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Mate recognition systems and species limits in a warbling-finch complex (*Poospiza nigrorufa/whitii*)

Emilio Ariel Jordan[a], Juan Ignacio Areta [b] and Ingrid Holzmann[b]

[a]Laboratorio de Ornitología. Materi y España, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CONICET-Prov. de Entre Ríos-UADER), Diamante, Argentina; [b]Laboratorio de Ecología, Comportamiento y Sonidos Naturales (ECOSON), Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO-CONICET), Salta, Argentina

ABSTRACT

Species limits in the *Poospiza nigrorufa/whitii* complex are not well understood. Three taxa formally described as species are now considered as subspecies (*nigrorufa*, *whitii* and *wagneri*) of a widespread species. The heavier *nigrorufa* has longer bill, tarsus and wings, is slightly dimorphic with males showing tawny rufous throat, breast and flanks, and brownish grey upper parts with a slate tinge, while females differ in the orange tinge of ventral parts and in the more olivaceous upper parts; inhabits shrubby open areas and wetlands with reeds and bulrushes in eastern southern South America, and gives a simple three-note pattern that repeats to form the song and diagnostic calls. The lighter *whitii* (including *wagneri* as a synonym) has a shorter bill, tarsus and wings, is highly dimorphic with males having dark chestnut throat, breast and flanks, and slate upper parts, while females exhibit tawny pale-orange ventral parts, and olivaceous light-brown upper parts; inhabits closed to semi-closed xerophytic to semi-humid scrub and woodlands in the western highlands, and has a complex multi-noted song and diagnostic calls. Reciprocal playback experiments indicate that both taxa are able to discriminate each other's songs. Locality data and ecological niche modelling show that *nigrorufa* and *whitii* are narrowly allopatric or parapatric in central Córdoba province (Argentina).This integrative evidence and the ~2.5% divergence in mtDNA show that *nigrorufa* and *whitii* possess different Specific Mate Recognition Systems and should be afforded full species status under any species concept.

A major issue in biology is to determine species limits in naturally occurring populations. There are many ideas on what species are, leading to a diversification of its operational counterpart of how avian species should be delimited (Zink and McKitrick 1995; Remsen 2005; de Queiroz 2007; Sangster 2014). Two main concepts define species in terms of fields of genetic recombination. The widely used Isolation Concept (IC, generally known as the Biological Species Concept, BSC) defines a species as groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1970). Importantly, the focus of the IC in adaptive reproductive isolation demands a phase of secondary contact and reinforcement to complete the speciation process through the development of so-called 'isolating mechanisms' (Paterson 1985). In the Recognition Concept (RC) species form when habitat changes in allopatry lead to adaptive changes in the Specific Mate Recognition System (SMRS) and hence in the Fertilization System that delimits species. The SMRS

is a co-adapted system of signalling whose goal is to bring members of a pair (or their gametes) together to allow copulation, and that operates correctly in the normal habitat of a species. Hence, habitat changes are thought to trigger the speciation process and two sister species are expected to differ in their normal habitats and in their SMRS. Under the RC, isolation between species is seen as an incidental effect of intrinsic changes in the SMRS and there would be no 'isolating mechanisms' evolved for their value in isolating any two species during the secondary contact phase of speciation (Paterson 1980, 1985).

Under both, the IC and the RC, reproductive isolation (whether adaptive or incidental) can be directly tested when members of populations of uncertain status occur in sympatry, leading to the interpretation of differences in phenotypic and genotypic traits of such populations as intrinsic barriers to gene flow. Since interbreeding of allopatric populations cannot be directly tested, allopatric populations pose a serious challenge to the IC, but not necessarily to the RC. To

overcome this problem, researchers frequently quantify differences in characters to infer whether two populations or taxa would remain perfectly distinct, exhibit essential reproductive isolation or interbreed freely in the case of a secondary contact (Isler *et al.* 1998; Assis *et al.* 2007; Tobias *et al.* 2010).The degree of divergence of allopatric taxa in comparison to those of closely related taxa known to have reached reproductive isolation provides a yardstick against which to evaluate whether or not allopatric taxa will remain distinct after secondary contact (Helbig *et al.* 2002; Remsen 2005; Gill 2014). Even though plumage and vocal traits are important pre-mating barriers in birds, analyses of differences in plumage and vocalisations frequently assume that the traits measured are the same that birds use in mate recognition, but this inference might not be valid for all cases (Pegan *et al.* 2015). Behavioural responses of birds to these differences are most relevant, and playback experiments provide useful (but underused) tools to evaluate the role of vocal traits as barriers to gene flow (Lanyon 1963; Ábalos and Areta 2009; Areta and Pearman 2013; Burbidge *et al.* 2015; Sangster *et al.* 2016).

Modern views argue that species limits are best evaluated by analysing several types of evidence in an integrative framework (Dayrat 2005; Padial *et al.* 2010). The Poospizinae tanagers (Burns *et al.* 2016) present several challenges for species delimitation: plumage and morphology exhibit marked convergences and are bad indicators of phylogenetic relationships (Lougheed *et al.* 2000; Shultz and Burns 2013), differences in vocal traits of geographically isolated populations may be a consequence of learning as in other tanagers making their interpretation as indicator of species limits difficult (Areta and Repenning 2011; Rising 2011), and the geographic ranges of possibly coexisting taxa and their boundaries are not known in detail (Hilty 2011; Jaramillo 2011; Rising 2011).

The Black-and-rufous/Chestnut Warbling-Finch (*Poospiza nigrorufa*/*whitii*) complex fits in the common pattern of allopatric sister taxa that may harbour more than one species, but no formal taxonomic study has addressed this possibility using an integrative approach. Currently three subspecies are recognised in this complex: *nigrorufa, whitii* and *wagneri*, the latter of which has been considered doubtfully distinct from *whitii* (d´Orbigny and Lafresnaye 1837; Sclater 1883; Sztolcmann 1926; Jaramillo 2011). Both *nigrorufa* and *whitii* were treated as full species (e.g. Sclater and Hudson 1888; Frenzel 1891; Stempelman and Schulz 1891; Lillo 1905; Friedmann 1927), until Hellmayr (1938) lumped them together, claiming that the taxon

whitii was the western representative of *nigrorufa*. Since then no critical review of their status has been undertaken, leading to their treatment as a single geographically variable species (e.g. Meyer de Schauensee 1966; Paynter 1970; Dickinson *et al.* 2004; Clements *et al.* 2016) or as a full species (e.g. Ridgely and Tudor 1989; Sibley and Monroe 1990; Mazar Barnett and Pearman 2001; del Hoyo *et al.* 2017). More recently, genetic data indicated that *nigrorufa* and *whitii* are well-differentiated sister taxa with levels of mtDNA divergence (*ca.*2.5% for cyt-b and ND2) similar to those of other Poospizinae sister species (Shultz and Burns 2013). The sister taxa *nigrorufa* and *whitii* share a general coloration pattern and are morphologically more similar in plumage than most pairs of sister species in their group with comparable genetic distances (Shultz and Burns 2013). For example, their sister clade is conformed by the Bolivian Warbling-Finch (*Poospiza boliviana*) and the Cinnamon Warbling-Finch (*Poospiza ornata*) that differ drastically in plumage (Lougheed *et al.* 2000; Jaramillo 2011; Shultz and Burns 2013; Burns *et al.* 2014). However, the plumage differences between *whitii* and *nigrorufa* are similar to those found between the recently split Grey-throated Warbling-Finch (*Microspingus cabanisi*) and Buff-throated Warbling-Finch (*M. lateralis*) (Assis *et al.* 2007), and exceed those of the genetically similar and morphologically very similar Cinereous Warbling-Finch (*M. cinereus*) and Black-capped Warbling-Finch (*M. melanoleucus*), whose specific status is not settled (Paynter 1970; Ridgely and Tudor 1989; Shultz and Burns 2013).

