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Taxonomic status of Paraguay's only endemic bird, the Chaco Nothura *Nothura chacoensis* (Aves: Tinamidae)

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Abstract

The Chaco Nothura *Nothura chacoensis* Conover is endemic to the Chaco of western Paraguay. Originally described as a subspecies of the Spotted Nothura *N. maculosa* (Temminck), it has been regarded by many authorities as a distinct species based on alleged sympatry with *N. maculosa*. However, an earlier study revealed no differences in cytochrome *b* sequences between the two taxa. We reanalyzed the geographic distribution and morphological variation of *N. chacoensis* and *N. maculosa* in western Paraguay based on museum specimens. There is no locality where specimens of both taxa were collected, thus there is no evidence for sympatry. Morphologically the two taxa did not differ in any size or shape variable. Plumage characters overlapped in a few specimens. We recorded vocalizations from at least four individuals of *N. chacoensis* within its known range. Its typical territorial song was a very rapid, relatively monotone trill that was virtually identical with the most frequent territorial song of *N. maculosa* in length, number of notes, rate of notes, and emphasized frequency, and differed substantially from the songs of other species of *Nothura*. Based on distributional, morphological, biochemical, and especially vocalization data, we conclude that *N. chacoensis* should be regarded as a subspecies of *N. maculosa*.

Key words: geographic distribution, geographic variation, morphological variation, *Nothura maculosa*, taxonomy, vocalizations

Introduction

Delimiting species boundaries among morphologically similar, geographically adjacent sister taxa of birds is premised upon a thorough understanding of geographic variation in biochemical, morphological, and behavioral traits, with the goal of evaluating the extent of gene flow between taxa to infer whether there is primary intergradation (clinal variation), secondary intergradation (hybridization), or an absence of intergradation (potential or complete reproductive isolation) (e.g., McKitrick & Zink 1988; Zink & McKitrick 1995; Johnson *et al.* 1999; Helbig *et al*. 2002; Tobias *et al*. 2010; Sangster 2013; Gill 2014).

The spotted tinamous of the genus *Nothura* (Aves: Tinamidae) inhabit open country of central and southern South America (Conover 1950; Short 1975; Cabot 1992; Davies 2002). Phylogenetic analyses confirm the close relationship among all species of *Nothura*, but most analyses reveal it to be a paraphyletic group whose relationships remain unresolved (Bertelli & Tubaro 2002; Bertelli *et al.* 2002, 2014; Porzecanski 2003; Tubaro & Bertelli 2003; Bertelli & Porzecanski 2004; Bertelli & Chiappe 2005; Bertelli & Giannini 2013; Bertelli 2016).

Five extant species of *Nothura* are currently recognized by the South American Checklist Committee (Remsen *et al.* 2017): (1) White-bellied Nothura *N. boraquira* (Spix) of eastern Bolivia, western Paraguay, and eastern Brazil; (2) Lesser Nothura *N. minor* (Spix) of southeastern Brazil and eastern Paraguay; (3) Darwin's Nothura *N. darwinii* G. R. Gray of southern Peru, western Bolivia, and western Argentina; (4) Spotted Nothura *N. maculosa* (Temminck) of southern Brazil, Paraguay, Argentina, and Uruguay; and (5) Chaco Nothura *N. chacoensis* Conover

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of western Paraguay. Of these, *N. chacoensis* has had the most controversial taxonomic history, being regarded as either a subspecies of *N. maculosa* (Conover 1937; Hellmayr & Conover 1942; Steinbacher 1962; Olrog 1963; Bump & Bump 1969; Short 1975, 1976; Blake 1979; Narosky & Yzurieta 1987, 1989, 2006; Hayes 1995; de la Peña & Rumboll 1998; Porzecanski 2003; del Castillo & Clay 2004, 2005; Rodríguez Mata *et al.* 2006; Smith 2006) or a distinct species (Conover 1950; Meyer de Schauensee 1966, 1970; Blake 1977; Sibley & Monroe 1990; Canevari *et al*. 1991; Cabot 1992; Monroe & Sibley 1997; Mazar Barnett & Pearman 2001; Bertelli & Tubaro 2002; Bertelli *et al.* 2002; Davies 2002; Tubaro & Bertelli 2003; Bertelli & Porzecanski 2004; Bertelli & Giannini 2013; Bertelli 2016; Remsen *et al.* 2018).

In this paper we review the taxonomic history and distribution of *N. chacoensis*, reexamine its distribution and morphological variation, and provide new evidence that it should be regarded as a subspecies of *N. maculosa*.

Taxonomic history and distribution

Nothura chacoensis was first described as a subspecies of *N. maculosa* by Conover (1937), based on 13 specimens from the dry Chaco of western Paraguay (*n* = 10) and north-central Argentina (*n* = 3). Conover (1937) described *N. chacoensis* as differing from typical *N. maculosa* by its grayer and less rufescent upperparts, buffier underparts, lighter and narrower dark streaking on the lower neck and breast, and less heavily barred flanks and sides.

In a subsequent taxonomic analysis of the genus, Conover (1950) elevated *N. chacoensis* to species rank after examining more specimens and increasing his sample size of Paraguayan specimens to 29; however, he also reassigned specimens of *N. chacoensis* from north-central Argentina to a new subspecies, *N. m. paludivaga* Conover. Despite Conover's (1950) belated recognition of specimens from Argentina previously attributed to *N. chacoensis* as *N. m. paludivaga*, *N. chacoensis* continued to be cited erroneously as occurring in Argentina (e.g., Olrog 1963; Meyer de Schauensee 1966, 1970; Bump & Bump 1969; Short 1975; Blake 1977, 1979; Sibley & Monroe 1990; Canevari *et al.* 1991; Cabot 1992; Hayes 1995; Davies 2002). Conover (1950:361–362) pointed out that the range of *N. chacoensis* "meets and may slightly overlap that of *N. m. paludivaga* and that there appears to be no area of intergradation between the two." Conover (1950) hypothesized that *N. chacoensis* evolved while isolated in the central Paraguayan Chaco by flood basins of the Paraguay River and Pilcomayo River, after which sediments filled the basins, facilitating the dispersal of *N. maculosa* westward across the Paraguay River and thus allowing formation of a secondary contact zone between *N. maculosa* and *N. chacoensis*.

