



Taxonomy and conservation: a tale of two tinamou species groups (Tinamidae, *Crypturellus*)

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Species delimitation has important consequences for the management of endangered species. Species-level taxonomy in the genus *Crypturellus* (Tinamidae) has been based largely on plumage characters and species limits in several groups have been difficult to establish. Because some of the forms of uncertain taxonomic status are currently threatened with extinction, a basic understanding of species limits is crucial not only for taxonomists but also for conservation biologists and managers. We analysed vocal variation to assess species limits in two *Crypturellus* species-groups, the red-legged complex (*Crypturellus erythropus* and allied forms) and the brown tinamou *Crypturellus obsoletus*. In the red-legged complex, where several species-level taxa have been recognized by some authors, there is no obvious geographic variation in vocalizations and populations appear mostly continuously distributed, with plumage variation largely explicable in terms of environmental conditions. In the brown group, a single species is recognized, but we found marked geographic variation in vocalizations and populations have disjunct distributions; we propose that at least one of the populations in this group likely merits recognition as a separate species. We conclude that incomplete knowledge of patterns of variation in relevant traits in addition to the momentum carried by traditional taxonomy may potentially mislead conservation actions.

Taxonomic, systematic, and evolutionary knowledge exerts a major influence on policy and decision-making in conservation biology (Samper 2004, Hendry et al. 2010). For example, species concepts and the criteria used to establish limits between species have important consequences regarding strategies for the management of endangered species and biodiversity (Agapow et al. 2004, Samper 2004, Frankham et al. 2012, Heller et al. 2013). Because species arguably represent the currency of biodiversity, much of conservation biology has relied on species as the main units for protection and management (but see Moritz 2002, Santamaría and Méndez 2012), and this requires that species be properly delimited. Furthermore, alternative criteria to recognize species can influence perceived priorities for conservation action (Cadena 2003, Agapow et al. 2004, Isaac et al. 2004, Dillon and Fjeldså 2005, Frankham et al. 2012) and could divert limited resources away from the conservation of threatened species of unquestionable taxonomic status (Garnett and Christidis 2007). Despite its critical importance, basing conservation action on sound species-level taxonomy is not always feasible: with regard to taxonomic knowledge, conservation biology is often a crisis discipline in which one must act before knowing all the facts (Soulé 1985). This is true even in well studied groups, such as birds.

Tinamous (Tinamidae) are terrestrial birds with limited flight abilities. The family is endemic to the Neotropics and

reaches its greatest diversity in tropical South America, with two major groups recognized: forest and steppe tinamous (Cabot 1992, Bertelli et al. 2002, Bertelli and Porzecanski 2004). Tinamous are cryptic, shy and elusive but their vocalizations are distinctive, being among the most characteristic sounds of Neotropical forests (Cabot 1992). The songs of tinamous are believed to be innate (i.e. genetically determined) and thereby unaffected by cultural evolution (Kroodsma and Miller 1996). Thus, assuming that vocalizations play an important role in species recognition and mating in tinamous (Cabot 1992), vocal variation could be used to establish species limits in tinamous under the biological species concept, much as has been done in other avian groups lacking song learning (e.g. subsocial passerines; Isler et al. 1998, Remsen 2005). However, to our knowledge, vocalizations have only been used in one study of species limits in tinamous (Maijer 1996).

The forest-tinamou genus *Crypturellus* is the most diverse in the family, with 21 species currently recognized (Cabot 1992, Remsen et al. 2014). However, high inter-specific similarity and ample intraspecific diversity have caused disagreement with regard to the number of species accepted (Cabot 1992). Tinamou species-level taxonomy is largely based on plumage characters and species limits among some populations of *Crypturellus* are not well established. Because some of the forms of uncertain taxonomic status are

currently threatened with extinction, an adequate understanding of species limits is crucial not only for taxonomists but also for conservation biologists and managers.