In this work we analyse the species limits in the *Poospiza nigrorufa*/*whitii* complex by combining morphological, plumage, habitat and distributional data, potential distribution models based on ecological niches, descriptions of vocalisations and the results of reciprocal playback experiments. We conclude that two monotypic species must be recognised in the complex based on their divergent SMRS.

Methods

Morphology

To evaluate whether warbling-finches differed in morphology we measured 106 specimens of *nigrorufa* and 91 specimens of *whitii* deposited at the Fundación Miguel Lillo (FML, Tucumán), Museo Argentino de Ciencias Naturales (MACN, Buenos Aires), and Museo de La Plata (MLP, La Plata). We also extracted weight data from labels of these specimens and those at the Field Museum of Natural History (FMNH,

Chicago) and National Museum of Natural History (NMNH, Washington, DC) (see Appendix A). We measured exposed culmen, bill length (distance from the posterior edge of the nostril to the bill tip), bill height at the anterior edge of the nostril, and tarsus length to the nearest 0.05 mm with digital callipers; and unflattened wing chord and tail length (base to tip of central pair of rectrices) with a metallic ruler to the nearest 0.5 mm. We compared morphological measurements of museum specimens with two-tailed *t*-tests (alpha = 0.01) when morphological variables were normally distributed (Shapiro–Wilks tests; alpha >0.05). Since wing chord measurements were not normally distributed we compared species values using the Mann–Whitney *U*-test (alpha = 0.01). When we found no differences between sexes (two-tailed *t*-tests; alpha = 0.01), morphological data from all specimens per taxon were lumped. For these analyses we used InfoStat/E (Di Rienzo *et al.* 2014).

We examined photographs of the type specimens of *Poospiza whitii* Sclater, 1883 and *Poospiza wagneri* Sztolcmann, 1926. There is no physical type specimen of *Emberiza nigro-rufa* d´Orbigny and Lafresnaye 1837 (currently *Poospiza nigrorufa*) that is a name based on Azara's (1802) description of the 'Chipíu negro y canela' (Hellmayr 1938) (see Taxonomic remarks).

Occurrence data

We compiled locality records for *nigrorufa* and *whitii* from three sources: (1) internet databases (eBird and Macaulay Library of Natural Songs, Cornell Lab of Ornithology, Ithaca, New York, USA; Xeno-canto, www.xeno-canto.org; Ecoregistros, www.ecoregistros.org), (2) publications in widely read journals and grey literature, and (3) label data of museum specimens examined or obtained through their online databases (Table S1).

Since in the central area of Córdoba province (Argentina) there are presumed records of both species in close localities, records between −64 and −62 degrees of longitude in this province were critically analysed to corroborate their specific identity. Records within this potential zone of overlap or parapatry were considered valid when documentation was available or when the author of the record provided good plumage or vocal descriptions that allowed for unambiguous identification. As a result, we obtained 781 locality records for *nigrorufa* and 322 for *whitii* (Online Resource 1).

Potential distribution models

We modelled the distributions of *nigrorufa* and *whitii* with MaxEnt 3.3.3k, using 500 iterations, 0.00001 convergence threshold, 10 000 maximum background points and all five auto-feature classes (Phillips *et al.* 2006). The program randomly withholds 25% of the presence locations to test performance of the model (Phillips *et al.* 2006). To avoid skewing the model's results, we rasterised locations to a 1 km^2 area, so that even if numerous presence locations were reported for within this area, presence data were reduced to a single record per 1 km^2 grid cell (Kramer-Schadt *et al.* 2013; Holzmann *et al.* 2015). After rasterisation, models were run using 678 presence localities for *nigrorufa*, and 304 for *whitii*.

For all taxa, we first ran a model in MaxEnt using all 19 bioclimatic variables of the set of WorldClim global climate layers with data collected between 1950 and 2000 at a resolution of 30 arc-seconds (*ca.*1 km^2; www.worldclim.org/; Hijmans *et al.* 2005). We evaluated the predictive efficacy of these 19 variables using the jackknife test of variable importance (training and test data) and variable response curves (Baldwin 2009). We eliminated variables that showed low (close to zero) or negative gain values for the training data. Low gains indicate that the variables did not have useful information by themselves for estimating distribution, while negative gains indicate that the variables make the model less transferable to other areas or conditions. With these variables removed, we ran a final model for each species using only informative variables. For final models we removed nine bioclimatic variables for *nigrorufa* (bio2, bio8, bio9, bio12, bio14, bio16, bio17, bio18 and bio19), and three for *whitii* (bio5, bio8 and bio10).

We evaluated the performance of the final model using the area under the curve (AUC; Fielding and Bell 1997). Whereas an AUC = 1 indicates that the model accurately discriminates between areas with presence and non-presence, an AUC = 0.5 indicates that the model predicts as well as a random model and an AUC <0.5 indicates that the model's predictive capability is worse than random (Elith *et al.* 2011). We used the logistic output that represents the potential habitat suitability of the species on a scale of 0–1, with higher values representing more favourable conditions for the presence of the species (Phillips *et al.* 2006). We applied the minimum training presence (MTP) as a threshold or 'cutoff' value for each model because it is the most conservative threshold, as it identifies the minimum predicted area possible while still maintaining a zero omission rate for both training and test data (Liu *et al.* 2005; Giovanelli *et al.* 2010; Bellamy *et al.* 2013). Ecologically, the MTP can be interpreted to contain those cells that are predicted to be at least as suitable as those where the species was identified as present.

We divided habitat suitability values in our final models into four discrete classes (unsuitable, low, moderate, and high suitability). In order to give classes representing low, moderate and high suitability visual representation we separated them into equal intervals by resting the lowest (MTP) value to the highest limit of the prediction set by the model and dividing this value by three.

Vocalisations

We compiled available recordings of *nigrorufa* and *whitii* in the Macaulay Library of Natural Sounds (MLNS, Cornell Laboratory of Ornithology, Ithaca, NY, USA), Xeno-Canto (XC, www.xeno-canto.org), Bird Sounds Database of the Florida Museum of Natural History (FLMNH, Florida, USA), and published sound tapes. We also recorded vocalisations with Telinga Pro 6 and Sennheiser ME-62 microphones mounted on Telinga Universal parabolas connected to Marantz PMD-661 and PMD-661 MKII digital sound recorders. Our recordings are deposited at the MLNS. We also searched for recordings at Borror Laboratory of Bioacoustics (Museum of Biological Diversity, Columbus, OH) and AVoCet (Michigan State University, MI), without success.

To find qualitative differences in vocalisations of *nigrorufa* and *whitii* we examined recordings aurally and visually with the aid of spectrograms. We analysed calls of 18 individuals (*nigrorufa* n = 14, *whitii* n = 4) and songs of 108 individuals (*nigrorufa* n = 81, *whitii* n = 27) (Appendix B). Spectrograms were built in Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY) with the following parameters: for *nigrorufa* Window – Type: Hann, Size: 1024 samples (=23.2 ms), 3dB Filter Bandwidth: 61.9 Hz; Time grid – Overlap: 50%, Hop size: 512 samples (=11.6 ms); Frequency grid–DFT size: 1024 samples, Grid spacing: 43.1 Hz. For *whitii* Window – Type: Hann, Size: 512 samples (=11.6 ms), 3 dB Filter Bandwidth: 124 Hz; Time grid – Overlap: 50%, Hop size: 256 samples (=5.8 ms); Frequency grid–DFT size: 512 samples, Grid spacing: 86.1 Hz. We used different window sizes that allowed us to accurately display enough of the fine structure of the notes of each species. The greater window size was used for the longer and whistled notes of the slower paced song of *nigrorufa*, while a smaller window size was better for the shorter, sometimes trilled, notes of the faster paced songs of *whitii*.

We applied Remane´s criteria (Wenzel 1992) to identify homologies among notes within species. According to these criteria, two notes are homologous when: (1) they share a position relative to the other in a sequence (Remane´s position criterion), and/or (2) share a distinctive form in a spectrogram (Remane´s special quality criterion).