Short (1975, 1976) reexamined specimens of *Nothura* and pointed out that *N. chacoensis* averages smaller in body size than most races of *N. maculosa*. However, Short (1975, 1976) concluded that *N. chacoensis* was a subspecies of *N. maculosa* because their differences are minor compared to the differences between other species of *Nothura*. Blake (1977) regarded *N. chacoensis* as a distinct species but later regarded it as a subspecies of *N. maculosa* (Blake 1979). Hayes (1995) reexamined specimens from Paraguay at the American Museum of Natural History (AMNH) in New York, New York, USA, the Field Museum of Natural History (FMNH) in Chicago, Illinois, USA, and the University of Michigan Museum of Zoology (UMMZ) in Ann Arbor, Michigan, USA, and concurred with Short (1975, 1976) that *N. chacoensis* is a subspecies of *N. maculosa*.

At the eastern edge of its range, *N. chacoensis* "abruptly meets and may slightly overlap that of *N. m. paludivaga*" according to Conover (1950). Hayes (1995) provided the most precise description of the possible zone of overlap, pointing out that *N. chacoensis* has been recorded as far east as 120 km W of Puerto Pinasco, Dpto. Presidente Hayes (≈59°00"W; FMNH, UMMZ), whereas *N. m. paludivaga* has been recorded as far west as Fort Wheeler, Dpto. Presidente Hayes (≈59°35'W; AMNH), 30 km NE of Fortín Isla Poi (Villa Militar), Dpto. Presidente Hayes (≈59°30'W; FMNH), and 235 km W of Río Negro (Estero Patiño), Dpto. Presidente Hayes (≈59°32'W; UMMZ). However, given the imprecise descriptions of these localities by the collectors, we have been unable to pinpoint their coordinates. Steinbacher (1962) reported three specimens of *N. chacoensis* from Laguna Escalante, Dpto. Presidente Hayes (23°50'S, 60°46'W; specimens in Zoologisches Forschunginstitut und Museum Alexander Koenig [ZFMK] in Bonn, Germany, and Naturmuseum und Forschungs-Institut Senckenberg [SMF] in Frankfurt-am-Main, Germany), but Short (1975) reidentified these specimens as *N. m. pallida* Olrog of the Argentinian dry Chaco (Olrog 1959).

The apparent sympatry of *N. chacoensis* and *N. m. paludivaga* has been argued as evidence that *N. chacoensis* is a distinct species (Blake 1977; Sibley & Monroe 1990; Cabot 1992), yet intermediate specimens have been collected in the narrow range of possible overlap. Conover (1950) described two possible hybrid specimens at FMNH, but did not state their museum catalog numbers or their localities; Hayes (1995) identified one possible hybrid specimen as *N. chacoensis* < *N. m. paludivaga* (FMNH 417655), collected at Laguna General Díaz, Dpto. Alto Paraguay or Presidente Hayes (22°18'N, 59°01'W), but was unable to locate the second putative intermediate specimen at FMNH. Short (1976) described another possible hybrid (AMNH 802523) collected 60 km E of Orloff, in Dpto. Presidente Hayes (≈59°27'W), which Hayes (1995) examined and identified as *N. chacoensis* > *N. m. paludivaga*. Given the imprecise localities of most *Nothura* specimens from the Paraguayan Chaco, the few specimens appearing to be intermediate between *N. chacoensis* and *N. m. paludivaga*, and the subjective nature of evaluating plumage variation among individuals of each taxon, we could not determine whether the possible zone of sympatry between *N. chacoensis* and *N. m. paludivaga* represents a cline (primary intergradation) or a hybrid zone (secondary intergradation) between two similar and closely related taxa.

In a study of morphological and genetic variation in tinamous, Porzecanski (2003) noted that, unlike other species of *Nothura*, *N. chacoensis* specimens lack diagnostic morphological characters. Despite average differences in underpart coloration and chest streaking, as well as slightly longer crural and caudal feathers, specimens of *N. chacoensis* were indistinguishable from *N. maculosa* when a single specimen was placed within a larger series of *N. maculosa*. Furthermore, the cytochrome *b* sequences of two *N. chacoensis* specimens (AMNH 811313, AMNH 305616) lack unique substitutions and are identical to those of *N. m. paludivaga* (AMNH SBB33) and nominate *N. m. maculosa* Temminck [KUMNH (University of Kansas Museum of Natural History) 3656, KUMNH 3842] from Paraguay. Porzecanski (2003) thus concluded that *N. chacoensis* should be synonymized with *N. maculosa*.

Several phylogenetic analyses of Tinamidae concluded that *N. darwinii* is more closely related to *N. maculosa* than *N. chacoensis*, implying that *N. chacoensis* should be considered a distinct species (Bertelli & Tubaro 2002; Bertelli *et al.* 2002; Tubaro & Bertelli 2003; Bertelli & Giannini 2013), but other analyses revealed that *N. chacoensis* and *N. maculosa* are sister taxa (Porzecanski 2003; Bertelli & Porzecanski 2004) or are equally related to *N. darwinii* (Bertelli 2016). A comprehensive phylogenetic analysis of tinamous did not include *N. chacoensis* because no skeletal specimens were available (Bertelli *et al.* 2014).

Anecdotal accounts differ on whether *N. chacoensis* is vocally distinct from *N. maculosa*. Robert S. Ridgely (pers. comm. in Hayes 1995) reported that the vocalizations of *N. chacoensis* "appear to differ slightly" from *N. maculosa*, but he did not record its vocalizations. Bertelli & Tubaro (2002) summarized data on the vocalizations of all *Nothura* tinamous except *N. chacoensis*, for which no recorded vocalizations were available. Smith (2006, pers. comm.) reported that all *Nothura* encountered in the central Paraguayan Chaco, presumed to represent *N. chacoensis*, appear indistinguishable from *N. maculosa* elsewhere in Paraguay in both plumage and vocalizations, but no vocalizations were recorded.

