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Article type : Original Paper

Running head: SPECIES DISTINCTIVENESS OF SNIPE SOUNDS

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

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as [doi: 10.1111/IBI.12795](https://doi.org/10.1111/IBI.12795)

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Accepted Article

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We analyzed breeding sounds of the two subspecies of South American Snipe *Gallinago p. paraguayiae* and *G. p. magellanica* to determine whether they may 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 *paraguayiae*, the calls are bouts of identical sound elements repeated rhythmically and slowly (about 5 elements per sec [Hz]) or rapidly (about 11 Hz). One call of *magellanica* is qualitatively similar to those of *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 *paraguayiae* is a series of sound elements that gradually increase in duration and energy; that of *magellanica* has two+ kinds of sound element that roughly alternate and are repeated as sets, imparting a stuttering quality. Sounds of the related Puna Snipe (*G. andina*) resemble but differ quantitatively from those of *paraguayiae*. Differences in breeding sounds of *G. p. paraguayiae* and *G. p. magellanica* are strong and hold throughout their geographic range. Therefore we suggest that the two taxa be considered as 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*, geographic 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 *G. 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 analyzed breeding displays of the two allopatric subspecies of the South American Snipe *G. 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; *S. magellanicus* King 1828; and *Gallinago andina* Taczanowski 1874) plus one subspecies of *G. 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 *G. 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 and 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*; the outer rectrix of *andina* is short and wide (Table 1).

TABLE 1 NEAR HERE

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 *paraguaiae* (Hellmayr 1932; supplementary material S1). Plumage of *andina* resembles that of *magellanica* more than *paraguaiae* (Hellmayr 1932, Tuck 1972; S1). The original descriptions of *paraguaiae* by Vieillot (1816) and *magellanica* by King (1828), with English translations, are provided in S2.

Acoustic differences among *paraguaiae*, *magellanica*, and *andina* also have been noted (Blake 1977, Hayman *et al.* 1986, Jaramillo 2003). Piersma (1996: 496) mused that *G. p. magellanica* “may be close to separate species status”, and Jaramillo (2003: 227) commented that the non-vocal *Winnow* sound 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 *Winnow* sound 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 analyzed 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 geographic 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 geographic coverage; sources of recordings

We analyzed our own audio recordings, those of several individual recordists (see Acknowledgments), and recordings in sound archives (S3). We screened nearly 1300 recordings: *paraguaiae* 625; *magellanica* 560; and *andina* 80. We obtained samples of ground calls or *Winnows* from 11 countries: *paraguaiae* 10; *magellanica* three; and *andina* three (Fig. 1; S3). For recordings duplicated across collections (see S3), 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 Tables 2-5.

FIGURE 1 NEAR HERE

We lacked recordings of *paraguaiae* from three countries within the known breeding distribution (Colombia, Ecuador, 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 xeno-canto (XC) 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, which are 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). 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 analyzed only those calls that were recorded from birds on the ground.

Descriptions, measurements and analyses

Descriptions and measurements on 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 one second 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: (a) five successive elements in *Chip* calls, plus the five Inter-element Intervals (variable names are in title case and are given in Tables 2-5) that preceded those call elements, and computed mean values for each individual bird; and (b) 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 Center Frequency: “The frequency that divides the selection into two frequency intervals of equal energy” (Charif *et al.* 2010: 171). Based on trial and error, to measure

Center 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 Center 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 midpoint). We selected high-amplitude call elements from long series or near the middle of bouts. Measures on Center Frequency varied substantially, presumably due mainly to variation in recording distance, background noise, 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: $DC = 100(\textit{Winnow} \textit{ duration}/(\textit{Winnow} \textit{ duration} + \textit{Inter-winnow} \textit{ Interval}))$; and $RR = (\textit{number of Winnows}/(\sum \textit{Winnow} \textit{ durations} + \sum \textit{durations of Inter-winnow} \textit{ Intervals that followed those Winnows}))$.

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 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 spectrograms in Figs. 2, 4, 5, 7, 9, and 11.

We screened each variable for normality of residuals, then conducted one-way ANOVAs (using 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: *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, 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 analyzed *Winnow* variables as for calls. As for calls, not all tests were independent. Only *Winnow Duration* and *Inter-winnow Interval* were significantly (but moderately) negatively correlated in each species.

RESULTS

Ground calls: *paraguaiiae* — Loud calls, comprising rhythmically repeated elements, were uttered in a 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 & 3). Element Duration is similar between the two call types (about 30 msec; figures given in the text are approximate), but intervals between successive elements average 2.8 times as long in *Slow Chips* (180 vs. 65 msec) 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 & 3).

FIGURES 2 & 3 NEAR HERE

TABLES 2 & 3 NEAR HERE

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 *paraguaiiae*, two kinds of call occur, which comprise either rhythmically repeated sound elements or repeated couplets, uttered in bouts or long series 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 & 5). As in *paraguaiiae*, acoustic structure varies substantially among birds, but within birds is uniform and similar between call types (Figs. 4 & 5).

FIGURES 4 & 5 NEAR HERE

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 msec) and are separated by silent intervals of more than a quarter of a second in *magellanica*; therefore both the Duty Cycle and Repetition Rate of sound elements are lower in *magellanica* than in *paraguaiiae* (Fig. 3; Tables 2 & 3). Finally, *Chip* calls of *magellanica* are higher in frequency than either kind of *Chip* call of *paraguaiiae* (2360 vs. 2000-2030 Hz, respectively).

The second type of ground call of *magellanica* (*Chipper*) is completely different from calls of *paraguaiiae*, 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 usually is followed by a longer silent interval (Figs. 5 & 6; Tables 2 & 3). These different attributes of the rhythmically repeated couplets impart the disyllabic audile quality to *Chipper* calls.

FIGURE 6 NEAR HERE

The longer and briefer of the two element types in *Chipper* calls average 63 and 48 msec in duration, respectively, longer than the *Chip* of this taxon or the *Slow Chip* or *Fast Chip* of *paraguaiae* (Fig. 3; Tables 2 & 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 ($r = 0.7567$, $P < 0.001$, $n = 44$; 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 Center Frequency of *Chipper* is higher than in *paraguaiae*: 2250-2270 Hz (Fig. 3; Tables 2 & 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 contrast, the descending-frequency portion is more prominent in sound elements of the *Chip* of *paraguaiae* and *magellanica* (compare Figs. 2, 4, & 7). In temporal variables, *G. andina* is closer to *paraguaiae* than to *magellanica*, but the Center Frequency of *andina* is the highest of all the taxa (2470 Hz; Fig. 3; Tables 2 & 3).

FIGURE 7 NEAR HERE

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 & 3). First, durations of and intervals between sound elements are longer in *magellanica* than in *paraguaiae* or *andina*. Repetition Rate and Duty Cycle of sound elements are very high in the *Fast Chip* of

paraguaiae: 11 Hz and < 30%, respectively, vs. 3-5 Hz and 12-18% for other calls/taxa. Calls of *magellanica* 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).

FIGURE 8 NEAR HERE

Flight Displays: General remarks — The “winnowing flight” (Mueller 1999; also termed “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 meters 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 hr 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 msec 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 & 5). Winnows of *paraguaiae* are 2.6 sec long, separated by intervals of 7.0 sec, for a repetition rate of 6.5 Hz and duty cycle of 28% (Fig. 10; Tables 4 & 5).

FIGURES 9 & 10 NEAR HERE

TABLES 4 & 5 NEAR HERE

The basic structure of *Winnows* 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 briefer 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 & 5). *Winnows* of *magellanica* are 3.4 sec long, separated by intervals of 8.9 sec; 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 & 5).

FIGURE 11 NEAR HERE

Winnows 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*'s temporal midpoint, or sometimes around or much later than at that point (Fig. 7). The silent intervals between sound elements sometimes are irregular in duration, causing audible breaks in rhythm (e.g. Fig. 7 I & J).

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

Winnow: Summary — *Winnows* 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 element that alternate and are repeated as sets. In addition, the sound elements in *magellanica* show pronounced (coupled) amplitude and frequency modulation. In the *Winnows* 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.

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 (EHM & JIA 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, *Winnows* 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 *Winnows* 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 *Winnows*). 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 be based only on observable traits like display traits (Peterson 1998, Helbig *et al.* 2002, Sangster 2014, Collar *et al.* 2016). Indeed, even if genetic information was available, “there is no fixed threshold of genetic divergence which can be used to determine whether two taxa are species or not” (Collar 2013: 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: (a) the three different kinds of long-distance breeding-season displays that we studied all differ; (b) some of the differing acoustic traits do not even overlap between *paraguaiae* and *magellanica*; (c) the acoustic structure of the displays is uniform throughout the geographic distribution of each form (West-Eberhard 1983, Wilkins *et al.* 2013); (d) 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 much greater also than differences between *paraguaiae* and *andina*; (e) the three taxa differ in morphology of outer rectrices, which is related to sound production (see Introduction); and (f) 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 analyze 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; relationship 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 geographic 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 *G. a. innotata*, a distinctively marked subspecies of *andina* known only from three specimens collected along Rio Loa (Antofagasta) in northern Chile in 1923 (Hellmayr 1932: 389-390).

Acoustic differences in the *Winnow* between different species presumably are related to how the rectrices are spread and controlled to produce sound, 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 and 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 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. Roesler, 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. EHM 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 Statement

Some recordings of the authors have been deposited in sound archives (see S3). We contributed all others vocalizations that we analyzed 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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TABLE 1. Descriptive statistics on body size in South American Snipe (*Gallinago p. paraguayiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*). Data are shown as mean \pm sd (n) (from Tuck 1972: 86).

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

TABLE 2. Descriptive statistics on ground vocalizations of South American Snipe (*Gallinago p. paraguaiiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*)^a. Cell entries are grand means across means of individuals \pm sd (n) range. Statistical test results are in Table 3.