Playback experiments

We carried out 20 reciprocal playback experiments in Argentina during the breeding season: 10 between September 2016 and February 2017 with *nigrorufa* as target (in Entre Ríos province: three experiments in Diamante, three in Aldea Protestante, one in Strobel; in Buenos Aires province: three in Reserva Natural Punta Lara), and 10 between January and February 2017 with *whitii* as target (all in Salta province: three in San Lorenzo, and seven in Reserva Natural Finca Las Costas).

Each experimental subject was treated with a single 'sandwich-playback trial'. Sandwich-playback tracks were of two types and each contained stimuli of both species, either conspecific–heterospecific–conspecific or heterospecific–conspecific–heterospecific. Each conspecific or heterospecific stimulus lasted 20 s and contained three songs. Successive stimuli within a sandwich were separated by 90 s of silence, during which playback responses were evaluated. In order to avoid pseudoreplication (Kroodsma 1989), each sandwich-playback track was built using different combinations and orders of songs taken from our extensive sound database. Sandwich-playback tracks were made with songs of 10 individuals of *whitii* from nine different localities, and 13 individuals of *nigrorufa* from 11 different localities (see Appendix B). In order to avoid possible responsiveness bias to local vocalisations (Kroodsma 1989), conspecific songs used in playback experiments were recorded more than 2 km away and frequently between 50 and 700 km from the target individual. Digital files were played back using a portable speaker set at 81–85 dB SPL at 1 m to approximately match the natural intensity of songs. We ranked the responses to each stimulus of a trial in four categories of increasing intensity: (1) lack of response (no change in behaviour), (2) silent approach, (3) vocalisation without approach (if the bird was not singing previously), and (4) approach with vocalisation. In some experiments, birds in response to conspecific playback approached and vocalised but continued singing beyond the 90 s gap. In these cases, the following heterospecific playback did not elicit any approach or change in behaviour. Hence, the heterospecific response was categorised as 'lack of response' and the homospecific as 'approach with vocalisation' (four individuals of *nigrorufa* and two of *whitii*). On the other hand, birds that were singing at the beginning of the experiment, and that approached the source and sang in response to conspecific vocalisations, were

categorised as 'approach with vocalisation' (three individuals of *nigrorufa* and five of *whitii*). Sandwich-playback trials allow testing for the effect of previous stimuli on subsequent stimuli. We expected that heterospecific vocalisations would not elicit any response, while homospecific vocalisations would always elicit strong responses regardless of stimuli order.

Results

Morphology

Plumage

All adult specimens of *nigrorufa* and *whitii* can be clearly identified by plumage traits, showing that there is no clinal connection between these forms. Both species are sexually dimorphic, but dimorphism is subtle in *nigrorufa* and very marked in *whitii* (Figure 1; Table 1). In the slightly dimorphic *nigrorufa*, males have a tawny rufous throat, breast and flanks, and are brownish grey with slate tinge upper parts

(crown, neck, back and rump), while females differ in the orange tinge of the ventral parts and in the more olivaceous upper parts. The sexes of *nigrorufa* are difficult to distinguish both in field and museum specimens. On the contrary, in the markedly dimorphic *whitii*, males have a dark chestnut throat, breast and flanks, and slate upper parts, while females exhibit a tawny pale-orange throat, breast and flanks, and olivaceous light-brown upper parts (Figure 1; Table 1).

Males and females of *nigrorufa* are easily distinguished from males of *whitii*, but differentiating females of *whitii* from both sexes of *nigrorufa* represents a challenge (Figure 1; Table 1). In the field, females of *whitii* exhibit paler ventral colours, and more olivaceous upper parts than both sexes of *nigrorufa*. However, these subtle differences in coloration might not be reliable field characters, as perception is likely to change under different lighting conditions. Instead, the key to correct identification seems to be the extent of the white tip of the tail, which is much greater in *whitii* than in any sex of *nigrorufa* (Figure 1; Table 1).
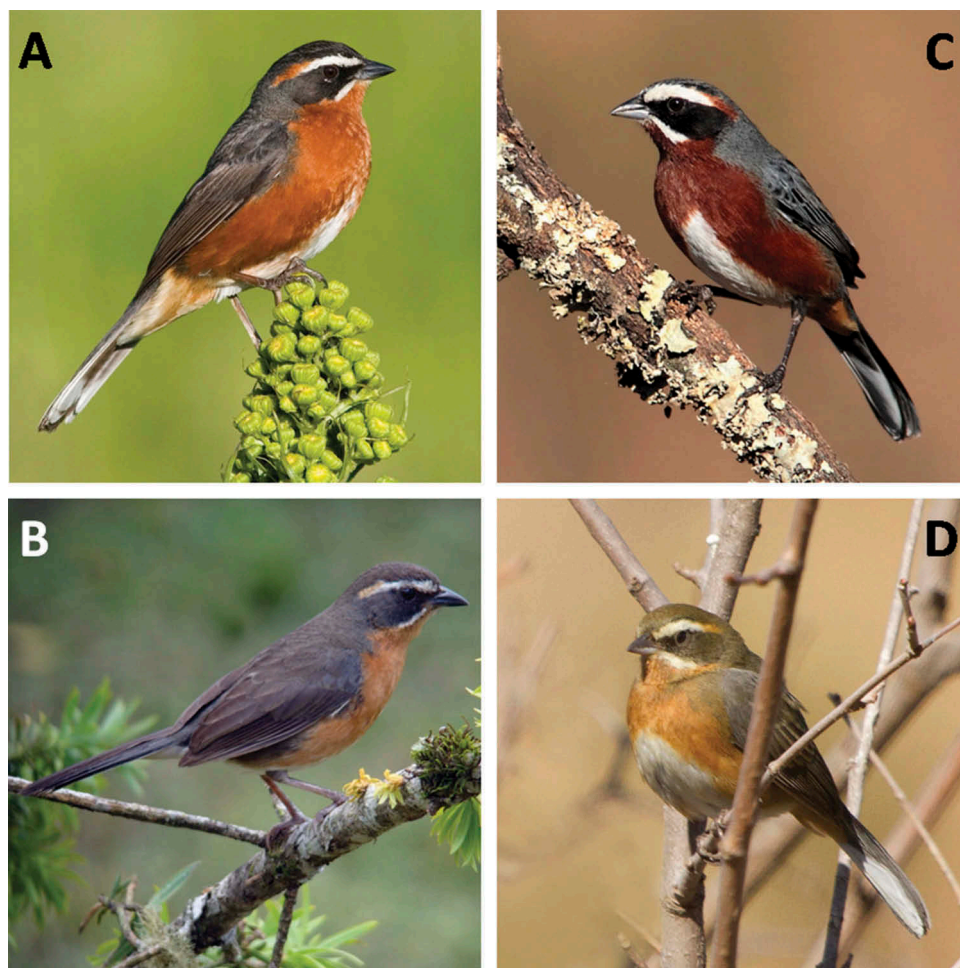

Figure 1. Adult individuals of Black-and-rufous Warbling-Finch (*Poospiza nigrorufa*) and Black-and-chestnut Warbling-Finch (*Poospiza whitii*). (A)–(B): Black-and-rufous Warbling-Finch, (C)–(D): Black-and-chestnut Warbling-Finch. (A) Male, Reserva Natural Punta Lara, Buenos Aires, Argentina, 12 October 2009. Photo: Sebastián Preisz. (B) Female, Bom Retiro, Santa Catarina, Brazil, 11 November 2008. Photo: Dario Lins. (C) Male, Vaqueros, Salta, Argentina, 10 August 2012. Photo: Gabriel Núñez. (D) Female, Salsipuedes, Córdoba, Argentina, 28 July 2012. Photo: Jorge La Grotteria.