Methods

Geographic distribution. We obtained the locality of each specimen of *Nothura* from the Paraguayan Chaco in the AMNH, FMNH, and UMMZ, plus specimens reported by Steinbacher (1962) and Short (1975) in SMF and ZFMK. For each locality we estimated its latitude and longitude based on Paynter (1989) and Hayes (1995), but in most cases we used Google Earth (www.google.com/earth; accessed 24 March 2017) to obtain a more precise estimate of each locality (Appendix 1). The localities were plotted on a map to evaluate the degree of sympatry among taxa.

Morphological variation. We examined 15 specimens of *N. m. paludivaga* and 28 of *N. chacoensis* from the Paraguayan Chaco in the FMNH and UMMZ to evaluate whether there are any specimens intermediate or overlapping between the two taxa in plumage color, which would be suggestive of primary or secondary intergradation. Given the subtle and complex differences in plumage coloration and pattern, we did not attempt to quantify this.

Using Vernier calipers, we measured (nearest mm) the following morphometric variables for each adult specimen: bill length (BL), from depression between cranium and maxilla to tip of maxilla; wing chord length (WL), from bend of folded wing to tip of longest primary feather; tarsus length (TL), from the anterior junction of tibiotarsus and tarsometatarsus to the distal junction of hind toe and tarsometatarsus; and middle toe length (MT), from proximal end to the distal end of the claw. In several specimens the bill or toe was slightly bent, in which case we took a measurement after straightening the bent bill or toe to a more normal position. We also recorded the sex of each specimen, as determined by the collector, from the attached label.

Vocalizations. During 29–30 Aug 2016 and 24–27 Feb 2017 we used playback of two previously recorded vocalizations of *N. maculosa* obtained from Xeno-Canto (XC; www.xeno-canto.org; accessed 24 March 2017) to elicit vocal responses of *N. chacoensis* at several localities in grasslands within the range of *N. chacoensis* in the central Paraguayan Chaco. The first vocalization used in playback was a "high pitched, continuous trill" (Bump & Bump 1969) from Patrocínio, Minas Gerais, Brazil (XC319690); the second vocalization was a series of "flutelike whistles, accelerating at the end" (Narosky & Yzurieta 1989) from Varjão, Goiás, Brazil (XC153782). Vocalizations of singing *N. chacoensis* were recorded with a Marantz Professional PMD 661 and a Sennheiser ME66/K6 microphone, cut and amplified with Audacity software (www.audacityteam.org; accessed 24 March 2017), converted from wav to mp3 files with OnlineVideoConverter software (www.onlinevideoconverter.com; accessed 24 March 2017), and uploaded to Xeno-Canto for archiving and analysis.

To compare vocalizations of *N. chacoensis* with those of other *Nothura* species posted on XC, we selected relatively clean recordings of the most frequently given territorial vocalization (not alarm calls) of each species (see Appendix 2). Sonograms were generated by XC and downloaded to measure the following variables: (1) length of song; (2) number of notes in song; (3) rate of notes; and (4) emphasized frequency (kHz).

Statistical analyses. A principal component (PC) analysis (Jolliffe 1981) was computed using the correlation matrix of raw data for four morphological variables (BL, WL, TL, and MT) to produce individual PC loadings for all specimens. Principal component 1 (PC1) and principal component 2 (PC2), often interpreted as body size and body shape axes in birds (e.g., Rising & Somers 1989), were calculated to compare two additional size and shape variables between *N. chacoensis* and *N. m. paludivaga*. Two-sample (Student's) *t* tests (Zar 2010) were used to compare the means of each morphological variable (BL, WL, TL, MT, PC1, and PC2) between the sexes for *N. chacoensis* and *N. m. paludivaga*. All statistical analyses were computed with Statistix 9 software (Anonymous 2008), with two-tailed probabilities and $\alpha = 0.05$.

Because multiple vocalizations were often recorded from the same bird, the number of samples was small, and some faint sonograms required estimates for the length of a song and the number of notes in a song, mean values were not calculated and inferential statistical tests were not used to compare species; instead, vocalizations among *Nothura* species were compared by the ranges of vocal characters.

Results

Geographic distribution. In the Paraguayan Chaco, *N. chacoensis* generally occurs to the north and west of *N. paludivaga* and overlaps in latitude and longitude with *N. paludivaga*, with some specimens of *N. paludivaga* collected between specimens of *N. chacoensis* to the north and south, but there is no locality from which specimens of both taxa were collected (Figure 1).

Steinbacher (1962) reported three specimens of *N. chacoensis* well to the west of other specimens in American museums, in the western Paraguay Chaco, but these were reidentified by Short (1975) as *N. m. pallida* (Figure 1).

Two specimens (FMNH 418091–418092) of nominate *N. m. maculosa* were collected at Chaco-í, on the west bank of the Paraguay River, in extreme southeastern Dpto. Presidente Hayes (Figures 1 and 2). These specimens were collected in 1942 (4 Sep and 30 Aug, respectively), but the locality was not reported by Conover (1950), suggesting they were acquired later.

Morphological variation. The plumage of *N. chacoensis* is more similar to *N. m. paludivaga* than to nominate *N. m. maculosa*, which is distinctly more rufescent (Figure 2). As described but somewhat exaggerated by Conover (1937, 1950), *N. chacoensis* specimens differ from *N. m. paludivaga* by their slightly paler upperparts, slightly paler and buffier underparts, and slightly finer streaking on the lower neck and breast. We could not discern any consistent difference in the pattern of barring on the flanks, which was described as lighter in *N. chacoensis* (Conover 1937, 1950). We concur with the identification of all 43 FMNH and UMMZ specimens of the two taxa as identified on their specimen labels (presumably by Conover 1950) by average differences in color, but the differences between them are subtle. Variation occurs within each series of specimens and there is overlap in the color of both the upperparts and underparts, and the extent of streaking on the lower neck and breast. For example, the specimen of *N. m. paludivaga* with the palest underparts (FMNH 16350), collected 17 km SW of Laguna General Díaz and only 10 km SW of the type locality of *N. m. paludivaga* (7 km SW of Laguna General Díaz; FMNH 17653), is as pale as some specimens of *N. chacoensis* (Figure 2) and only slightly paler than other specimens of *N. m. paludivaga*. Furthermore, the specimen of *N. chacoensis* with the darkest underparts (FMNH 12113), which is one of 15 specimens collected at the type locality of *N. chacoensis* (265 km W of Puerto Casado; FMNH 12501), is as dark as some specimens of *N. m. paludivaga* (Figure 2) and only slightly darker than other specimens of *N. chacoensis*. When a specimen of one taxon was placed among a series of specimens of the other taxon it was barely discernible as being different, as noted by Porzecanski (2003). Hayes (1995) previously identified a possible hybrid specimen as *N. chacoensis* < *N. m. paludivaga* (FMNH 417655), but this specimen did not appear to be any more intermediate than other specimens. As described above, the two specimens appearing to be the most intermediate are the specimen of *N. m. paludivaga* with the palest underparts (FMNH 16350), which could be considered *N. m. paludivaga* > *N. chacoensis*, and the specimen of *N. chacoensis* with the darkest underparts (FMNH 12113), which could be considered *N. chacoensis* > *N. m. paludivaga*. There was no discernible zone of hybridization, which should be characterized by an increase in intermediacy and variability, between the taxa (Schueler & Rising 1976).