We conducted analyses of vocal variation to assess species limits in two *Crypturellus* species groups, the red-legged complex (*Crypturellus erythropus* and allied forms) and the brown tinamou *Crypturellus obsoletus*. The taxonomy of the red-legged, medium-sized *Crypturellus* inhabiting lowland areas in northern South America has been controversial for decades; this group has received much attention in part because two forms (*columbianus* and *saltuarius*) have been suggested to be at risk of extinction and some authors consider them to be good species (Cabot 1992, Renjifo et al. 2002, Birdlife International 2008, Remsen et al. 2014). On the other hand, the taxonomy of the brown tinamou has not been evaluated recently and it is considered of least concern from a conservation standpoint (Birdlife International 2008). Our interest in the brown tinamou was spurred by the rediscovery of one of its members in Colombia (Alvarez-Rebolledo et al. 2007), where it was formerly known only from 'Bogotá' trade skins. Because preliminary analyses indicated this population was vocally distinct, we suspected that the brown tinamou could include species-level taxa at risk of extinction that had been overlooked owing to the lack of modern taxonomic studies.

Methods

Study taxa

Crypturellus erythropus (red-legged tinamou) is widespread in the lowlands of northern South America (Fig. 1); it is found in wet to dry forest and also in disturbed habitats (Olivares 1958, Schwartz and Lentino 1984, Cabot 1992, Remsen et al. 2014). Seven subspecies of *C. erythropus* have been described (Clements et al. 2010) and are currently considered as such by the South American Classification Committee of the American Ornithologists' Union (Remsen et al. 2014). However, some of these forms have often been regarded as separate species (Storz et al. 1996, Renjifo et al. 2002, Donegan et al. 2003) and two of them, *C. e. columbianus* (Colombian tinamou) and *C. e. saltuarius* (Magdalena tinamou), are currently considered threatened (Collar 1992, Renjifo et al. 2002). *Crypturellus e. saltuarius* was described from a single male specimen on the basis of its stronger pattern of barring in the plumage, but because this type of pattern is characteristic of immature males in this group, the taxonomic distinctness of this form has been questioned (F. G. Stiles pers. comm.). The taxonomic status of *Crypturellus kerriae* (choco tinamou) has also been matter of dispute, but it has not been treated