Table 1. Morphological measurements and plumage features of both sexes of Black-and-rufous Warbling-Finch (*Poospiza nigrorufa*) and Black-and-chestnut Warbling-Finch (*Poospiza whitii*). Values (in mm) are mean ± SD; [range]; (*n*)

	Poospiza nigrorufa		*Poospiza whitii*	
	Males	Females	Males	Females
Throat, breast and flank colour	Tawny rufous	Tawny rufous with pale-orange tinge	Chestnut	Tawny pale-orange
Crown, neck, back and rump colour	Brownish grey with slate tinge	Brownish grey with olive tinge	Slate	Olivaceous light-brown
Extent of white tips on tail	At most one-third of tail		More than half of tail	
Culmen	7.63 ± 0.43 [5.91–8.85] [78]		7.34 ± 0.42 [6.31–9.27] [97]	
Bill height	5.09 ± 0.28 [4.48–5.811] [76]		5.03 ± 0.25 [4.44–5.70] [96]	
Tarsus length	20.67 ± 1.08 [18.27–23.81] [81]		19.47 ± 0.77 [17.36–21.41] [100]	
Wing chord	63.52 ± 2.16 [58.5–68.5] [45]	61.57 ± 1.75 [59.5–64.0] [14]	62.52 ± 2.04 [58.0–65.5] [63]	59.67 ± 2.09 [55.5–63.5] [33]
Tail length	55.18 ± 2.51 [52.0–59.5] [14]	56.96 ± 3.52 [49.0–63.5] [46]	57.37 ± 3.93 [45.5–67.0] [64]	54.73 ± 2.67 [49.5–60.5] [33]
Weight	17.31 ± 0.95 [16.0–19.5] [13]		15.35 ± 1.56 [12.0–17.5] [13]	

Morphometry

Specimens of *nigrorufa* had a significantly higher and longer bill, longer tarsus and wings, and were ~10% heavier than *whitii*. Both species were sexually dimorphic, with males exhibiting longer wings and tails than females. Within-sex comparisons between species show that *nigrorufa* had longer wings, but not longer tails, than *whitii* (Figure 2; Table 1).

Distribution

The distribution of *nigrorufa* extends from the state of Paraná in southern Brazil, southward to southern Buenos Aires province in Argentina, and westwards to the Paraná River basin in Paraguay, reaching eastern Córdoba province in Argentina (Figure 3(B)). The distribution of *whitii* is from La Paz department in Bolivia, south through the Andes to Mendoza province, and Sierras Centrales (highlands of western Córdoba and San Luis provinces), Argentina (Figure 3(B)).

Populations of *nigrorufa* and *whitii* are narrowly allopatric. Their distributions approach closely in central Córdoba province (Argentina) without overlapping. The closest records were separated by ~70 km and pertain to a male of *whitii* at Monte del Rosario (near the end of the eastern foothills of the Sierras Centrales; −30.913° S, −63.423° W) and a singing male of *nigrorufa* at Laguna del Plata (where the Pampas plains begin; −30.927° S, −62.886° W) (see Table S1 for more details on localities).

The distribution of *nigrorufa* extends mostly across the open eastern Pampas plains of southern South America, where it ranges from sea level to 100 m a.s.l. (Figure 3). However, it reaches higher altitudes in southeast Brazil following the availability of open Pampas-like habitats that occupy the higher elevation Atlantic Forest plateau (e.g. 870 m a.s.l. in Curitiba). On the other hand, *whitii* inhabits montane wooded areas in the west (east of the Andes) between 200 and 900 m a.s.l. in the southern portion of its distribution and between 1500 and 2500 m a.s.l. in the northern portion, following the altitudinal ascent of its preferred habitats above the more tropical rainforests (e.g. 3800 m a.s.l. in Lake Titicaca, Bolivia) (Figure 3).

Seasonal movements of *nigrorufa* and *whitii* require more study. In general, both species seem to be year-round residents across most of their ranges. Hayes (1995) considered *nigrorufa* as a rare Austral Migrant in southern Paraguay, but Smith (2006) reports it as a scarce inhabitant of grassy marshes there. Supporting its resident status in this region, it was recorded between October and January in Asunción (Paraguay), and in five localities of Argentina, very close to the boundary of
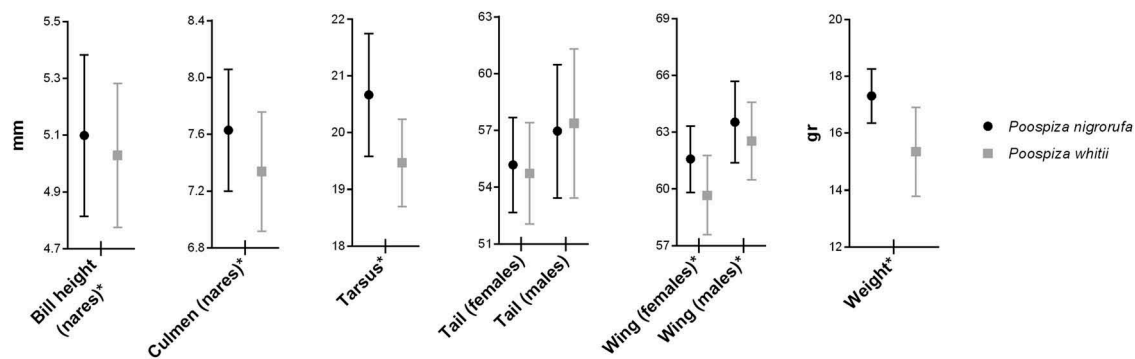
Figure 2. Morphological measurements and weight of Black-and-rufous Warbling-Finch (*Poospiza nigrorufa*) and Black-and-chestnut Warbling-Finch (*Poospiza whitii*) showing mean and standard deviation. Asterisks denote significant differences with alpha = 0.05 (*t*-test for all variables except for wing length that was compared with Mann-Whitney *U*-test). Black-and-rufous Warbling-Finches have significantly higher and longer bill, longer tarsi and wings, and are heavier than Black-and-chestnut Warbling-Finches.

Paraguay (Nemesio Parma and PP Araucaria, Misiones; Rincón Ombú Chico, RP 12 E of Itá-Ibaté and San Cayetano, Corrientes) (see Appendix S1). Locally, *whitii* apparently makes short-distance seasonal movements, descending in altitude during the winter. For example, in Tambo (Bolivia) it was fairly common during the wet season but a rare visitor in the dry season (Schmitt *et al.* 1997), and in Villa María (Argentina) some birds move downslope from the Sierras Centrales during the Austral winter (Salvador and Salvador 2014).

Potential distribution

The distributional model successfully discriminated areas of species presence and absence of *nigrorufa* and *whitii* (Figure 3(A)), with strong model performance (AUC = 0.957 and AUC = 979, respectively) for both training and test data sets. The MTP threshold for *nigrorufa* was 0.08 and for *whitii* was 0.007. The categorisation of suitability values (as explained in Methods) resulted in the following categories for each species: 0.008–0.25 = low suitability, 0.25–0.50 = moderate suitability, 0.50–0.75 = high suitability for *nigrorufa*; 0.007–0.26 = low suitability, 0.26–0.52 = moderate suitability, 0.52–0.79 = high suitability for *whitii*. Our final model of potential distributions indicates that the most suitable areas of both species are clearly allopatric, showing high to moderate presence probabilities for *nigrorufa* on eastern plains, and those of *whitii* on western highlands (Figure 3).

Vocalisations

The songs and calls of *nigrorufa* and *whitii* differed dramatically (Figure 4). Individuals of both species usually sing exposed from the highest available perches, and their songs begin with low-intensity phrases that

increase as the song progresses. According to our field experience, only the males of *nigrorufa* sing, but the subtle sexual dimorphism precludes a definitive statement. Instead, it is easier to assert that only males of *whitii* sing since the differences between the sexes are evident (see Morphology).