Element Variable ^b	<i>paraguaiiae</i>		<i>magellanica</i>			<i>andina</i>
	Slow Chip	Fast Chip	Chip	Chipper element		Chip
				Long	Short	
Duration (ms)	31.4 \pm 5.18 (29) 19-42	29.1 \pm 5.36 (47) 16-42	36.5 \pm 5.00 (71) 27-51	64.2 \pm 13.83 (44) 34-101	46.8 \pm 12.24 (44) 26-68	27.0 \pm 2.93 (17) 23-32
Inter-element Interval (ms)	178 \pm 14.3 (29) 155-206	64.1 \pm 5.61 (47) 51-75	264 \pm 20.2 (71) 229-315	245 \pm 43.9 (44) 165-339	216 \pm 31.8 (44) 152-288	194 \pm 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	
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	
Center Frequency (Hz)	2000 ± 324 (30) 1292-2672	2110 ± 301 (39) 1500-2498	2340 ± 280 (60) 1547-2842	2247 ± 393 (38) 1464-2885	2235 ± 403 (37) 1421-2928	2468 ± 370 (13) 1680-2885

^a One unidentified bird whose *Chip* was recorded in the Atacama Desert had means (for n = 5 calls) on the variables Element Duration to Center Frequency, respectively, of: 41.2 ± 3.19 (sd) msec, 238 ± 2.28 msec, 14.7%, 3.58 Hz, and 1981 Hz (Figs. 1, 3).

^b 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*, A). Descriptive statistics are summarized in Table 2.

Comparison of sound elements	ANOVA results	<i>P</i> - estimates from Tukey multiple comparison of means ^{a, b}		
		<i>paraguaiiae-magellanica</i>	<i>paraguaiiae-andina</i>	<i>magellanica-andina</i>
<i>G. andina</i> Chip and:	<i>P, F, (df)</i>			
<i>P Fast Chip, M Chip:</i>				
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
Center 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
Center Frequency	< 0.001, 8.12, (2, 86)	0.034 ^c	< 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 ^c	< 0.001
Inter-element Interval	< 0.001, 287, (2, 115)	< 0.001	0.009 ^c	< 0.001
Center 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 ^c	< 0.001
<i>P Slow Chip, M Chipper:</i>				
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
Center Frequency	< 0.001, 7.82, (2, 76)	0.032 ^c	< 0.001	0.13
Duty Cycle	< 0.001, 20.4, (2, 85)	< 0.001	0.026 ^c	< 0.001
Repetition rate	< 0.001, 114, (2, 91)	< 0.001	0.16	< 0.001

^a Computed on means of individual birds with R functions aov and TukeyHSD.

^b Tests within comparison groups are not all independent (see Methods).

^c 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.

TABLE 4. Descriptive statistics on *Winnows* of South American Snipe (*Gallinago p. paraguaiiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*). Cell entries are grand means across individuals \pm sd (n (birds)) range. Statistical test results are in Table 5.

Variable ^a	<i>G. p. paraguaiiae</i>	<i>G. p. magellanica</i>	<i>G. andina</i>
<i>Winnow</i> Duration (sec)	2.54 \pm 0.531 (92) 1.4-4.5	3.39 \pm 0.733 (55) 1.8-5.5	3.33 \pm 0.478 (19) 2.8-4.2
Inter- <i>winnow</i> Interval (sec)	6.55 \pm 1.536 (65) 2.3-9.8	7.25 \pm 1.21 (22) 4.3-9.3	7.20 \pm 1.260 (16) 4.5-8.8
<i>Winnow</i> Repetition Rate (per min)	6.72 \pm 1.229 (63) 4.8-12	5.87 \pm 0.687 (21) 4.8-8.1	5.78 \pm 0.856 (16) 4.7-7.7
<i>Winnow</i> Duty Cycle (%)	29.0 \pm 7.66 (62) 16-55	29.5 \pm 5.99 (21) 18-42	32.2 \pm 5.25 (16) 23-45
<i>Winnow</i> Center Frequency (Hz)	1499 \pm 206 (57) 1163-2282	1784 \pm 150 (47) 1464-2067	1534 \pm 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) ^b	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

^a See Methods.

^b For regular temporal parts of *Winnows* only; parts with irregular timing (e.g. Fig. 8I, J) were excluded for this measure.

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. paraguayiae*, *G. p. magellanica*) and Puna Snipe (*G. andina*). Descriptive statistics are summarized in Table 4.

Variable	ANOVA results	<i>P</i> – estimates from Tukey multiple comparison of means ^{a, b}		
	<i>P</i> , <i>F</i> , (df)	<i>paraguayiae-magellanica</i>	<i>paraguayiae-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 ^c	0.007 ^d	~ 1
<i>Winnow</i> Duty Cycle	0.27, 1.34, (2, 96)	0.95	0.23	0.49
<i>Winnow</i> Center Frequency	< 0.001, 15.9, (2, 131)	< 0.001	0.025 ^e	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

^a Computed on means of individual birds with R functions aov and TukeyHSD.

^b Tests within comparison groups are not all independent (see Methods).

^{c, d, e} 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.

FIGURE 1. Geographic distribution of samples of ground calls (A) and *Winnows* (B) of South American Snipe (*Gallinago p. paraguaiae* and *G. p. magellanica*) and Puna Snipe (*G. andina*) used in the study. One sample of calls from the Atacama region is also shown in panel A (see text). The Monte Desert of Argentina separates the distributions of *Gallinago p. paraguaiae* and *G. p. magellanica* in Argentina. Map prepared by D. J. Mercer, Map Room, Memorial University of Newfoundland.

FIGURE 2. The South American Snipe *Gallinago p. 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. Panel A: *Slow Chip* followed immediately by *Fast Chip*, illustrating that no intermediates occur in the transition between the two call types. Recording data: A, B, and 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, (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 within ground calls of the South American Snipe *Gallinago p. paraguaiae* and *G. p. magellanica*, and Puna Snipe *G. andina*. *Chipper* sound elements and the intervals between sound elements in both *Chip* and *Chipper* are notably longer in *magellanica* than in the other taxa (panels A, B), and *magellanica*'s calls are uttered more slowly (panel C). The duty cycle also is higher in *magellanica*, especially in the *Chipper* (panel 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 4. The South American Snipe *Gallinago p. 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 panels B-I; the natural intervals between them are reduced for graphical purposes. 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, EHM; 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.

FIGURE 5. A second type of loud ground call given by breeding South American Snipe *Gallinago p. 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 panels 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 (XC19484), 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.

FIGURE 6. The *Chipper* of breeding South American Snipe *Gallinago p. magellanica* is characterized by rhythmically repeated couplets of sound elements, one of which is always longer than the other (panel A). Usually the interval following the long element also is longer than that following the brief element within each couplet (panel B). In contrast, the sound elements in the *Chip* calls of *magellanica* are uniform in duration and in the periods of silence that separate them; the ranges of values for *Chip* Element Duration (panel A) and Inter-

element Interval (panel 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 *magellanica* is used in other graphs.

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 (panels 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 *G. p. paraguayiae* or *G. p. magellanica*, in consisting of brief rhythmically repeated sound elements that increase gradually in duration and amplitude to the center 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. panels I, J); we did not measure inter-element intervals in such parts. Recording data: A and C (Macaulay Library 171896), Peru (11.5 S 74.9 W), 3 October 2008, P. A. Hosner; B and 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; 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.

FIGURE 8. *Chip* calls of the South American Snipe *Gallinago p. paraguayiae* and *G. p. 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 *magellanica* (see text). 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 p. paraguayiae* 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 S), 26 August 1964, P. A. Schwartz; B, Suriname (2.3 N 54.6 W), 17 June 2017, K. Zyskowski; C

