. & Zimmer, K.J. 2019. A classification of the bird species of South America. American Ornithologists’ Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm (accessed 15 March 2019).

Rheindt, F.E., Szekely, T., Edwards, S.V., Lee, P.L.M., Burke, T., Kennerley, P.R., Bakewell, D.N., Atrashidi, M., Kosztolanyi, A., Weston, M.A., Liu, W.T., Lei, W.-P., Shigeta, Y., Javed, S., Zefania, S. & Kupper, C. 2011. Conflict between genetic and phenotypic differentiation: the evolutionary history of a ‘lost and rediscovered’ shorebird. PLoS One 6: e26995.

Sangster, G. 2014. The application of species criteria in avian taxonomy and its implications for the debate over species concepts. Biol. Rev. 89: 199–214.

de Schauensee, R.M. 1966. The Species of Birds of South America and Their Distribution. Narberth: Livingston.

Short, L.L. 1972. Systematics and behavior of South American flickers (Aves, Colaptes). Bull. Am. Mus. Nat. Hist. 149: 1–110.

Sibley, C.G. & Monroe, B.L., Jr 1990. Distribution and Taxonomy of Birds of the World. New Haven: Yale University Press.

Sick, H. 1993. Birds in Brazil: A Natural History. Princeton: Princeton University Press.

Sutton, G.M. 1981. On aerial and ground displays of the World’s snipes. Wilson Bull. 93: 457–477.

Thoen, W. 1969. Auffallender Unterschied zwischen den instrumentalen Balzlauten der europäischen und nordamerikanischen Bekassine Gallinago gallinago. Der Ornithol. Beob. 66: 6–13.

Tuck, L.M. 1972. The Snipes: A Study of the Genus Capella. Monograph Series No. 5. Ottawa: Canadian Wildlife Service.

Ura, T., Azuma, N., Hayama, S. & Higashi, S. 2005. Sexual dimorphism of Latham’s Snipe (Gallinago hardwickii). Emu 105: 259–262.

Vieillot, L.J.P. 1816. Dictionnaire d’Histoire Naturelle, appliqué aux Arts, à l’Agriculture, à l’Economie rurale et domestique, à la Médecin, etc, 3 edn: Paris: Chez Deterville.

West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. Q. Rev. Biol. 58: 155–183.

Wilkins, M.R., Seddon, N. & Safran, R.J. 2013. Evolutionary divergence in acoustic signals: causes and consequences. Trends Ecol. Evol. 28: 156–166.

Winkler, H. & Short, L.L. 1978. A comparative analysis of acoustical signals in pied woodpeckers (Aves, Picoides). Bull. Am. Mus. Nat. Hist. 160: art.1.

Wodarczyc, R., Minias, P., Gogga, P., Kaczmarek, K., Remisiewicz, M. & Janiszewski, T. 2011. Sexing Common Snipe Gallinago gallinago in the field using biometric criteria. Wader Study Group Bull. 118: 10–13.

Zink, R.M., Rohwer, S., Andreev, A.V. & Dittmann, D.L. 1995. Trans-Beringia comparisons of mitochondrial DNA differentiation in birds. Condor 97: 639–649.

Received 23 March 2019; Revision 6 June 2019; revision accepted 17 October 2019. Associate Editor: Frank Rheindt.

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 paraguaiae and Gallinago paraguaiae 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 paraguaiae paraguaiae* and *Gallinago paraguaiae magellanica*.

Table S2. Summary of publicly accessible archived recordings of *Winnows* and ground calls of South American Snipe (*Gallinago paraguaiae paraguaiae, Gallinago paraguaiae 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, AVoCeta; BL, British Library; FM, Florida Museum; IBC, The Internet Bird Collection; ML, Macaulay Library; and XC, xeno-canto. Some catalogue errors in taxonomic designation are noted in “Remarks”.

© 2019 British Ornithologists' Union