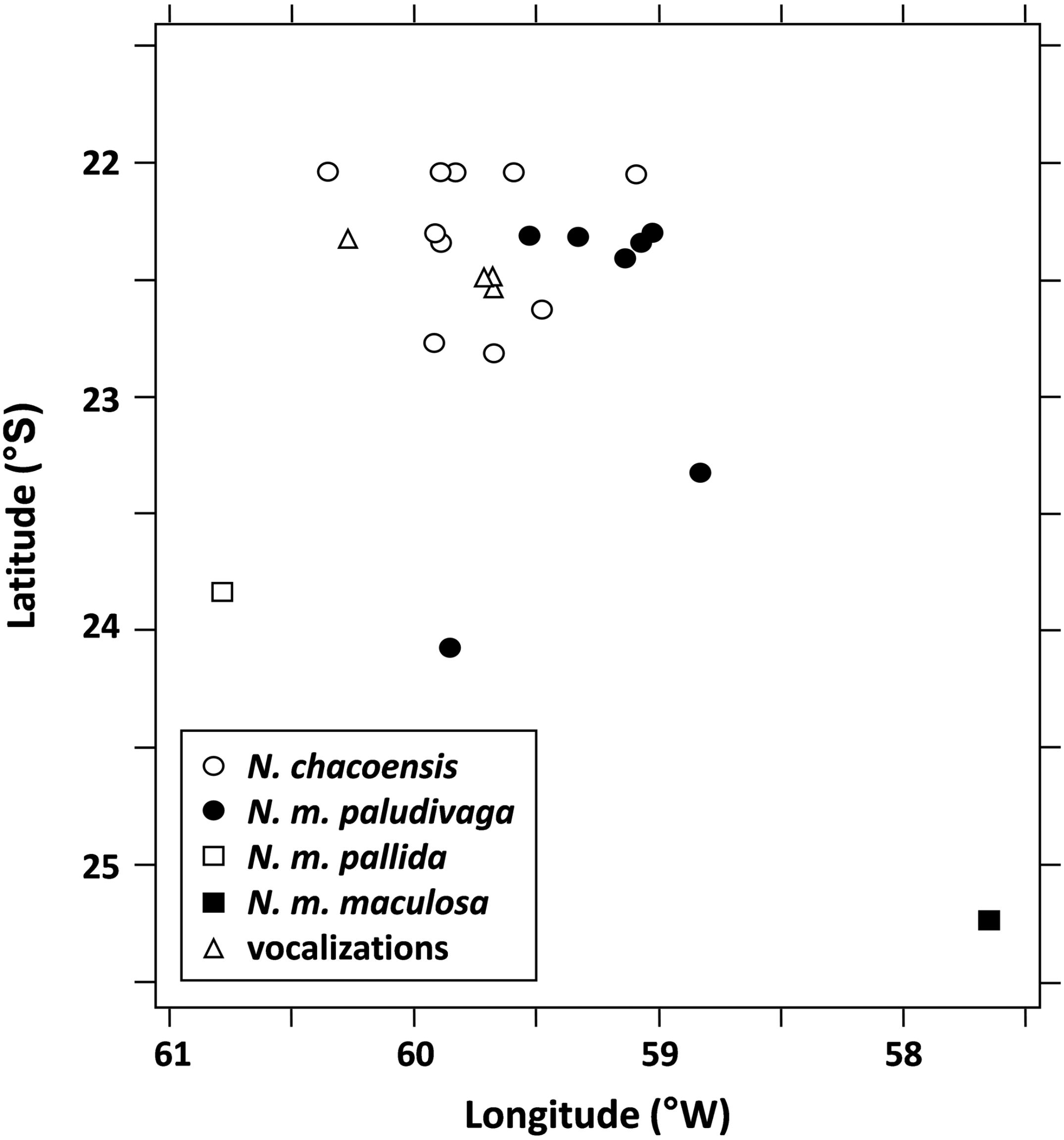

FIGURE 1. Distribution of *Nothura chacoensis* and three subspecies of *N. maculosa* in the Paraguayan Chaco, based on specimens examined in this study at the AMNH, FMHN, UMMZ, and specimens examined by Steinbacher (1962) and Short (1975) at SMF and ZFMK. The locations of our recordings of *Nothura* tinamou vocalizations are also plotted, demonstrating that they were within the geographical range of *N. chacoensis* but not that documented for *N. maculosa*.

FIGURE 2. Ventral and dorsal views of *Nothura* specimens (all in FMNH) from the Paraguayan Chaco. From left to right: *N. m. paludivaga* with the palest underparts (16350), the type specimen (17653), and the darkest underparts (17657); *N. chacoensis* with the palest underparts (13665), the type specimen (12501), and the darkest underparts (12113); and a specimen of nominate *N. m. maculosa* (418092). Photo by Justin Ling.