The simple song of *nigrorufa* consists of one phrase with three pure whistled notes, which is repeated a variable number of times (Figure 4(A, B)). This phrase is usually transliterated as *pleased to meet you* in English or *quem te vestiu* in Portuguese. The first note (alpha = α) distributes most of its energy in a V-shaped spectrogram tracing, which represents the main part of the note and the most conserved part among individuals. The second note (beta = β) is similar to the α-note but lower pitched. The third one (gamma = γ) is a rapid descending note.

The general shape and order of the three notes of the song of *nigrorufa* are very consistent throughout the range of the species. Individuals at some localities share fine-structural details in the notes suggesting the existence of at least some minor geographic variation in the shape of the notes within the general sequence template. Many of these fine-structural variations are aurally imperceptible. Thereby, these individuals usually add small variations to the beginning and the end of the main (V-shaped) part of α- and β-notes, and minor variations occur in the beginning of the γ-note (Figure 4(A, B)) (for more examples see Appendix B recordings from Entre Ríos: MLNS-132389, 217718, 217719 and Rio Grande do Sul: MLNS-67702, 19321).

Some individuals of *nigrorufa* sing faster songs than others by making the notes shorter and diminishing the duration of silences between notes. Fast and slow songs can be found in any location throughout its range without a geographic pattern. These differences in rhythm may stem from intra-
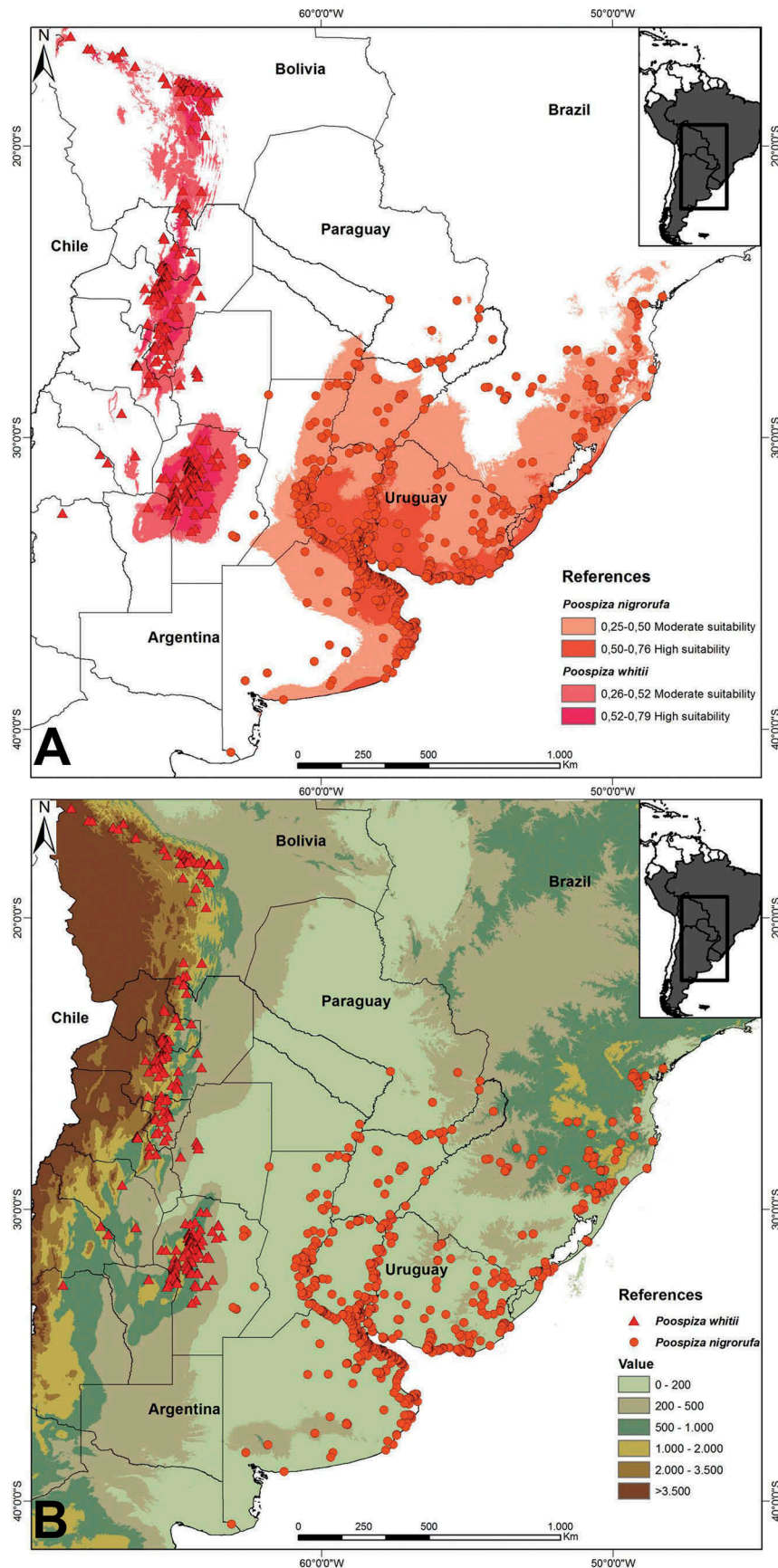
Figure 3. Presence localities and potential distribution of Black-and-rufous Warbling-Finch (*Poospiza nigrorufa*) and Black-and-chestnut Warbling-Finch (*Poospiza whitii*). Presence localities: orange circles, Black-and-rufous Warbling-Finch (*n* = 678); red triangles, Black-and-chestnut Warbling-Finch (*n* = 304). (A) Exact presence localities and potential distribution as predicted by MaxEnt. (B) Presence localities on a level-curves map highlighting the altitudinal range of both species.
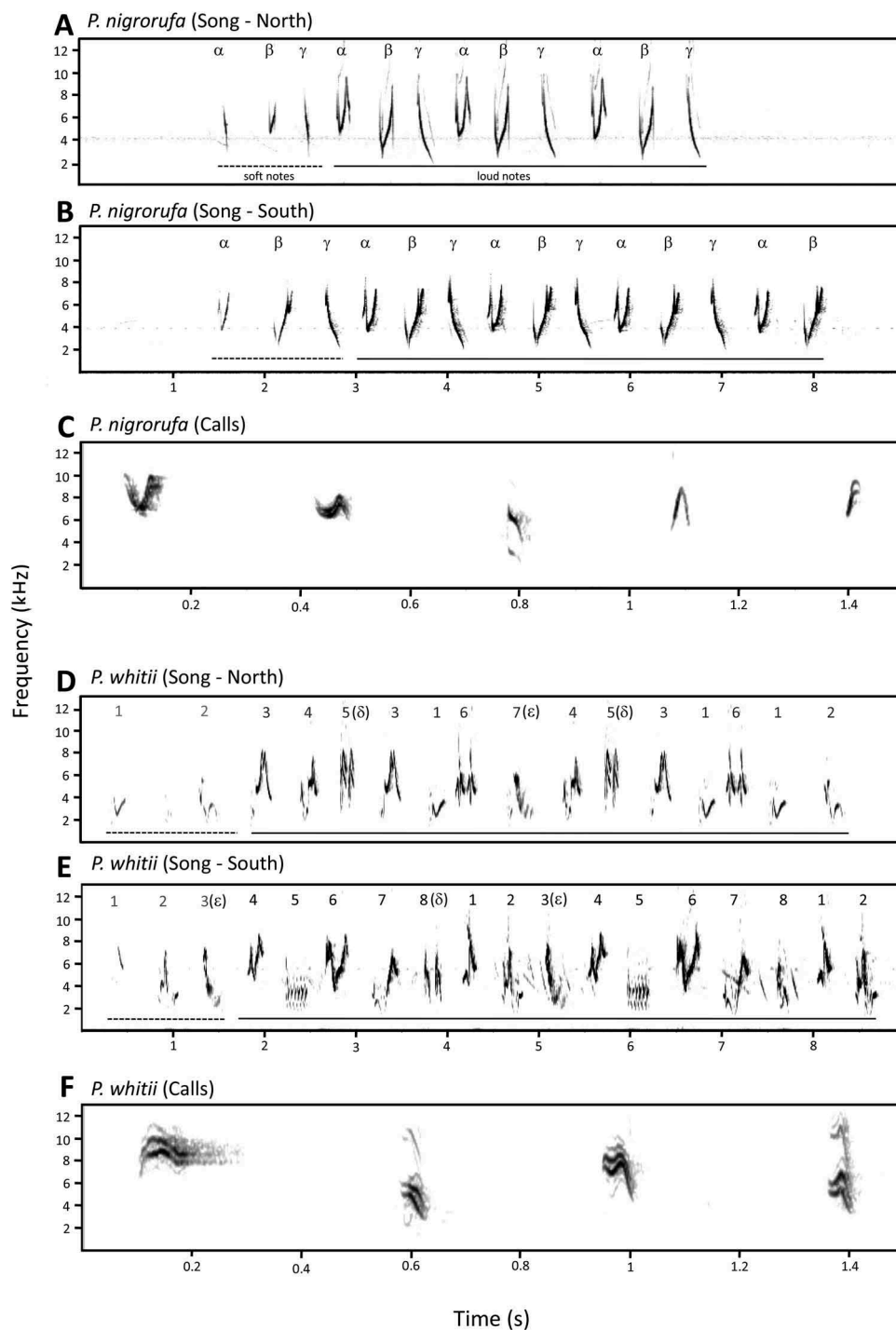
Figure 4. Spectrograms depicting songs (A, B, D, E) and calls (C, F) of adult males of Black-and-rufous Warbling-Finch (*Poospiza nigrorufa*) and Black-and-chestnut Warbling-Finch (*Poospiza whitii*). (A) Passo Fundo, Rio Grande do Sul, Brazil, 29 November 1971 (P. A. Schwartz MLNS-67602). (B) Reserva Natural Punta Lara, Buenos Aires, Argentina, 12 November 2014 (E. A. Jordan MLNS-213132). (C) Two first notes: Aldea Protestante, Entre Ríos, Argentina, 13 December 2013 (E. A. Jordan MLNS-217778), three final notes: Reserva Natural Punta Lara, Buenos Aires, Argentina, 26 December 2015 (E. A. Jordan MLNS-catalogue number pending). (D) Reserva Natural Provincial Finca Las Costas, Salta, Argentina, 27 March 2016 (J. I. Areta MLNS-catalogue number pending). (E) Villa General Belgrano, Córdoba,Argentina, January (Straneck 1990). (F) First note: Mataral, Santa Cruz, Bolivia, 16 August 2013 (A. Spencer XC-189909), three final notes: San Marcos Sierra, Córdoba, Argentina, 25 October 2016 (J. I. Areta MLNS-catalogue number pending). Greek letters designate homologous notes (α, β, γ, δ, ε), Arabic numerals designate sequences of notes without implying homology (1–8). Note the conservatism of the three notes in the song of the Black-and-rufous Warbling-Finch in two localities over 850 km away in contrast to the complex and variable song of the Black-and-chestnut Warbling-Finch in two localities 800 km away. While homologies between all the notes of the Black-and-rufous Warbling-Finch can be traced, only some homologies can be certainly recognised between the notes of the Black-and-chestnut Warbling-Finch.