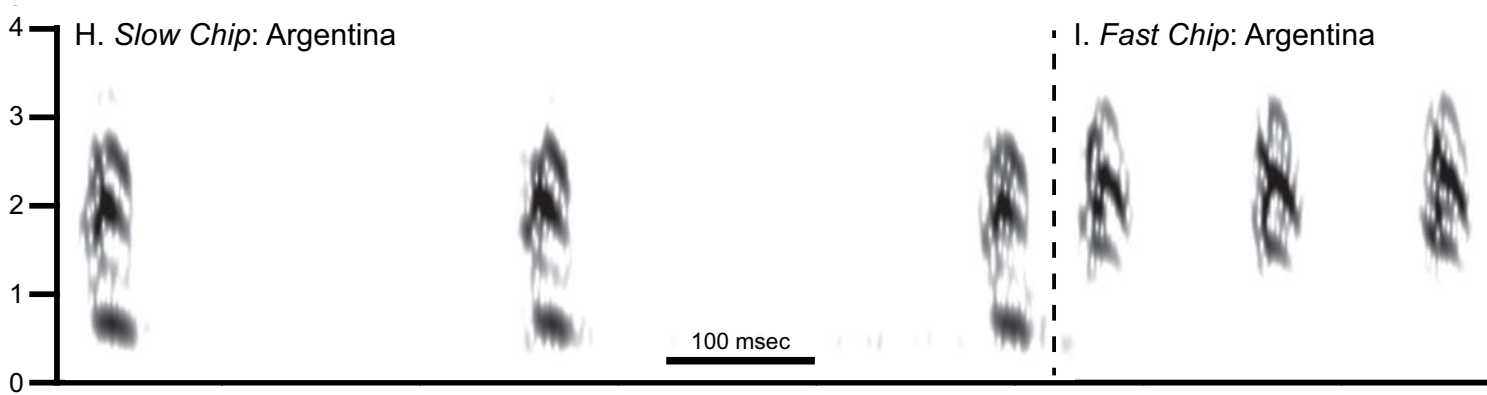
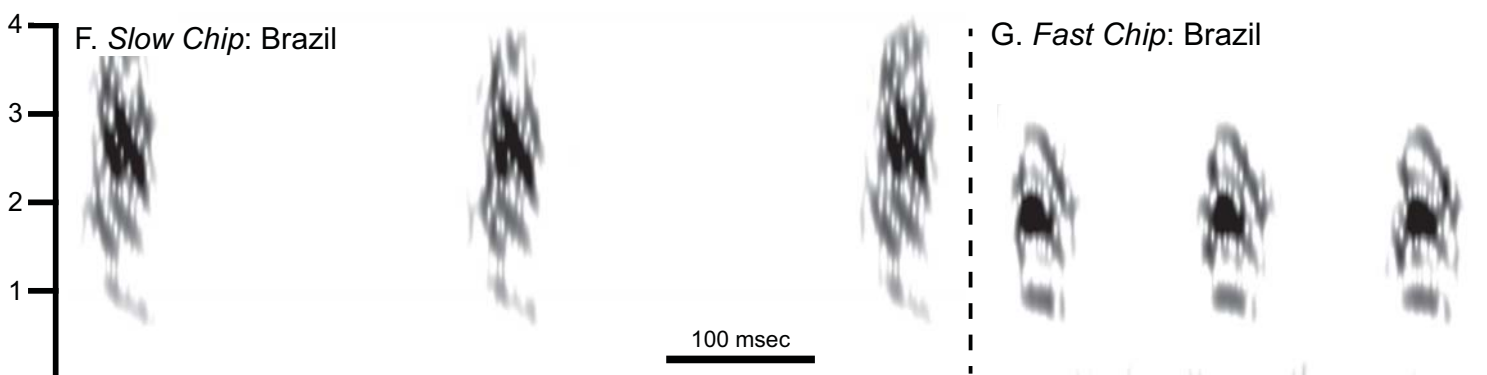
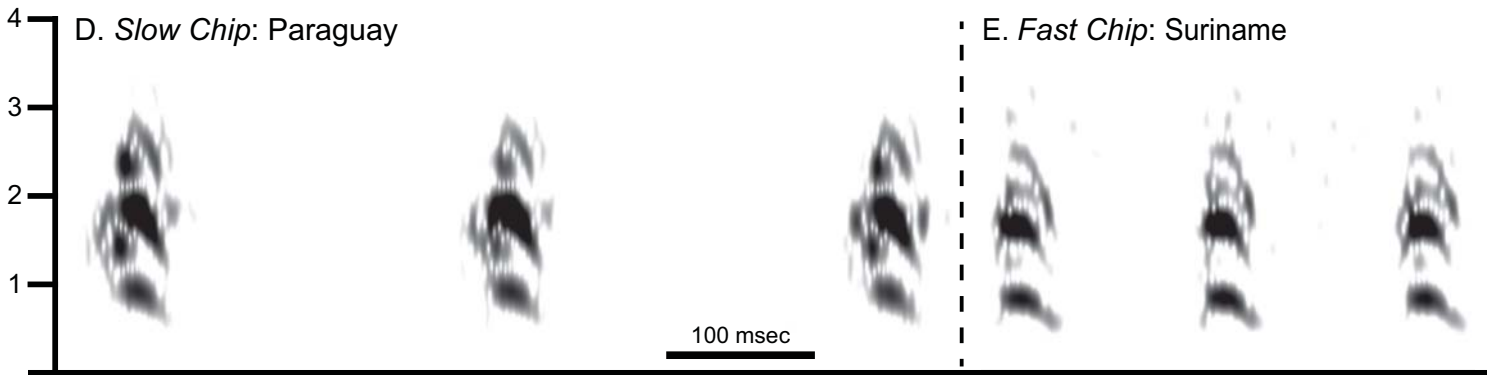
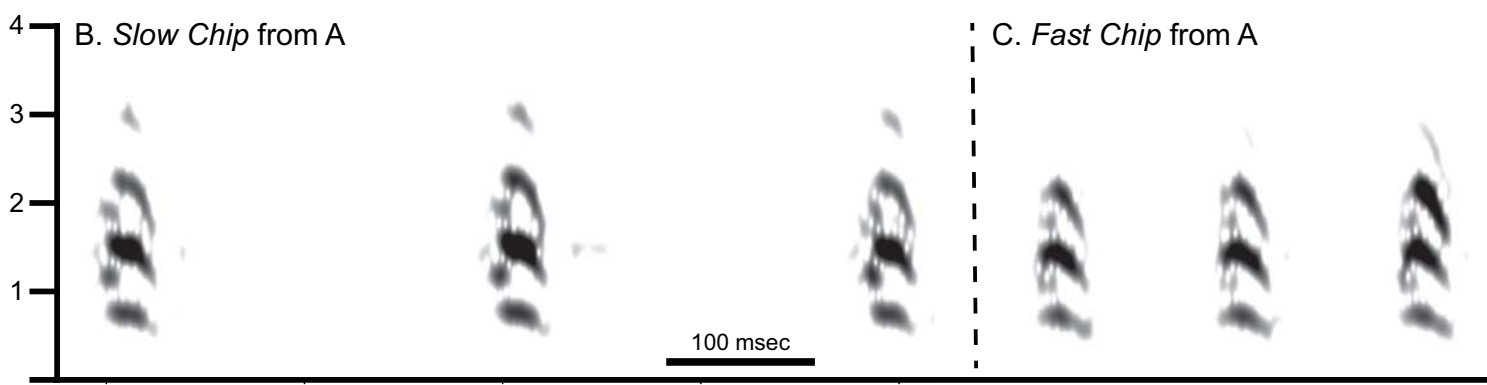
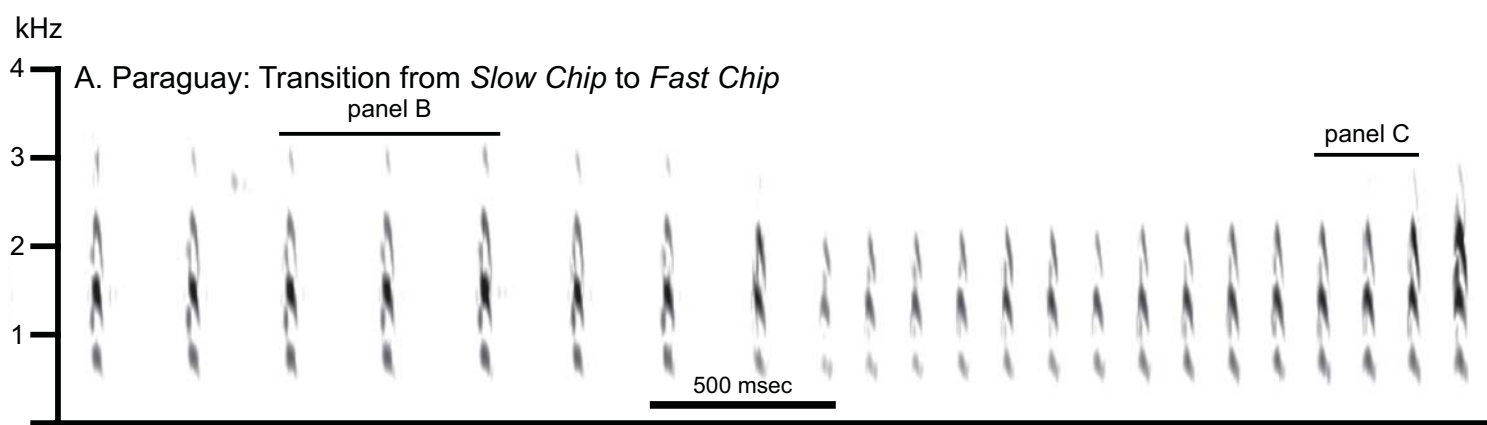
(Macaulay Library 52421), Bolivia (13.8 S 68.2 W), 3 June 1990, T. Parker; D (ML68409), Brazil (31.0 S, 51.5 W), 19 August 1993, D. W. Finch; E, Paraguay (26.5 S 58.0 W), 11 November 2008, E. H. Miller.

FIGURE 10. Graphical summary of trends in temporal characters measured on *Winnows* of the South American Snipe *Gallinago p. paraguayiae* and *G. p. magellanica*, and Puna Snipe *G. andina*. *Winnows* and inter-*Winnow* intervals averaged briefest in *G. p. paraguayiae* among the three taxa (panels A, B), so *Winnows* were given at the highest rate (panel C; the duty cycle was similar across the taxa). Duration of pulses (as defined operationally; see Methods) was greatest in *G. p. paraguayiae* (panel D), and the interval between pulses was brief (panel E), so the pulse duty cycle was very high (panel F; pulse-repetition rate across the taxa was ~5, ~7, and ~9, respectively). The inter-pulse interval in *Winnows* was substantially higher in *G. p. magellanica* than in the other taxa (panel 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 below 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.

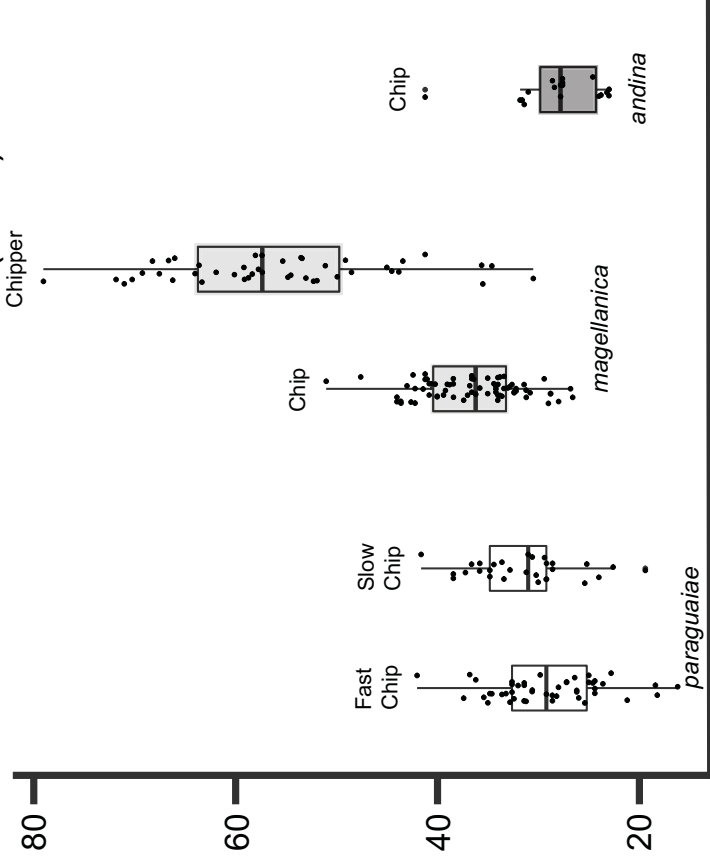
FIGURE 11. The *Winnow* of the South American Snipe *Gallinago p. magellanica* consists of sound elements that are briefer than in *G. p. paraguayiae* and often appear as repeated couplets (e.g. panels C, D) or triplets (e.g. panels B, E) of elements that differ in duration; elements between sound elements also vary. The sound elements (especially longer ones) often show frequency modulation (panel D). As in *G. p. paraguayiae*, 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. Kroodsmas.