Nothura chacoensis and *N. m. paludivaga* do not differ significantly in BL, WL, TL, MT, PC1, or PC2 for either sex or for both sexes combined (P > 0.05 for all variables; Table 1). No significant sexual dimorphism occurs for any measurement within each taxon or for both taxa combined (P > 0.05 for all variables; Table 1). A scatterplot of PC1 (eigenvalue = 1.57 with 39.3% of variation) versus PC2 (eigenvalue = 1.20 with 30.1% of variation) for both sexes combined reveals complete morphological overlap between the two taxa (Figure 3).

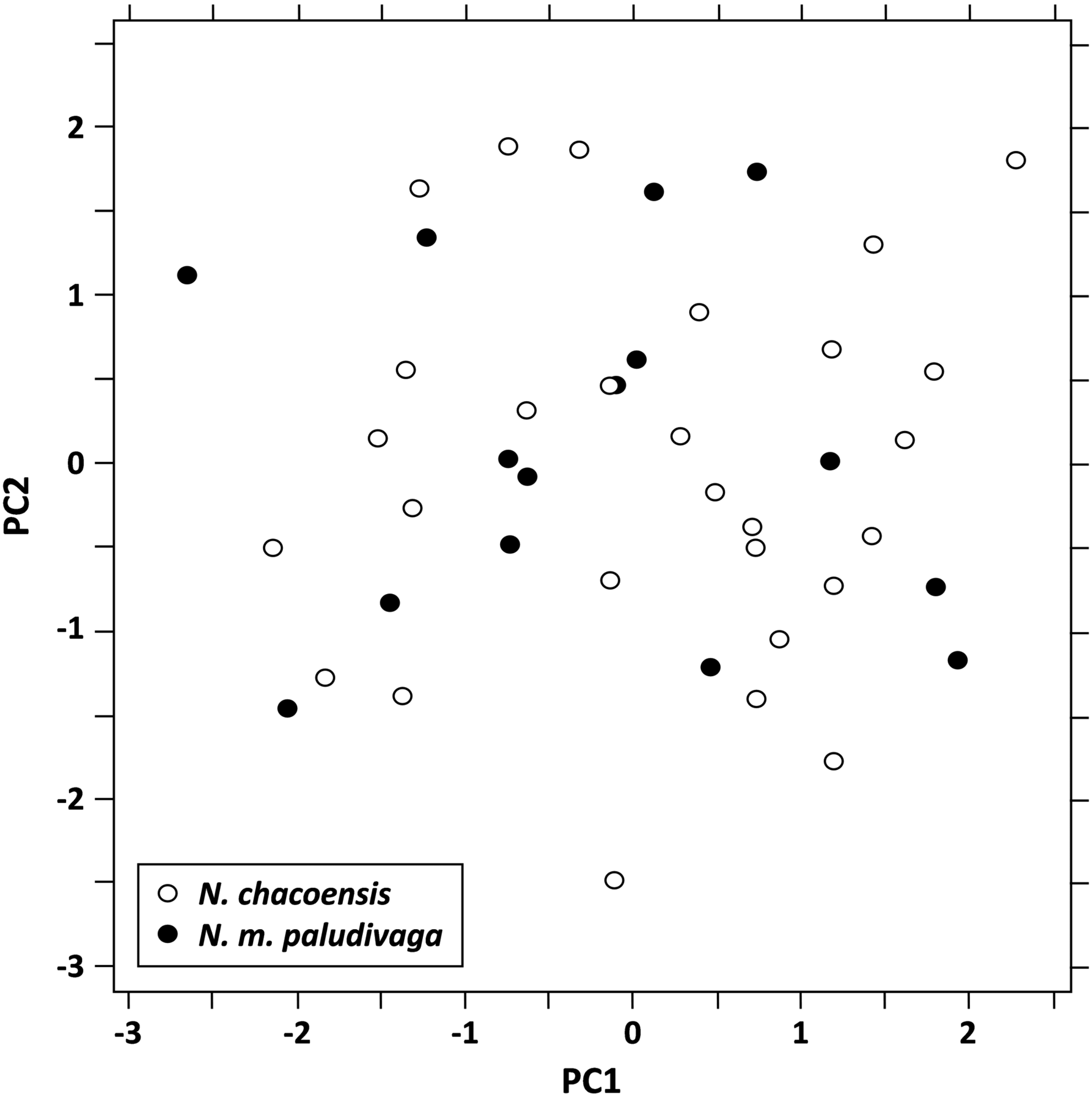

FIGURE 3. Principal component analysis of four morphometric variables for *Nothura m. paludivaga* and *N. chacoensis*.

Vocalizations. *Nothura chacoensis* readily responded to playback of *N. maculosa* recordings. On 29 Aug 2016 we recorded vocalizations of *N. chacoensis* at three localities near Laguna Capitán, Dpto. Presidente Hayes (22°32'37"S 59°40'27"W): 22°30'48.8"S 59°42'16.8"W, 22°29'41.1"S 59°42'25.0"W, and 22°29'41.5"S 59°41'34.6"W. Although we heard at least five different individuals at the first locality, three at the second, and three at the third, we are uncertain how many individuals were recorded at each site. On 30 Aug 2016 we heard two more *N. chacoensis* at Laguna Capitán (22°32'36.9"S 59°40'25.1"W), but the vocalizations were too distant to obtain a quality recording, and we observed two others nearby. On 27 Feb 2017 we recorded vocalizations of one *N. chacoensis* 7 km ENE of Fortín Toledo, Dpto. Boquerón (22°20'23"S 60°15'41"W). Despite searching for *N. chacoensis* at several other localities, including the type locality, on 25 Feb 2017, we were unable to obtain any additional recordings.

TABLE 1. Morphological variation (mean, SD, range) in bill length (BL), wing length (WL), tarsus length (TL), middle toe length (MT), inferred body size (PC1), and inferred body shape (PC2) in N. m. paludivaga (n = 5 m#, 10 f#) and N. chacoensis (n = 13 m#, 15 f#) specimens from the Paraguayan Chaco. All measurements are in mm except PC1 and PC2 (see Methods).