individual variation due to internal motivation (e.g. hormonal) or external stimuli (e.g. presence of another male); or to inter-individual variation, which suggests that birds might be broadly classified as either slow or fast singers.

The complex song of *whitii* is composed of a succession of a variable number of notes whose quality and order varies greatly from individual to individual (Figure 4(D, E)). In stark contrast to *nigrorufa*, the number of notes performed by each analysed individual of *whitii* varied between 8 and 12. We identified three general types of notes: single melodious notes, paired melodious notes, and trills (Figure 4(D, E)). A complete song is a rhythmic series of single melodious notes, among which paired melodious notes and a few trills are irregularly interspersed that might be represented as *choo we, tip-tip, sweet peer, tweak, trrree, sweet peer*. The single melodious notes are highly variable in shape and pitch, but usually show two or more inflection points. Paired melodious notes consist of two identical or nearly identical short and rapidly delivered notes. Trills can be dry and flat or harsh and descending; they occur less often than the other note types but are very distinctive and clearly set *whitii* apart from *nigrorufa*. Songs vary markedly from individual to individual and this variation may also extend to successive songs in the same individual. Notes in a complete song can either follow a certain sequence that is repeated to form phrases (Figure 4(E)), or may have no discernible phrase pattern (Figure 4(D)). Despite the large variation, clearly homologous notes can be identified in all the individuals (Figure 4(D, E)).

The numerous calls of both species are easily distinguished with the aid of spectrograms, but are virtually impossible to distinguish in the field (Figure 4(C, F)).

Playback experiments

In all reciprocal sandwich-playback experiments, 10 males of *nigrorufa* and 10 males of *whitii* responded aggressively to conspecific vocalisations approaching to the sound source and singing (i.e. the highest category of intensity), while ignoring heterospecific ones (i.e. lack of response), regardless of stimulus order (*n* = 15 conspecific and 15 heterospecific stimuli for each species). While males of *nigrorufa* approached the song source through direct eye-level flights and gave full songs from the onset, *whitii* frequently responded by descending close to the ground to approach the sound source and gave soft renditions of the song while searching for the playback source.

Discussion

Current views on species limits argue that they are better established by integrating several sources of evidence (Padial *et al.* 2010; Yeates *et al.* 2011; Sangster 2014). Accordingly, in this work we evaluated the taxonomic status of taxa in the *P. nigrorufa/whitii* complex by providing data from various sources. Our data set shows that *nigrorufa* and *whitii* differ in (1) plumage coloration and degree of dimorphism, (2) morphometric traits, (3) habitat preferences, (4) vocal characters, and that (5) in reciprocal playback experiments they ignore the other taxon while answering strongly to their own vocalisations. Integration of these lines of evidence clearly shows that *nigrorufa* and *whitii* belong to different species under many species concepts (Mayr 1963; Cracraft 1985, 1992). However, this pair of species fits especially well in the features expected for sister species under the RC (Paterson 1980, 1985), since two sister species should differ in their normal habitats and in the specific set of features that conform their SMRS.

Habitat differences between *P. nigrorufa* and *P. whitii* are marked. While *P. nigrorufa* inhabits shrubby open areas in wetlands with reeds (*Typha, Schoenoplectus*) and bulrushes (*Scirpus, Rhynchospora*) and grassy plains with Pampas Grass (*Cortaderia selloana*), *P. whitii* inhabits closed to semi-closed xerophytic to semi-humid scrub (*Prosopis, Geoffroea*) and woodlands (*Podocarpus, Alnus*) (Hayes 1995; Jaramillo 2011; Herzog *et al.* 2016; pers. obs.) far from wetlands. Their bioclimatic niches also differ, as testified by the models that predict non-overlapping of most suitable areas. In the Poospizinae, both plumage brightness and colour have evolved under selective regimes favouring different features in open than in closed habitats (Shultz and Burns 2013). Although Shultz and Burns (2013) considered *P. whitii* as a species of open habitats, we suggest that it is more appropriately considered a species of closed to semi-closed habitats. The darker males of *P. whitii* in more closed habitats in comparison to the lighter males of *P. nigrorufa* in open habitats are in agreement with the adaptive plumage changes expected for plumage crypsis (Shultz and Burns 2013). This in turn is consistent with the view of the RC that adaptive changes in SMRS features in novel habitats (in this case plumage in relation to environmental light) may lead to speciation. Additionally, other selective pressures appear to have acted differently in males and females, leading to a marked sexual dimorphism in *P. whitii* and to a minor to almost absent dimorphism in *P. nigrorufa*. Among Thraupidae the evolution of sexual dichromatism is driven more often by changes in male coloration than in female coloration, and although decreases in sexual dichromatism are much

more common than increases among tanagers (Shultz and Burns 2013), the direction of the change in this particular case is difficult to assess. It might involve a change from less to more dimorphism by the acquisition of darker males in *P. whitii* or a change from more to less dimorphism by the evolution of paler males in *P. nigrorufa*.