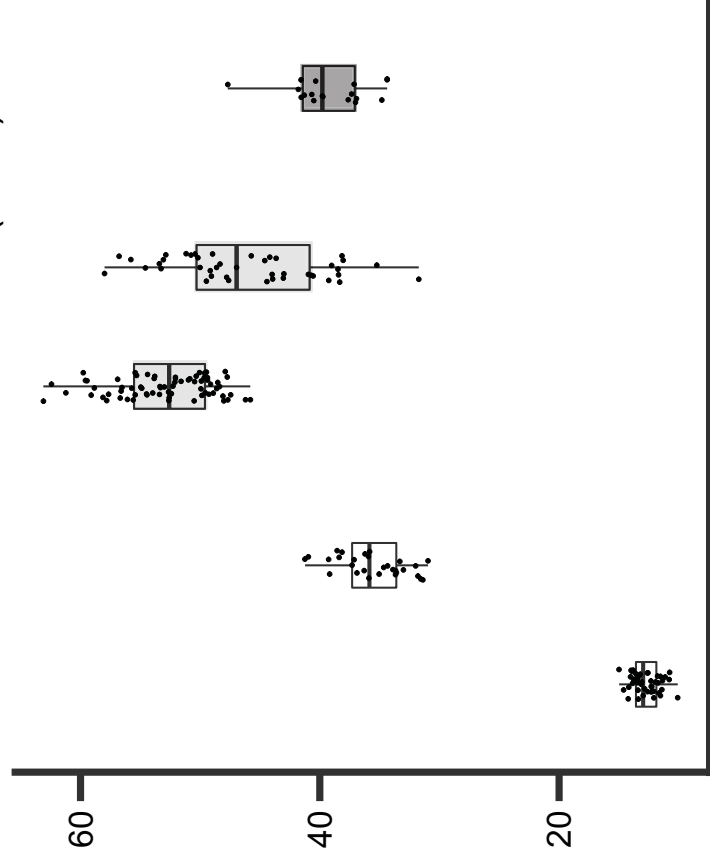




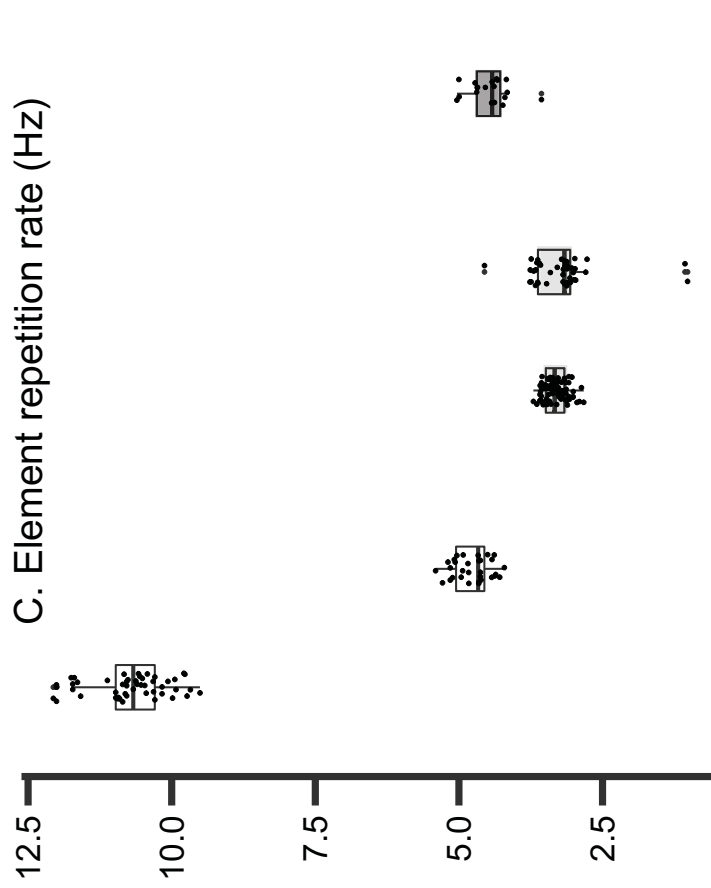
A. Element duration (msec)



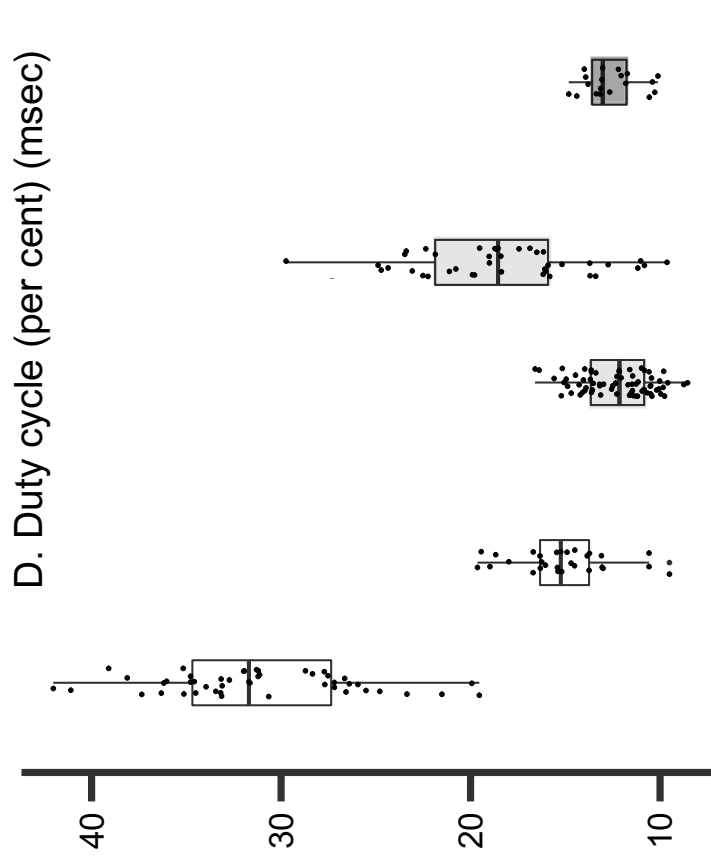
B. Inter-element interval (msec)



C. Element repetition rate (Hz)



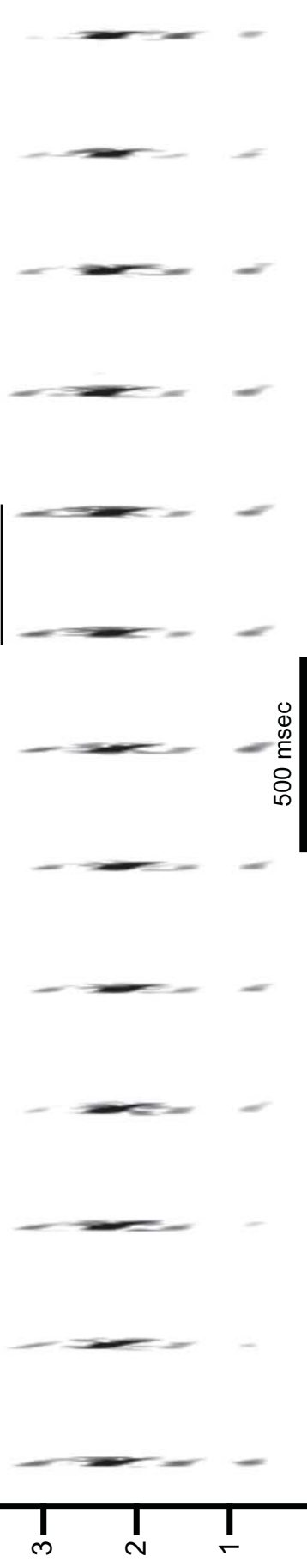
D. Duty cycle (per cent) (msec)



kHZ

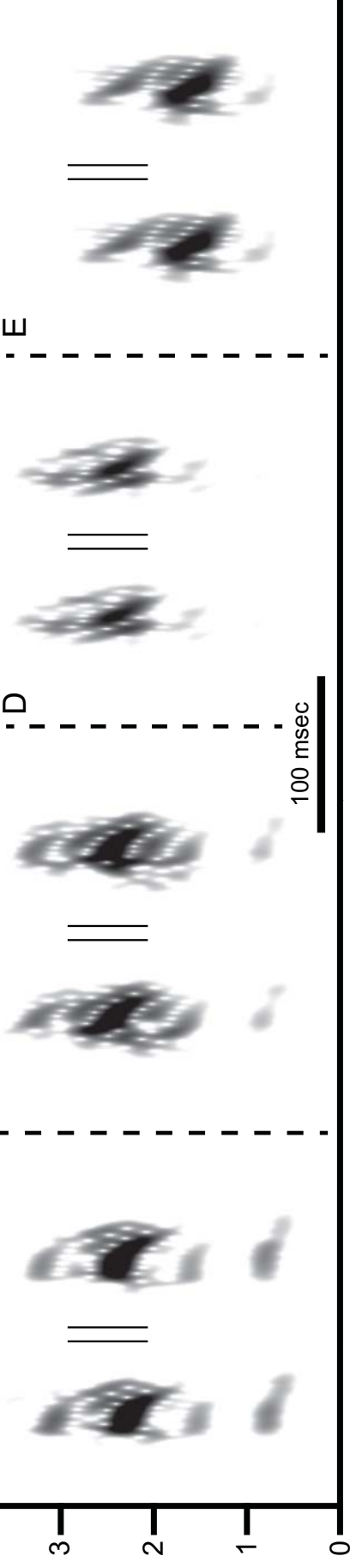
A. Chile: Magallanes

panel B



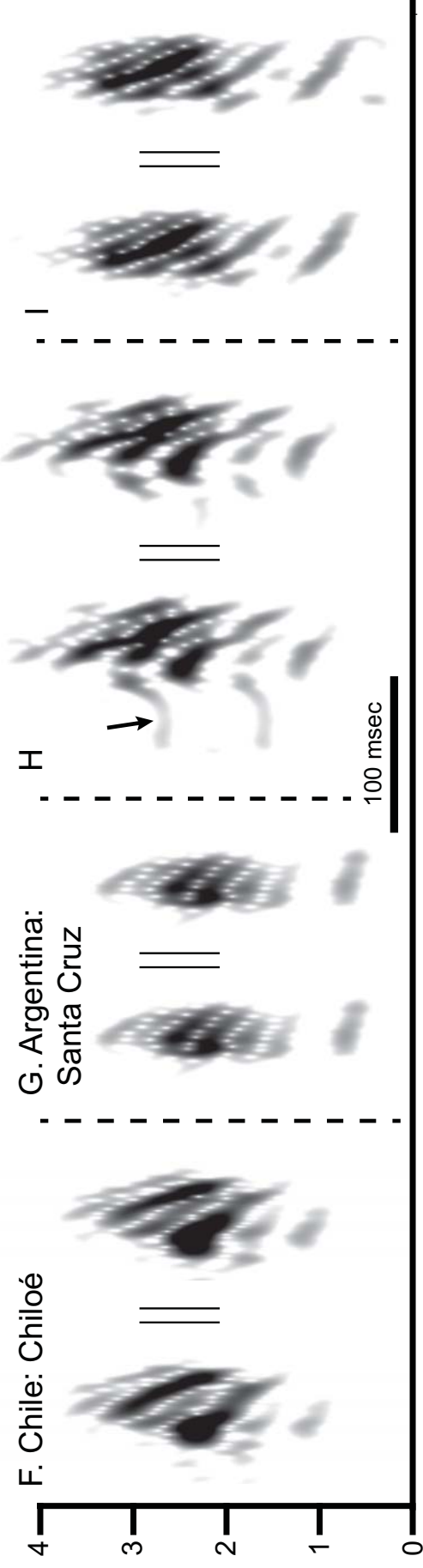
B. from A

Chile: Magallanes (C, D, E)