		N. m. paludivaga			*N. chacoensis*		
Variable	Sex	Mean	SD	Range	Mean	SD	Range
BL	♂	19.2	1.3	18–21	19.1	0.8	18–20
	♀	19.8	1.3	18–22	19.3	1.2	18–21
WL	♂	122.8	4.2	119–130	121.7	4.4	116–129
	♀	124.6	2.8	119–128	122.2	6.0	105–131
TL	♂	32.0	2.7	29–36	32.1	1.6	30–36
	♀	33.2	2.4	29–38	32.3	2.5	28–38
MT	♂	28.4	1.8	26–30	28.4	1.5	27–32
	♀	28.7	1.3	27–31	28.9	1.5	26–31
PC1	♂	0.2	1.6	-2.1–1.8	0.27	1.2	-1.8–1.8
	♀	-0.4	1.2	-2.7–1.9	-0.0	1.3	-2.1–2.3
PC2	♂	-0.2	1.2	-1.5–1.7	-0.19	0.9	-1.4–1.6
	♀	0.2	1.0	-1.2–1.6	0.1	1.3	-2.5–1.9

All recorded vocalizations of *N. chacoensis* consisted of a very rapid, relatively monotone trill, starting faintly, increasing in volume, and ending abruptly. The recorded vocalizations fall entirely within the range of the "high pitched, continuous trill" (Bump & Bump 1969) of *N. maculosa* in length, number of notes, rate of notes, and emphasized frequency (Figure 4, Table 2). At the locality 7 km ENE of Fortín Toledo we also recorded "flutelike whistles" (Narosky & Yzurieta 1989) which sounded very similar to those of *N. maculosa*, but because of background noise the quality of the recordings was insufficient for comparison with those of *N. maculosa*.

The typical song of *N. darwinii* in XC recordings, described by Bump & Bump (1969) as the "trill call," is similar to the presumably homologous trill of *N. chacoensis* and *N. maculosa*, but is usually longer and always slower in the rate of notes per sec (Figure 4, Table 2).

TABLE 2. Range of variation in vocal characters of typical territorial songs of *Nothura* tinamous: song length (sec); number of notes in song; rate of notes (notes/sec); emphasized frequency (kHz); and number of songs (minimum number of individuals) analyzed. See Appendix 2 for a list of recordings analyzed.

Species	Song length	Notes in song	Rate of notes	Emphasized frequency	Songs (individuals)
N. boraquira	29.8–51.6	12–27	0.4–0.7	2.1–2.9	5 (4)
N. minor	10.2–12.4	9–17	0.9–1.6	3.9–4.1	3 (3)
N. darwinii	4.0–8.1	43–74	8.2–11.7	2.3–2.7	23 (4)
N. maculosa	3.0–6.6	51–98	14.3–21.3	2.3–2.9	25 (13)
N. chacoensis	3.3–4.5	56–77	15.3–17.5	2.8–2.9	12 (4)

The typical songs of *N. boraquira* and *N. minor* in XC recordings are much longer and slower than the trills of *N. darwinii*, *N. maculosa*, and *N. chacoensis* (Table 2), as well as the slower "flutelike whistles" of *N. darwinii* and *N. maculosa* (Narosky & Yzurieta 1989, Bump & Bump 1969; XC). Because multiple individuals appeared to be calling on most relatively clean recordings of *N. boraquira*, we selected five in which we were confident that the songs of one individual could be isolated from other individuals and measured (Appendix 2). The typical song of *N. boraquira* consists of a series of one- or two-noted calls (sometimes slurred together) up to 0.6 sec long with intervals of 2.1–8.7 sec between calls; when two notes were given, the first note is usually longer, louder, and sometimes differs slightly in frequency from the second note (Figure 4, Table 2). *Nothura boraquira* apparently lacks the rapid trill call of *N. darwinii*, *N. maculosa*, and *N. chacoensis* (Bump & Bump 1969; Davies 2002; XC).