The narrow (70 km) parapatry of *P. nigrorufa* and *P. whitii*, if confirmed by more refined geographic sampling, would provide conclusive evidence to recognise them as a full biological species (Remsen 2005). Even so, allopatric taxa can be ranked as species under the RC if they differ in habitat use and in their SMRS, without the need of sympatry to pass a species-level test as in the IC (Paterson 1980, 1985).

Vocalisations are thought to be a key component of the SMRS in birds (Marler 1957; Isler *et al.* 1998; Price 2008). Geographic variation in vocalisations in birds that learn their vocalisations complicates the task of deciding whether any geographically structured vocalisation should be interpreted as indicative of a breeding barrier or simply as a local feature that would not have a profound effect in limiting or impeding gene flow between other vocally different populations (Slabbekoorn and Smith 2002; Areta and Repenning 2011). Our data show that the simple three-note song of *P. nigrorufa* contrasts markedly with the complex multi-noted song of *P. whitii*. Despite some minor geographic variation (which deserves further study), the structural differences in song and calls are consistent throughout their geographic ranges and their break coincides with the break in plumage, habitat use and morphology. Reciprocal playback experiments to assess the role of songs of *P. nigrorufa* and *P. whitii* as a mate recognition cue and as a potential barrier to gene flow show that they respond to their own songs but ignore those of the other taxon, acting at the same time as an intra-specific mating signal and as a barrier to inter-specific mating.

Taxonomic remarks

The lack of a type specimen for *P. nigrorufa* (d´Orbigny and Lafresnaye 1837) demands a careful analysis of the history of the name. We concur with Hellmayr's (1938) interpretation that *Emberiza nigro-rufa* d'Orbigny and Lafresnaye 1837 is a mere naming of Azara's (1802) number 142 '*Chipíu negro y canela*'. Azara (1802, p. 529) described the adults and some 'varieties' whose lower throat, belly and sides had dark brushstrokes ('*. . . y en lo inferior de la garganta, pecho y costados había pinceladas oscuras*') and suspected that these varieties were the product of age rather than sexual ('*. . . sospecho que las mencionadas variedades son mas bien de edad que sexuales*'). d

´Orbigny and Lafresnaye (1837) only described an immature bird from Santa Fé and referred it erroneously to Azara's bird number 162 (instead of 142) due to a numbering error in Walckenaer's French edition of Azara's work (Hellmayr 1938). Thus, Azara (1802) described the immature plumage contra Hellmayr (1938) who considered that d´Orbigny and Lafresnaye (1837) were the first to describe this plumage. Further supporting this point, Azara thought that his '*Chipíu negro y canela*' could be the *Fovette tachetée de Luisiana* (sic), described and illustrated in Martinet's *Planche enluminée* number 752 (1), which shows a brown-backed bird with a short pale supercilium and dark striped underparts on a whitish background. *Pipillo personata* Swainson 1837 from Brazil is a junior synonym of *Emberiza nigro-rufa* d´Orbigny and Lafresnaye 1837, since it was published in December 1837 (Hellmayr 1938; see illustration in Gould 1839). Finally, Cabanis (1847) included *E. nigro-rufa* in *Poospiza*. However, the junior synonym *Poospiza personata* was used to refer to *P. nigrorufa* by many authors at least until 1924 (Hellmayr 1938).

The doubtfully valid subspecies *wagneri* was described as a full species by Sztolcmann (1926) based on a single male type and three females from Chulumani (Bolivia). The male differed from males of *whitii* by a chestnut instead of a white chin, more extensive white moustache, and a black basal outer vane instead of a completely white outer vane of outer rectrices. However, these alleged differences become less obvious when comparing the type specimen of *wagneri* against museum and living specimens of *whitii*. The type specimen of *wagneri* shows a small white spot on the chin, slightly smaller than in the males of nominate *whitii* with less white; the white moustache in *wagneri* is as extensive as in many males of *whitii*; and finally, both the type specimen of *wagneri* and almost all specimens of *whitii* coincide in their black basal outer vane to the outermost tail feather. Given these similarities, we concur with those who argue that, based on our current knowledge, *wagneri* is better considered as a synonym of *P. whitii*.

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ORCID

Juan Ignacio Areta http://orcid.org/0000-0001-8588-3030

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Appendices

Appendix A

Museum specimens of Black-and-rufous Warbling-Finch (*Poospiza nigrorufa; n* = 132) and Black-and-chestnut Warbling-Finch (*Poospiza whitii; n* = 149) examined and/or measured for this study. Specimens are held at the American Museum of Natural History (AMNH, New York), British Natural History Museum (BNHM, London), Fundación Miguel Lillo (FML, Tucumán, Argentina), Field Museum of Natural History (FMNH, Chicago), Museo Argentino de Ciencias Naturales (MACN, Buenos Aires, Argentina), Museum and Institute of Zoology – Polish Academy of Sciences (MIZ, Warsaw, Poland), Museo de Ciencias Naturales de La Plata (MLP, La Plata, Argentina), and National Museum of Natural History (NMNH, Washington, DC).

Black-and-rufous Warbling-Finch (*Poospiza nigrorufa*)

AMNH: 518453, 799541, 799542, 799542, 799543, 799545, 799546, 799547, 799548, 799549, 799550, 799551, 799552, 799553, 799554, 799555, 799556, 799557, 799558, 799559, 799560, 799561, 799562, 799563, 799564, 799565. FML: 2160, 2169, 2170, 4326, 6705, 8805. MACN: 701a, 39184, 45487, 54954, 5700, 37961, 33383, 53468, 6799, 8915, 2503a, 2503a, 9291, 4202, 33959, 9232, 28827, 40063, 3192a, 3031a, 31473, 8965, 31474, 2568a, 33294, 33973, 1457a, 870a, 37959, 280a, 1129a, 3570a, 37960, 3112a, 3112a, 43560, 57041, 229a, 111a, 167a, 2873a, 1166a, 43561, 3218a, 45489, 54905, 55017, 55940, 66647, 67032, 2503a, 6295a, 2912a, 52573, 5591a, 5861a, 6273a, 33323, 29180. MLP: 234, 4416, 5990, 9312, 9313, 9506, 13335, 243, 244, 236, 2844, 4415, 5988, 5989, 6055, 6651, 6710, 7560, 6652, 8283, 9116, 9504, 12931, 13336, 13603, 13852, 13853, 13854, 10751, 12583. NMNH: 630237, 630398, 614757, 614758, 614759, 615431.

Black-and-chestnut Warbling-Finch (*Poospiza whitii*)

AMNH: 139692, 139693, 139694, 139694, 139695, 139695, 139696, 139698, 139699, 142331, 142332, 142333, 142334, 142335, 142336, 142337, 142338, 142339, 142340, 142341, 142342, 142343, 142344, 142345, 142346, 518459, 518460, 518461, 518462, 518463, 518465, 786565. FML: 419, 420, 422, 571, 603, 620, 922, 1018, 1154, 1257, 1339, 1375, 1499, 1958, 2038, 2040, 2146, 2147, 2151, 2152, 2299, 2376, 3351, 3483, 5621, 6296, 7703, 9137, 9138, 9139, 9633, 9665, 9667, 9669, 9721, 9848, 9851, 9852, 10587, 10595, 11205, 12614, 12615, 14083, 14084, 14085, 14446, 14985, 15155, 17342, 17499. FMNH: 295170, 295171, 295172, 295173, 295174, 295176, 295177, 295178, 295180. MACN: 217a, 22202, 22203, 22204, 22205, 22206, 22207, 22208, 22209, 18342, 18347, 18348, 18349, 18350, 18351, 18352, 18353, 18354, 18355, 18357, 18356, 7a, 6329a, 53029, 53031, 53032, 53030, 9451C, 9648, 9648D, 8428, 8884, 9648C, 9451, 9451A, 9451B, 9648C, 9648A, 9648B, 272a, 8132, 40157, 799a, 34041, 34042. MIZ: 33827, 33829, 33830, 33831. MLP: 10944, 10945, 11273, 11313, 11601, 13404, 10578. BNHM: 1885.2.10.321.