F. Chile: Chiloé

Falkland Is./Is. Malvinas (H, I)



KHZ

A. Chile: near Punta Arenas

panel B



500 msec

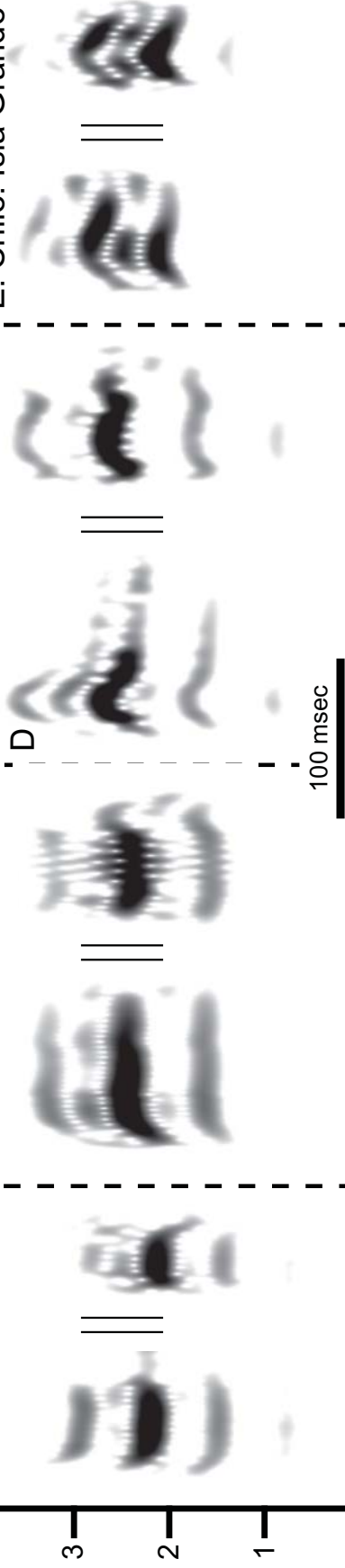
Chile: near Punta Arenas (C, D)

B. from A

D

C

E. Chile: Isla Grande



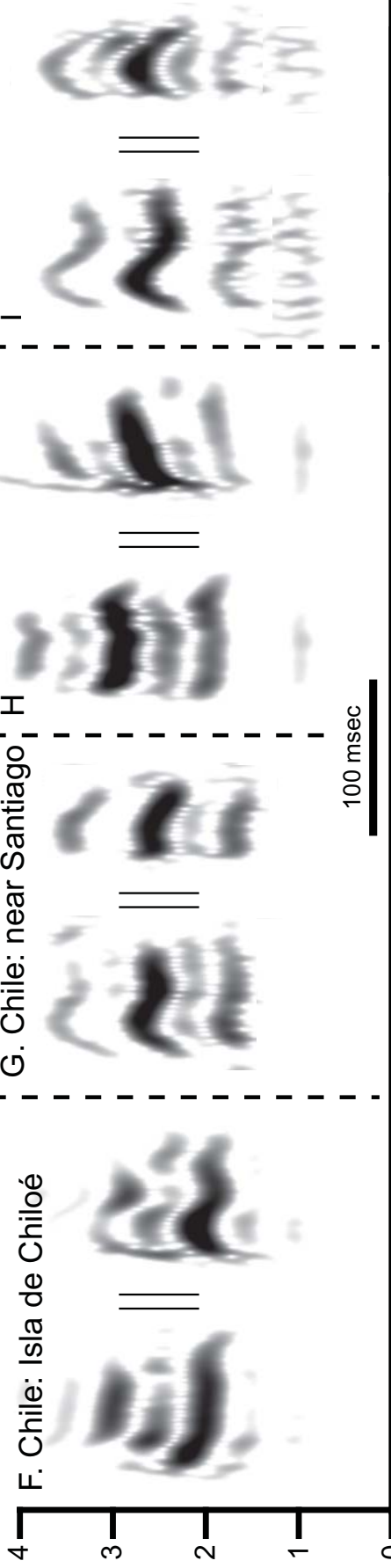
Falkland Is./Is. Malvinas (H, I)