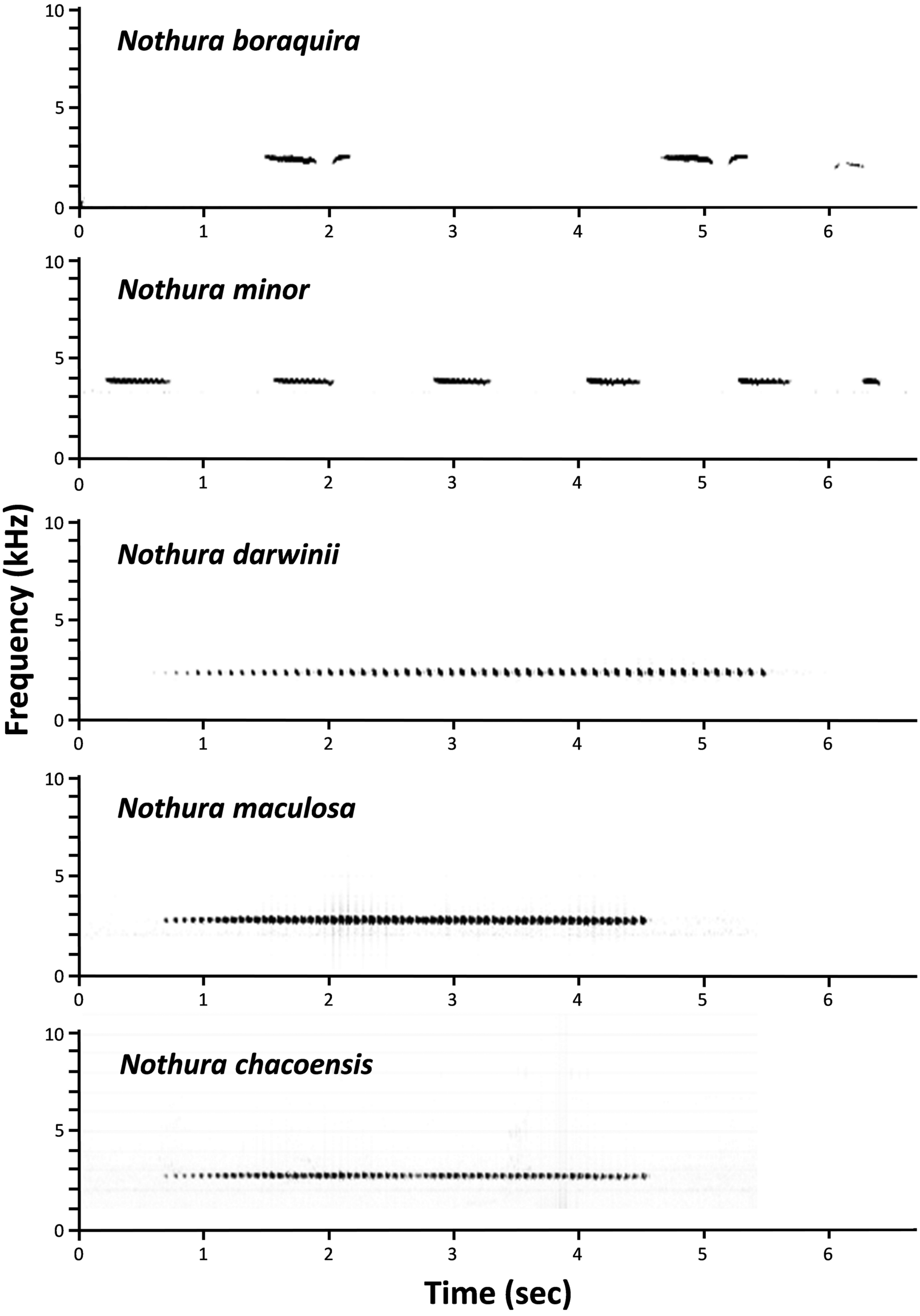

FIGURE 4. Typical territorial vocalizations of *Nothura* tinamous: *N. boraquira* (partial song of XC15370 from Bolivia by Juan Mazar Barnett); *N. minor* (partial song of XC283242 from Brazil by Robson Silva e Silva); *N. darwinii* (XC226707 from Peru by Peter Boesman); *N. maculosa* (XC319690 from Brazil by Robson Silva e Silva); and *N. chacoensis* (XC345716 from Paraguay by Oscar Rodríguez).

Only three XC recordings of the territorial songs of *N. minor* were usable in this analysis. Its typical song consists of a series of long notes up to 0.5 sec long or a shorter series of long notes with intervals of 0.6–1.4 sec between notes, followed by a faster series of shorter notes, all at a higher frequency than that of any other *Nothura* species (Figure 4, Table 2). Davies (2002) mentioned *N. minor* giving a trill similar to *N. maculosa.* A recording of a trill attributed to *N. minor* (XC 36840) may have been misidentified because it appears identical to that of *N. maculosa* (2.7 kHz, 2.9 sec long, 54 notes, 18.6 notes/sec).

Discussion

Geographic distribution. Although Conover (1950) suggested that *N. chacoensis* and *N. m. paludivaga* may overlap in distribution, which others used as evidence that they were distinct species (Blake 1977; Sibley & Monroe 1990; Cabot 1992), there is no locality at which specimens of both taxa were collected. Thus, the criterion of sympatry cannot be used to consider *N. chacoensis* a distinct species.

The previously unreported specimens of nominate *N. m. maculosa* from Dpto. Presidente Hayes represent the first records west of the Paraguay River in the Paraguayan Chaco. Although the nominate race occurs east of the Paraguay River and Paraná River, Conover (1950) reported specimens of nominate *N. m. maculosa* from west of the Paraná River in Santa Fe Province in the Argentinian Chaco. The Paraguay River does not appear to have formed a historical barrier to its distribution.

Morphological variation. The plumage of *N. chacoensis* is more similar to *N. m. paludivaga* than to nominate *N. m. maculosa*, suggesting that *N. maculosa* is a paraphyletic taxon if *N. chacoensis* is excluded. *Nothura m. paludivaga* and *N. chacoensis* do not differ in any size or shape measurement, suggesting a very close relationship. Although most specimens of *N. m. paludivaga* and *N. chacoensis* are separable by subtle differences in plumage color, overlap between the taxa in plumage color and the absence of a discernible zone of hybridization are more suggestive of primary intergradation than secondary intergradation. The slightly paler coloration of *N. chacoensis*, which occurs in a drier part of the Paraguayan Chaco than areas inhabited by *N. paludivaga* and nominate *N. m. maculosa* (Hayes 1995), is consistent with Gloger's "rule," which predicts that populations in more humid areas are more heavily pigmented than those in drier areas (Zink & Remsen 1986).

Vocalizations. Each species of tinamou has a unique repertoire of vocalizations, consisting of a few different songs and calls, which are important for intraspecific recognition (Cabot 1992; Davies 2002). Three distinct vocalizations have been described for *N. maculosa*, including: (1) a "high pitched, continuous trill," considered the most frequent vocalization and thought to represent its territorial song (Bump & Bump 1969); (2) a series of "flutelike whistles, accelerating at the end" (Narosky & Yzurieta 1989) or "short, impressive whistling (to us peeping) notes" (Bump & Bump 1969), often given while trilling but more frequently when disturbed, possibly representing low-intensity alarm calls by alerting other individuals to the presence of danger (Bump & Bump 1969); and (3) high-intensity alarm calls, consisting of "high pitched 'quit, quit, quit' notes," given when disturbed (Bump & Bump 1969). Similar calls were described for *N. darwinii*, but the "trill call" song was given less often than the "flutelike whistles" (Bump & Bump 1969).

We recorded mostly one song type of *N. chacoensis*, which is indistinguishable from the "high pitched, continuous trill" song (Bump & Bump 1969) of geographically widespread *N. maculosa*. We also recorded "flutelike whistles" of *N. chacoensis* that are similar to those of *N. darwinii* and *N. maculosa* (Bump & Bump 1969; XC), but the recording quality was insufficient for analysis. The extreme similarity, as first reported on the basis of unrecorded aural comparisons by Smith (2006), in the trill songs of *N. chacoensis* and *N. maculosa*, especially compared with the longer and slower homologous trill song of *N. darwinii* and the much different songs of *N. boraquira* and *N. minor*, provides strong evidence that *N. chacoensis* and *N. maculosa* are conspecific.