Appendix B

List of recordings of Black-and-rufous Warbling-Finch (*Poospiza nigrorufa; n* = 84) and Black-and-chestnut Warbling-Finch (*Poospiza whitii; n* = 31) examined for this study. Capitalised names refer to provinces, departments or states; localities in bold are followed by the name of the recordist, number of individual

birds recorded (in parentheses), and catalogue number. Acronyms: MLNS, Macaulay Library of Natural Sounds, Cornell Lab of Ornithology, Ithaca, New York, USA; XC, Xeno-Canto, www.xeno-canto.org; FLMNH, Bird Sounds Database of Florida Museum of Natural History, Florida, USA. Asterisks denote recordings with calls, and underlines indicate recordings used in playback experiments.

Black-and-rufous Warbling-Finch (Poospiza nigrorufa)

Argentina. CORRIENTES. **Campo Avalos, Rio Mirinay**: B. Lopez-Lanus (1) XC-61237. ENTRE RÍOS. **20.0 km E of Ibicuy**: M. J. Andersen (1) MLNS-132389. **28.0 km W of Ibicuy**: E. A. Jordan (1) MLNS-217718, 217719. **Aldea Brasilera**: E. A. Jordan (1) MLNS-217705. **Aldea Protestante**: E. A. Jordan (6) MLNS-213157, 213158*, 217775, 217778*, 217782*, 217783. **Diamante, zona rural**: E. A. Jordan (3) MLNS-213156*, 213155, 213154. **Estación San Martín (near Ibicuy)**: E. A. Jordan (2) MLNS-217726*, 217727*. **Ibicuy**: E. A. Jordan (1) MLNS-217722. **Mazaruca**: E. A. Jordan (1) MLNS-217772. **Parque Nacional Predelta**: E. A. Jordan (1) MLNS-217790. **Salto Ander-Egg**: E. A. Jordan (2) MLNS-213148, 213149. **Strobel**: E. A. Jordan (2) MLNS-217789, 217786. MISIONES. **Posadas**: Aves del NEA (1) XC-253253. SANTA FE. **Arroyo Pájaro Blanco (desembocadura), Alejandra, San Javier**: B. López-Lanús (1) XC-57615, 57616, 57617. **Puerto Piracuacito**: J. I. Areta (1) MLNS-216261; E. A. Jordan (1) MLNS-217731. BUENOS AIRES. **Atalaya**: J. I. Areta (2) MLNS-523266*, 523264*; E. A. Jordan (4) MLNS-177554, 177552, 177556, 177551; P. L. Tubaro (1) FLMNH 15544. **Isla Santiago**: J. I. Areta (3) MLNS-catalogue numbers pending; E. A. Depino (1) MLNS-201682. **La Plata**: L. R. Macaulay (1) MLNS-139134. **Otamendi**: B. Lopez-Lanus (2) XC-52522, 52523. **Parque Provincial Pereyra Iraola**: J. I. Areta (1) MLNS-171005. **Reserva Natural Punta Lara**: J. I. Areta (1) MLNS-523232; E. A. Depino (3) MLNS-213852, 179287*, 179238; E. A. Jordan (11) MLNS-177541, 177537, 177534*, 177544, 179287*, 197259*, 213169, 213166, 213132, 213164, 213115. **Saladillo**: M. A. Roda (1) XC-50178.

Brasil. PARANÁ. **Wetland along the Iguaçu River – Curitiba**: B. Tavener (1) XC-111980*; R. Sobania (1) XC-10312. SANTA CATARINA. **Iomerê**: R. B. Stringari (1) XC-195891. **Restingas do Farol de Santa Marta, Laguna**: J. Gava (1) XC-187119. **Salete**: D. Meyer (1) XC-173311. RIO GRANDE DO SUL.

10.0 km N of Taim: W. Belton (1) MLNS-19321. **30.0 km N of Passo Fundo**: P. A. Schwartz (1) MLNS-67602. **40.0 km SW of Encruzilhada do Sul, Faz. Sao Jose**: W. Belton (1) MLNS-20241. **5.5 km S of Sao Fransisco Da Paula**: T. A. Parker III (1) MLNS-34014. **Aparados da Serra**: P. Boesman (2) XC-228551, 228552, 228553, 228554. **Banhado do Maçarico region**: R. Antunes Dias (2) XC-84300*, 91534. **Estância Santa Maria – Jaguarão**: F. Jacobs (1) XC-7395. **Ijuí**: F. I. de Godoy (1) XC-211756. **Reserva Biológica do Mato Grande – Arroio Grande**: F. Jacobs (1) XC-20608*. **Rio Carreiro, Serafina Corrêa**: A. E. Rupp (1) XC-42155. **RPPN Pontal da Barra – Pelotas**: F. Jacobs (1) XC-17403. **Santa Isabel (across canal)**: W. Belton (1) MLNS-19322.

Uruguay. ARTIGAS. **Calnu**: P. A. Hosner(1) MLNS-117973. MALDONADO. **Minas**: A. Riccetto (1) XC-5739. **Caracoles**: B. Lopez-Lanus (1) XC 52526. **Laguna del Diario**: A. Silveira (1) XC-100808. **Maldonado**: A. Silveira (1) XC-209519. MONTEVIDEO. **Santiago Vázquez**: J. P. Culasso (2) MLNS-197259*, XC-54203, 54204. SALTO. **Desembocadura del Arroyo San Antonio**: P. Rinaldi (1) XC-191068.

Black-and-chestnut Warbling-Finch (Poospiza whitii)

Argentina. JUJUY. **Termas de Reyes, 17 km W of Jujuy**: N. Krabbe (1) XC-16000, 47465. **Los Molinas, Grande River**: M. Nelson (1) XC-48281. **Lozano**: R. Fraga (1) XC-49945. **Valle Colorado**: F. Burgos (1) MLNS-catalogue number pending. SALTA. **Chicoana, Chorro Blanco**: J. C. Arvin (1) FLMNH-15060; J. I. Areta (2) MLNS-catalogue number pending. **Lagunilla**: J. I. Areta (1) MLNS-catalogue number pending. **Reserva Natural Provincial Finca Las Costas**: J. I. Areta (2) MLNS-catalogue numbers pending; E. A. Jordan (5) MLNS-catalogue numbers pending*. **San Lorenzo**: J. I. Areta (3) MLNS-catalogue numbers pending*. **El Durazno, comunidad Lule**: E. A. Jordan (1) MLNS-catalogue number pending. **Escuela República de Venezuela, 6 km SSW of Campo Quijano**: J. I. Areta (1) MLNS-catalogue number pending. CATAMARCA. **Las Juntas**: C. Ferrari (1) XC-53155, 53156. CÓRDOBA. **Capilla del Monte**: M. Castelino (1) XC-61052; C. Ferrari (1) XC-53160. **La Cumbre**: C. Ferrari (1) XC-53157. **Villa General Belgrano**: R. Straneck (1) Straneck 1990; B. López-Lanús (1) XC-52518. **San Marcos Sierra**: J. I. Areta (2) MLNS-catalogue numbers pending*.

Bolivia. CHUQUISACA. **7 km N of Sopachuy**: N. Krabbe (2) XC-16125, 19983. SANTA CRUZ. **Mataral**: A. Spencer (1) XC-189909*.