G. Chile: near Santiago

H

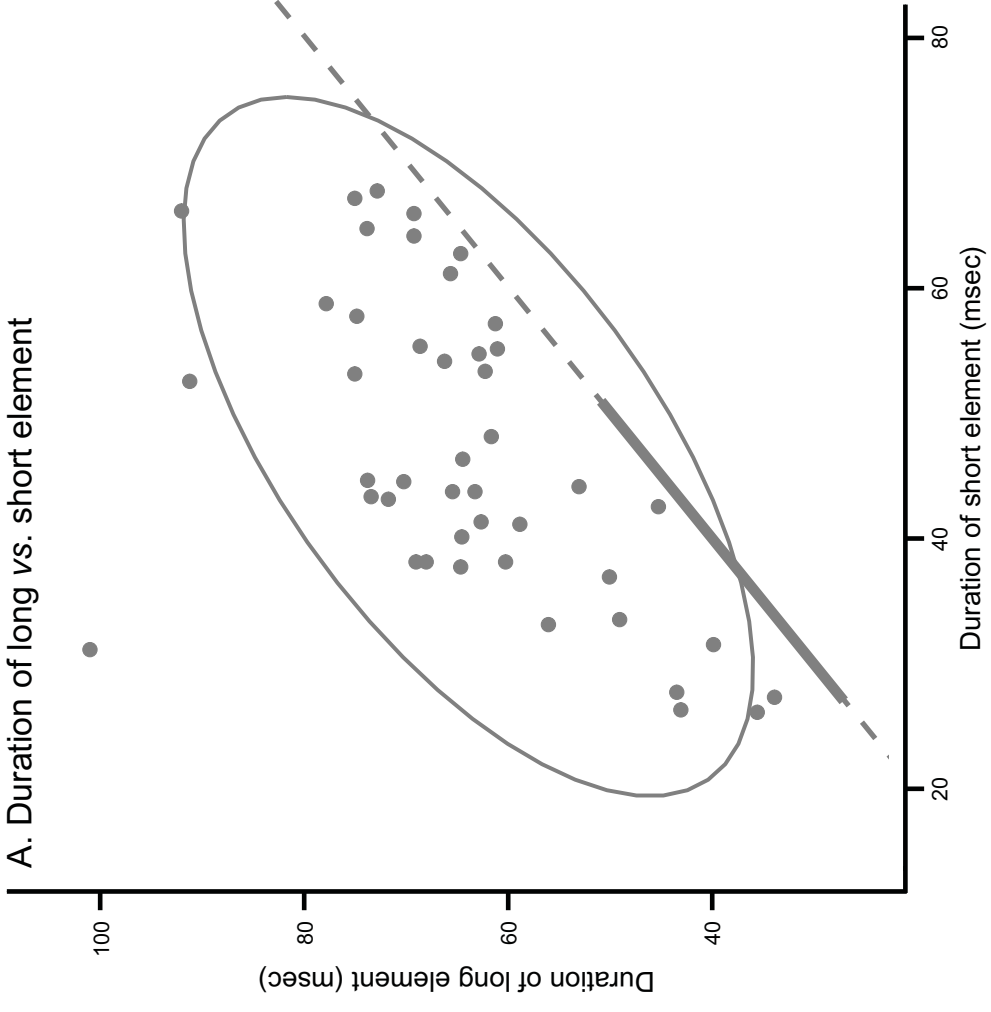
F. Chile: Isla de Chiloé

I

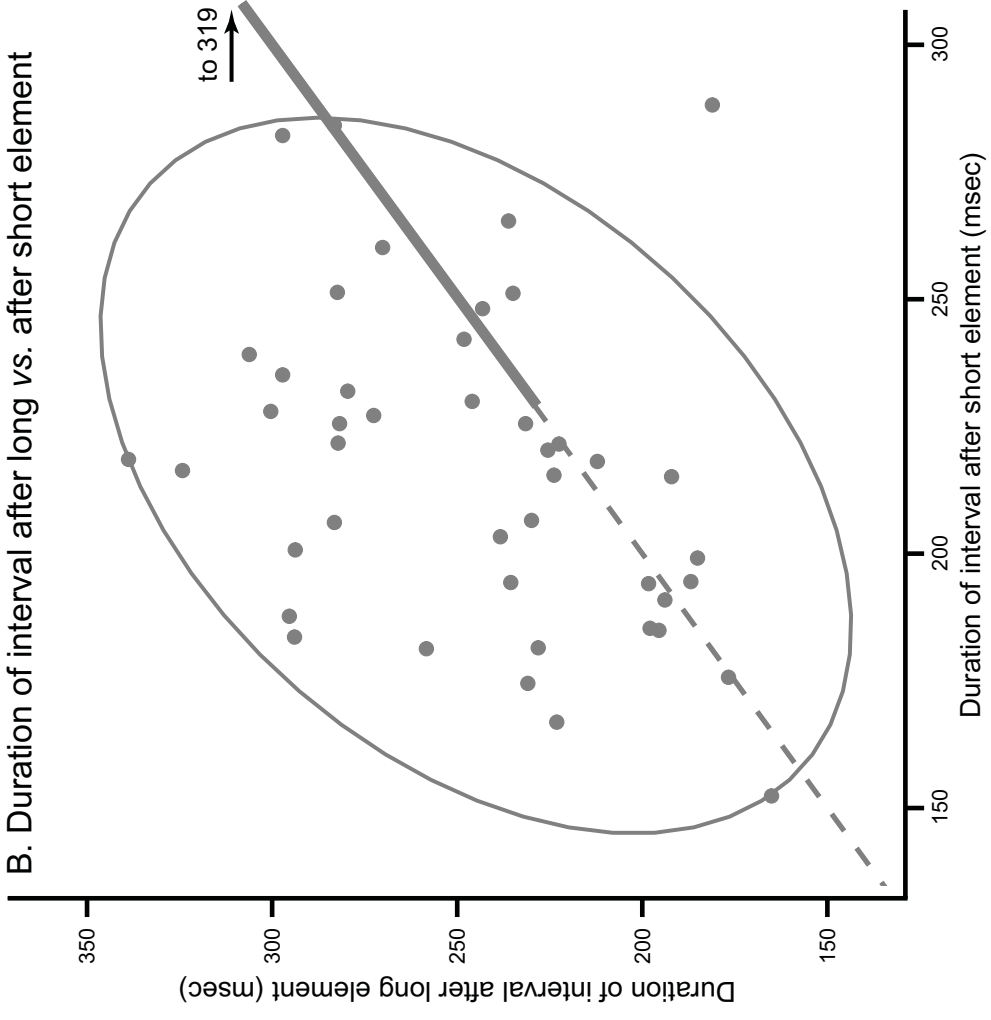


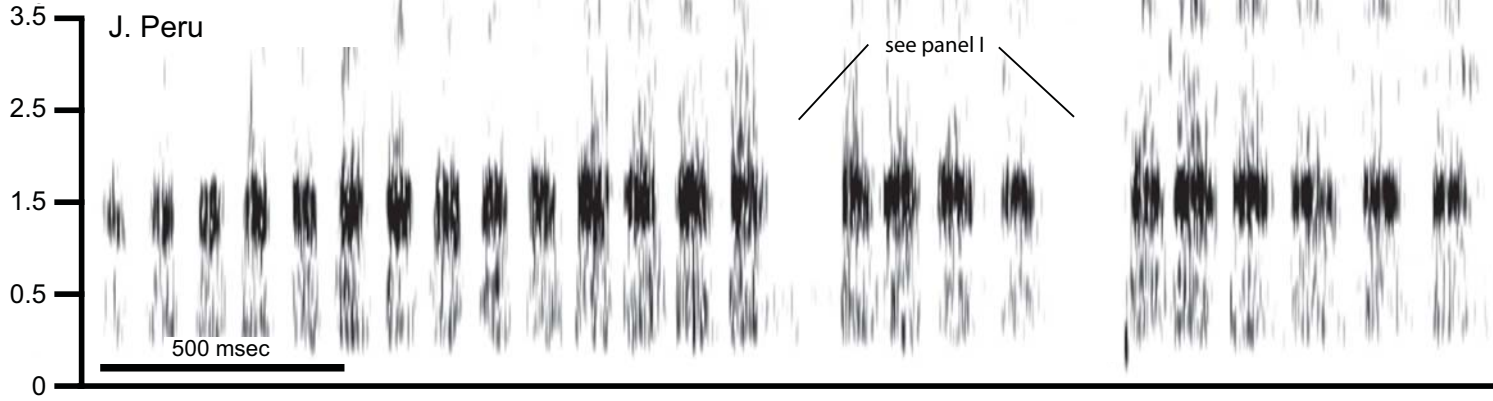
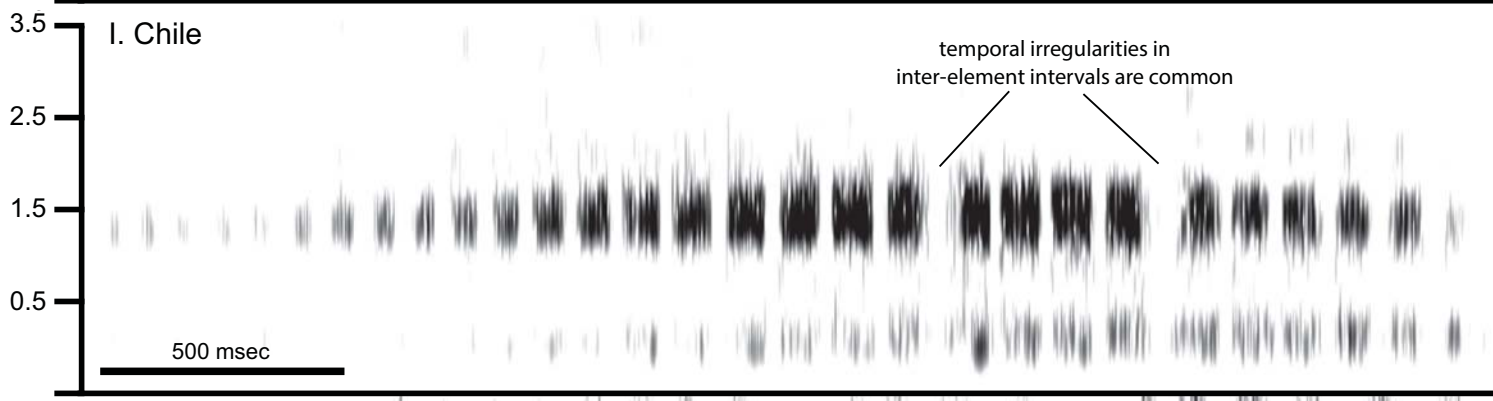
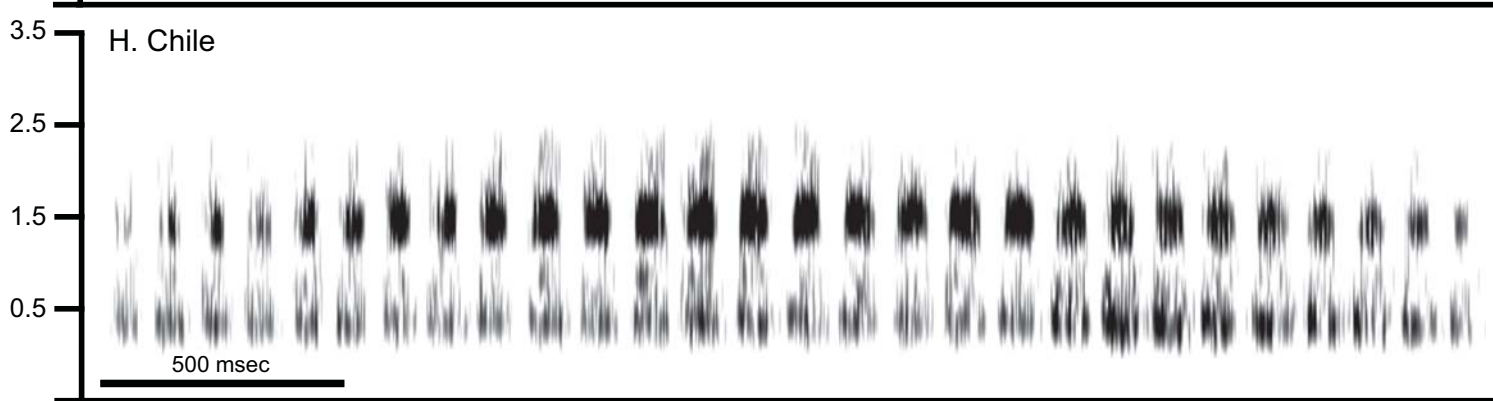
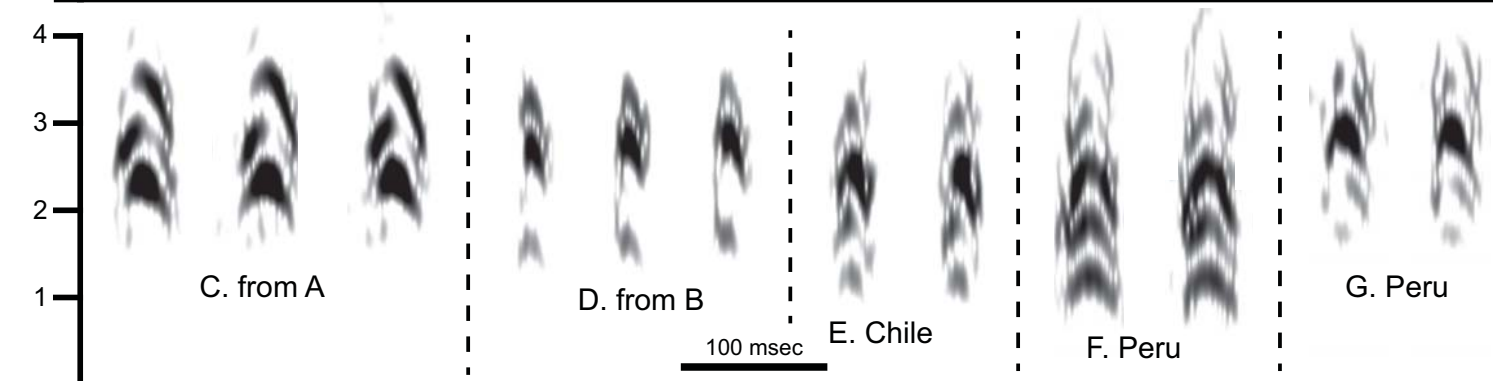
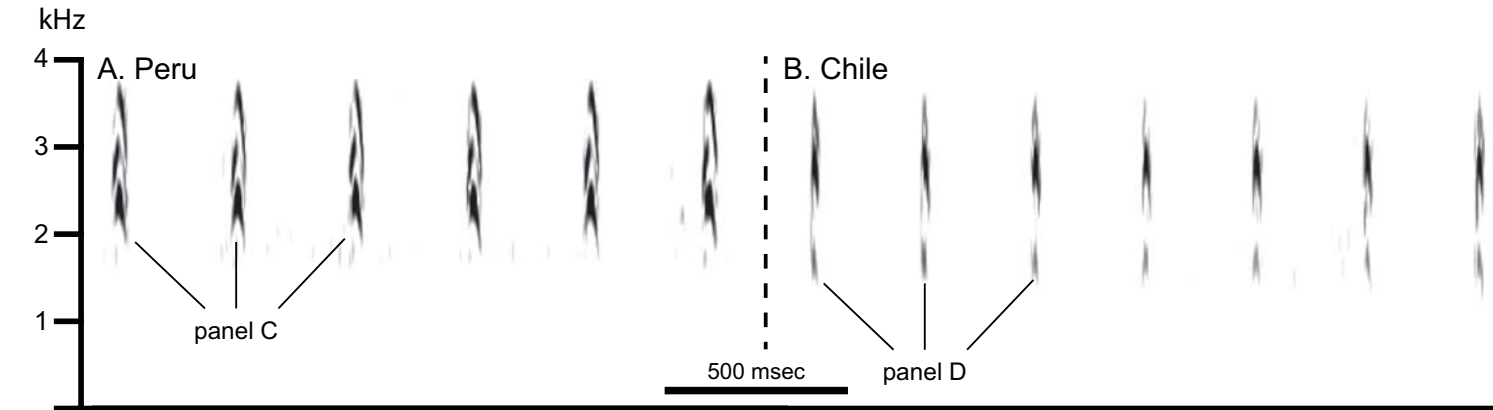
100 msec