The strong similarity in trill songs between *N. darwinii* and *N. maculosa*, which we analyzed (Table 2), and in a slower series of flutelike calls (XC), which we did not analyze, are consistent with some phylogenetic analyses concluding that *N. darwinii* and *N. maculosa* represent sister taxa when *N. chacoensis* and extinct *Nothura* species are ignored (Bertelli *et al.* 2002; Porzecanski 2003; Bertelli & Tubaro 2002; Tubaro & Bertelli 2003; Bertelli & Porzecanski 2004; Bertelli 2016), but not in other analyses (Porzecanski 2003; Bertelli *et al.* 2014). The less striking similarity of songs between *N. boraquira* and *N. minor* suggest that they may also represent sister taxa, which is consistent with some phylogenetic analyses (Bertelli *et al.* 2002; Bertelli & Tubaro 2002; Tubaro & Bertelli 2003), but not others (Porzecanski 2003; Bertelli & Porzecanski 2004; Bertelli *et al.* 2014; Bertelli 2016).

Conclusions. Based on the lack of known sympatry between *N. chacoensis* and *N. maculosa*, combined with their similarities in morphology, cytochrome *b* sequences, and vocalizations, we conclude that *N. chacoensis* is unlikely to be reproductively isolated from *N. maculosa* as required for species status under the biological species concept (e.g., Johnson *et al.* 1999), or sufficiently diagnosable from *N. maculosa* as required for species status under the phylogenetic species concept (e.g., McKitrick & Zink 1988). Given the average differences in plumage coloration of *N. chacoensis* from adjacent subspecies of *N. maculosa* to the east and south (*N. m. paludivaga*) and southwest (*N. m. pallida*; Conover 1937, 1950; Short 1975, 1976), and the overlap of plumage coloration between the two forms, we conclude that primary intergradation (clinal variation) occurs and that *N. chacoensis* should be regarded as a subspecies of *N. maculosa*, with the trinomial *N. m. chacoensis*, as it was originally described (Conover 1937). Despite the similarity in plumage coloration between *chacoensis* and *paludivaga* and the presence of a few intermediate specimens with overlapping plumage traits, we concur with the identification of 100% of the specimens as subjectively identified (presumably by Conover 1950) by their museum labels, which meets the traditional "75 per cent rule" for diagnosability of subspecies (Amadon 1949) and even the more stringent "95 per cent rule" advocated by Patten & Unitt (2002).

The Chaco biogeographical region is considered a major center of endemism for numerous species and subspecies of birds (Short 1975; Cracraft 1985; Haffer 1985). Conover's (1950) hypothesis that *N. chacoensis* evolved while isolated in the central Paraguayan Chaco by flood basins of the Paraguay River and Pilcomayo River is supported by geological evidence for multiple periods of extensive flooding in the past (Kruck *et al.* 2011; McGlue *et al.* 2012). However, there is scant biogeographical evidence that the Paraguay River has ever formed a substantial barrier to bird dispersal (Hayes 1995), even in the case of weak-flying tinamous. *Nothura m. paludivaga* occurs to the west of the Paraguay and Paraná Rivers in the Chaco of Paraguay and Argentina, but crosses the Paraguay River in northeastern Paraguay, and *N. m. maculosa* occurs to the east of the Paraguay River in Paraguay and Argentina, but crosses the Paraguay River in Paraguay and the Paraná River in Argentina, with no evidence of differentiation on opposing sides of the river (Conover 1950). The distributional, morphological, genetic, and vocal evidence in *Nothura* tinamous suggests that past periods of inundation of the Paraguay and Pilcomayo rivers did not form a sufficient barrier for speciation to occur within the genus in the Paraguayan Chaco.

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APPENDIX 1.

Localities and approximate coordinates of adult *Nothura maculosa* and *N. chacoensis* specimens from the Paraguayan Chaco examined during this study (FMNH, UMMZ) and earlier by FEH (AMNH). *Nothura maculosa maculosa*: Chaco-í (25°14'S, 57°44'W; FMNH 418091, 418092). *Nothura maculosa paludivaga*: Laguna General Díaz (22°18'S, 59°01'W; FMNH 416352–416354, 417655–417657); 7 km SW of Laguna General Díaz (22°21'S, 59°04'W; FMNH 417653–417654); 17 km SW of Laguna General Díaz (22°25'S, 59°08'W; FMNH 416346–416350); 30 km NE of Villa Militar (22°19'S, 59°32'W; FMNH 416351); Makthlawaiya (23°20'S, 58°50'W; AMNH 320742–320743); 235 km W of Riacho Negro, Estero Patiño (24°05'S, 59°49'W; UMMZ 105232). *Nothura chacoensis*: 265 km W of Puerto Casado (22°03'S, 60°21'W; FMNH 412108–412115, 412501, 413259, UMMZ 90889, 92573–92574, 93029–93030); 200 km W of Puerto Casado (22°03'S, 59°53'W; AMNH 305616, FMNH 413666, 418093); 195 km W of Puerto Casado (22°03'S, 59°50'W; FMNH 413667, UMMZ 93782); 170 km W of Puerto Casado (22°03'S, 59°36'W; FMNH 413260); 120 km W of Puerto Casado (22°03'S, 59°50'W; FMNH 413665, 415650, UMMZ 96004–96005); 16 km E of Filadelfia (22°21'S, 59°53'W; FMNH 417648–417650); Orloff (22°19'S, 59°55'W; FMNH 417651–417652); 60 km E of Orloff (22°19'S, 59°19'W; AMNH 802523); Lichtenau (22°50'S, 59°40'W; AMNH 803133, 809555–809559); 120 km W of Puerto Pinasco (22°38'S, 59°28'W; UMMZ 96005–96006). *Nothura maculosa maculosa*: Chaco-í (25°15'S, 57°39'W; FMNH 418091–418092).

APPENDIX 2.

Sonograms of vocalizations measured in this study. *Nothura boraquira*: Bolivia (XC15370); Brazil (XC40026, XC49563, XC103787, XC103788). *Nothura minor*: Brazil (XC283242, XC298304, XC303547). *Nothura darwinii*: Argentina (XC90300, XC90304, XC90306); Peru (XC39787, XC226706–XC226707). *Nothura maculosa*: Argentina (XC273214, XC273216–273217); Brazil (XC5208, XC8586, XC17082, XC36591, XC105632, XC176452, XC211654, XC226708, XC319690); Uruguay (XC51594). *Nothura chacoensis*: Paraguay (XC345712–345716, XC361091–361092).