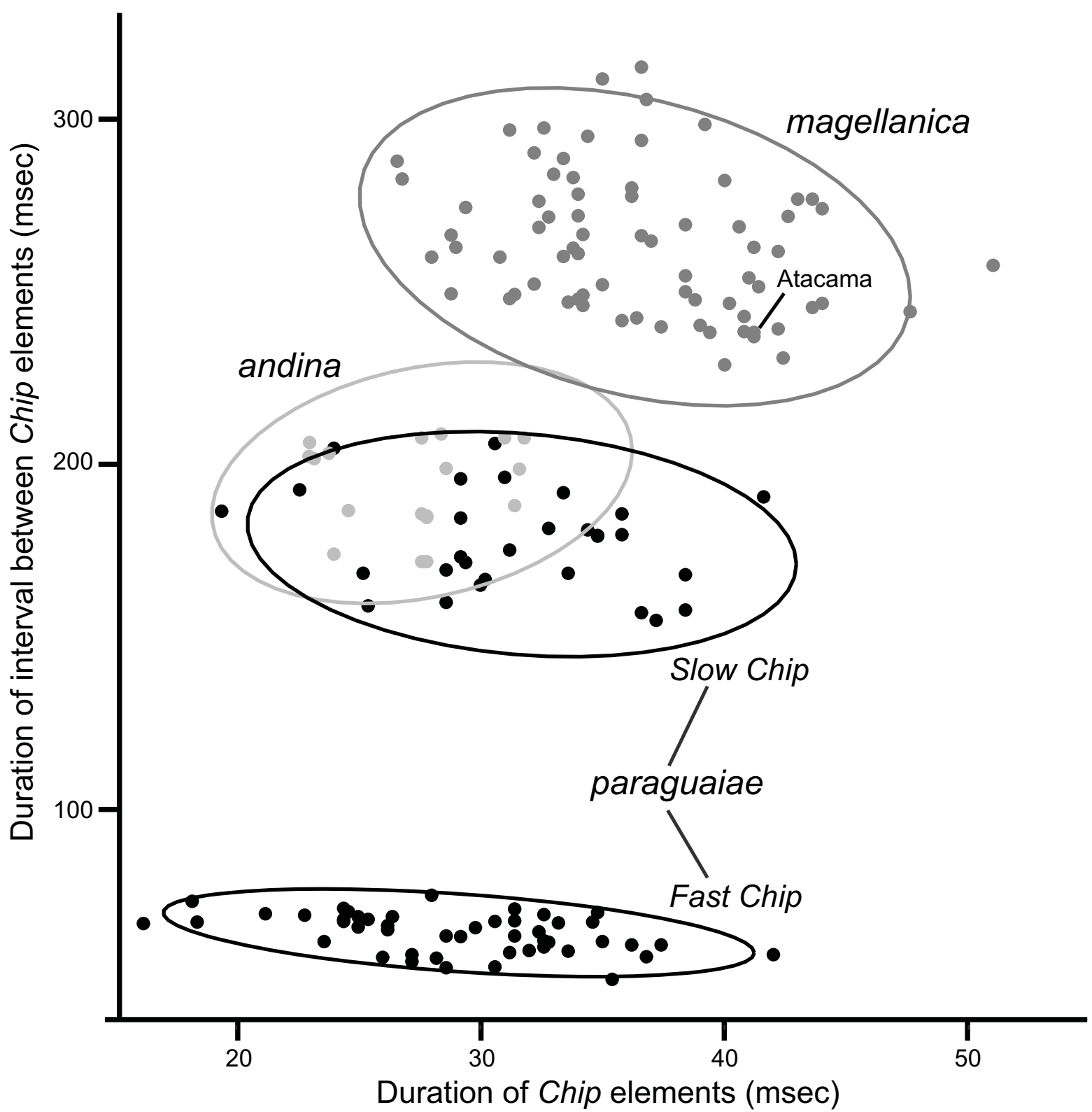
A. Duration of long vs. short element



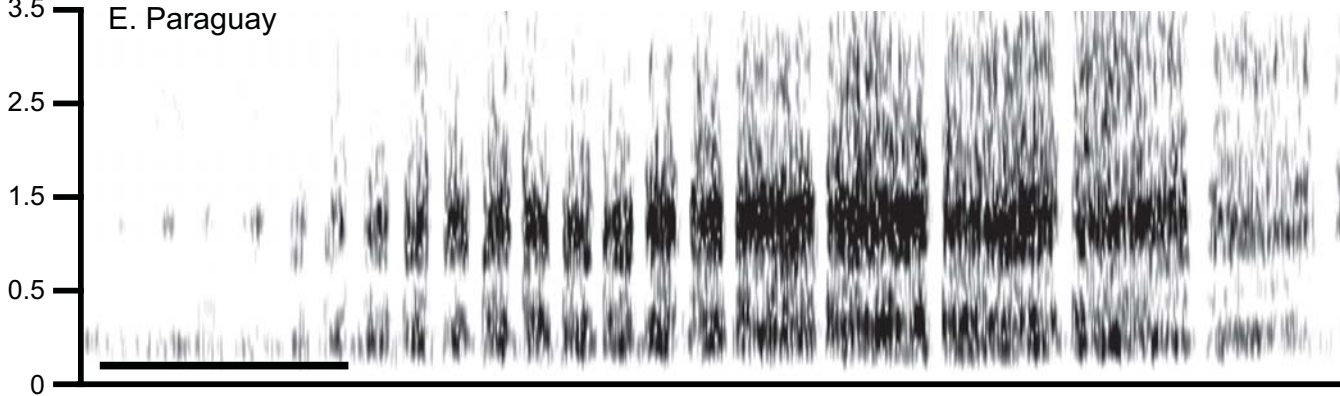
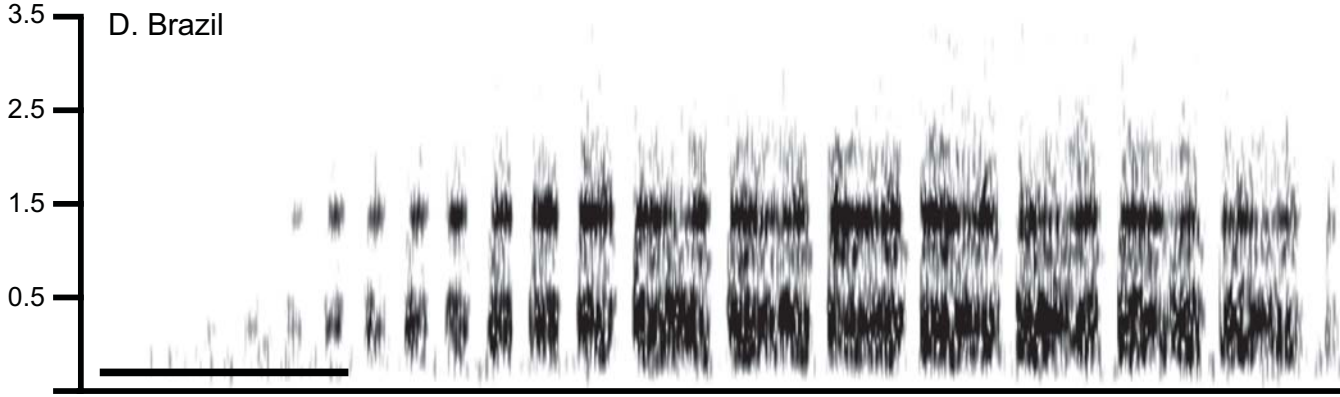
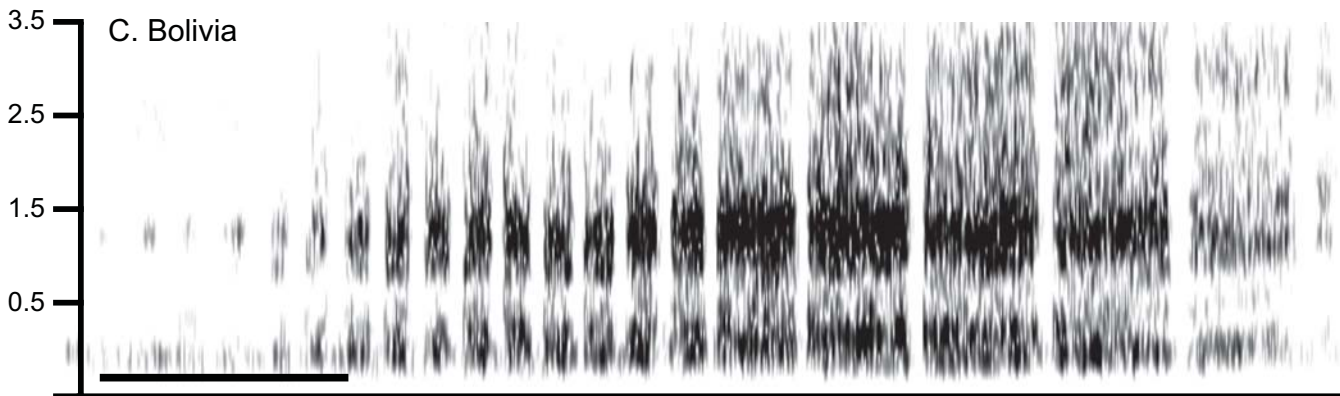
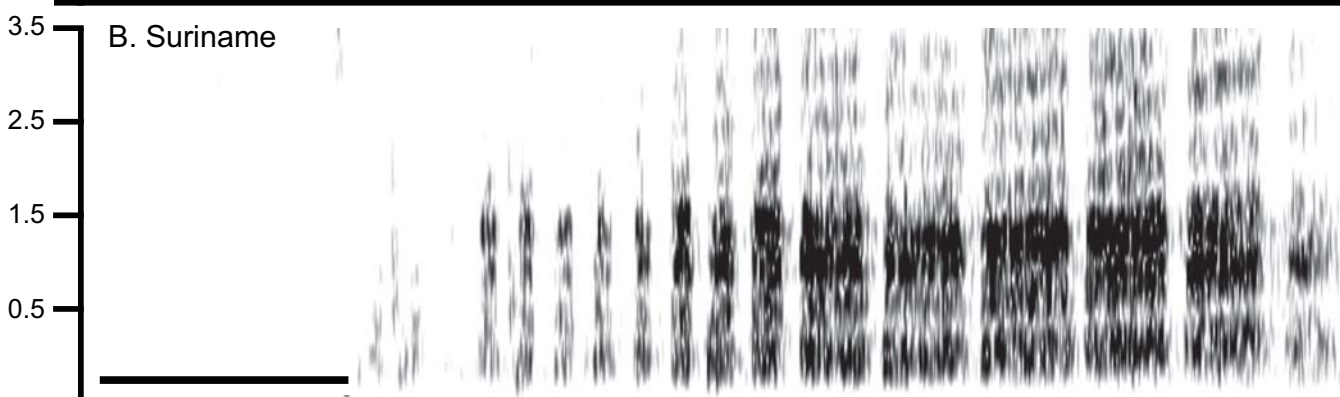
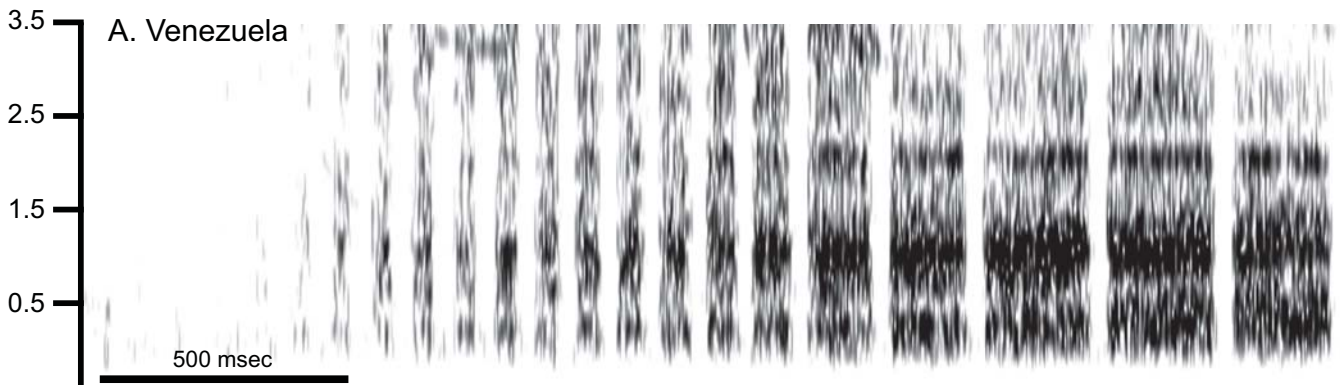
B. Duration of interval after long vs. after short element



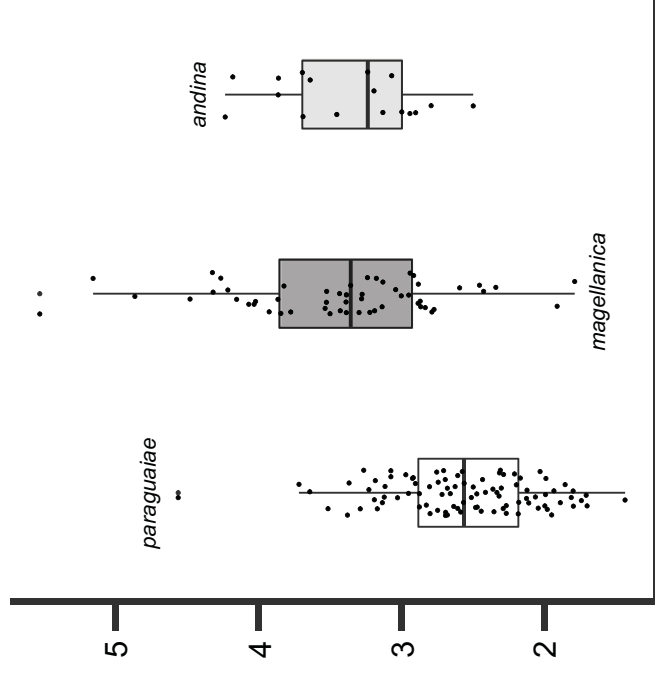




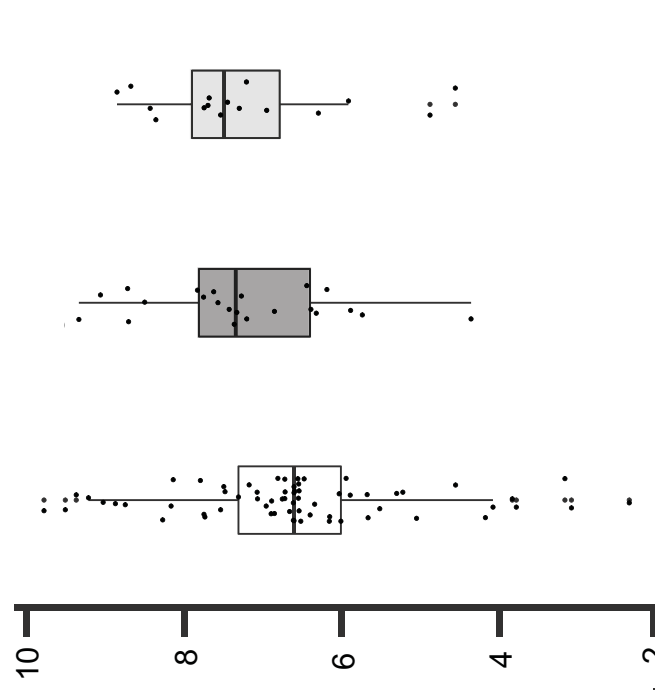
kHz



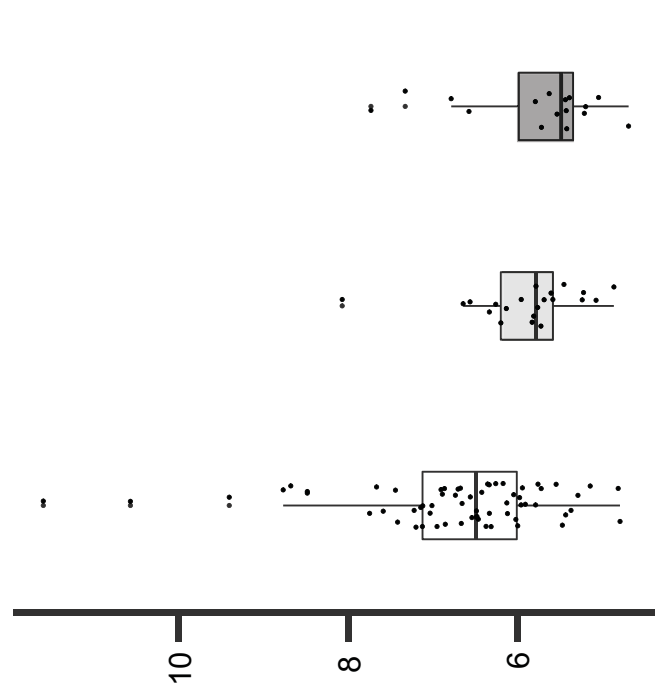
A. Winnow duration (sec)



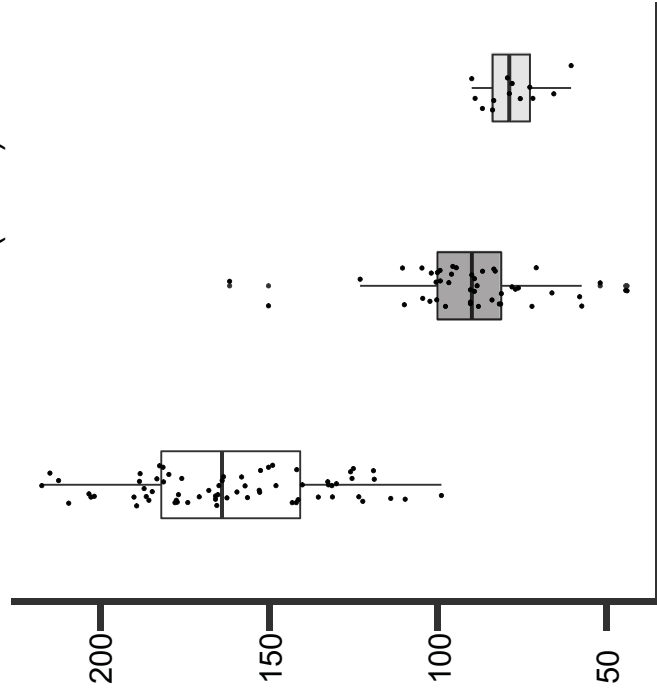
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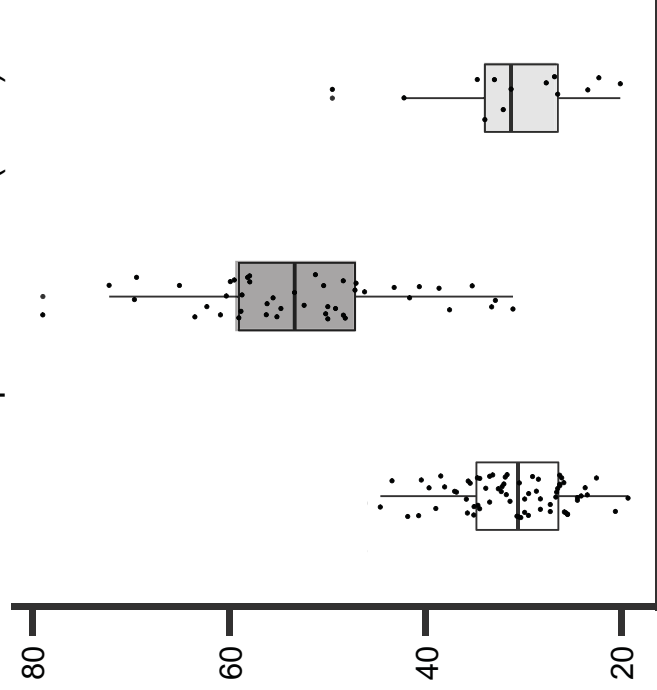
C. Winnow repetition rate (Hz)



D. Pulse duration (msec)



E. Inter-pulse interval (msec)



F. Pulse duty cycle (per cent)