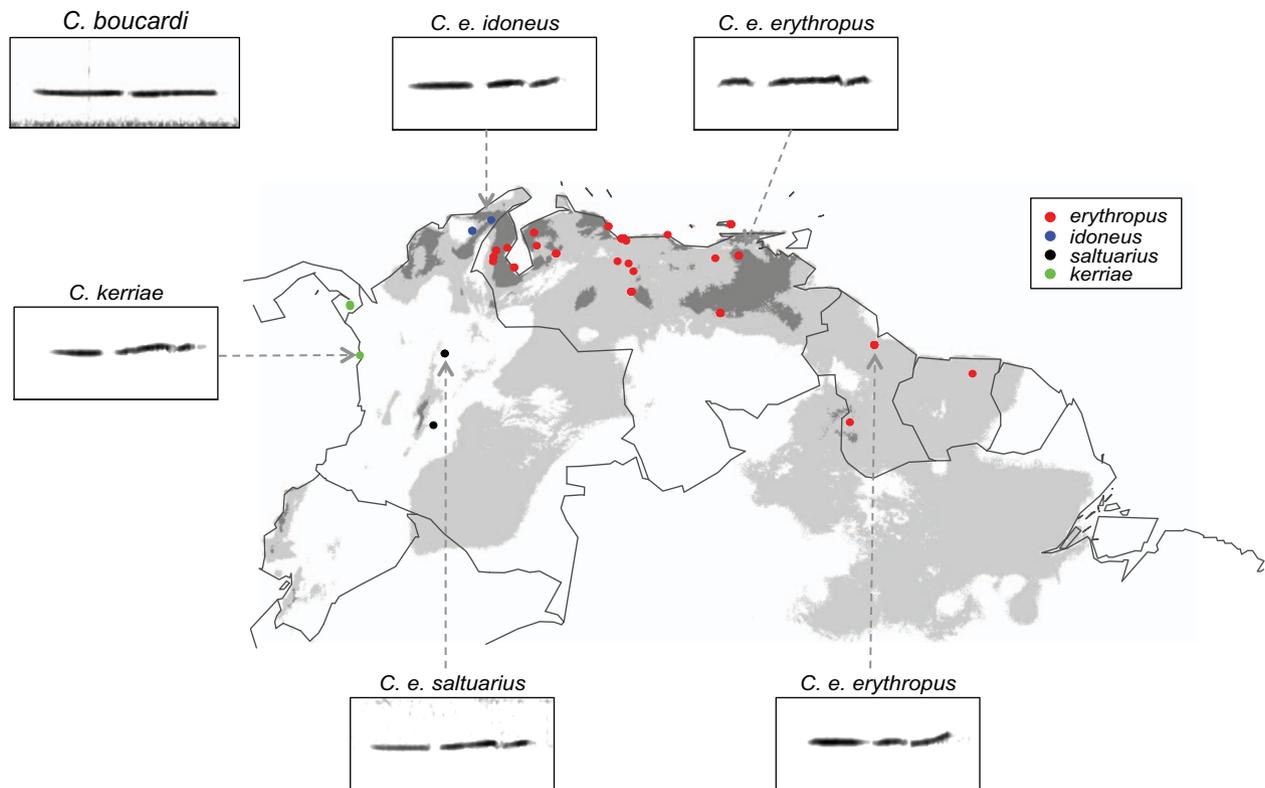


Figure 1. Geographic distribution and vocal variation of the red-legged tinamou complex in northern South America. Circles represent the location of recordings used in acoustic analyses. A potential distribution map is shown in grayscale, with darker tones indicating greater probability of presence. The map was constructed using the maximum entropy method implemented in package DISMO for R (Hijmans et al. 2011) based on the localities from which recordings were available and using 19 climate surfaces obtained from WORLDCLIM, ver. 1.2 (Hijmans et al. 2005). Representative sonograms of two-second sections of songs of each form are shown: the horizontal axis indicates time and the vertical axis indicates frequency (range 0–2 kHz). A sonogram for the extralimital Central American species *C. boucardi* is shown but its geographical distribution is not depicted in the map.

as conspecific with *C. erythropus*. Some authors have considered *C. kerriae* and *C. erythropus* as sister taxa, forming a superspecies with the Middle American *C. boucardi* (slaty-breasted tinamou; Sibley and Monroe 1990, Bertelli et al. 2002). It has been suggested that *C. e. saltuarius* might be a subspecies of *C. kerriae* (Blake 1977), but also that *kerriae* could instead be a subspecies of *C. boucardi* (Remsen et al. 2014).

Crypturellus obsoletus (brown tinamou) is a polytypic species with nine recognized subspecies inhabiting disjunct areas in both the highlands and lowlands of South America (Venezuela, Colombia, Ecuador, Peru, Bolivia, Brasil, Paraguay and Argentina; Fig. 2; Olivares 1958, Cabot 1992, Clements et al. 2010). The nominate form *C. o. obsoletus* was described based on skins from localities in southeastern Brazil (Ipanema, Itararé, Mato-Dentro; Hellmayr and Conover 1942). Four decades later, *C. o. castaneus* was described based on ‘Bogotá’ skins of uncertain geographic origin (Sclater 1858 in Hellmayr and Conover 1942), and specimens from Peru and Ecuador were later referred to this taxon (Hellmayr and Conover 1942). In September 2006 an expedition of the Inst. Alexander von Humboldt to a cloud forest site on the western slope of the

Cordillera Oriental west of Bogotá obtained the first recordings of *C. o. castaneus* (Alvarez-Rebolledo et al. 2007). Since this discovery, this form has been repeatedly recorded at this locality and a few others in the same region (O. Cortés, A. Hernández, O. Laverde. and C. D. Cadena unpubl.).

Vocal analysis

We examined good-quality tinamou recordings deposited in the Macaulay Library of Natural Sounds (MLS), Xeno-Canto (XC), and the Banco de Sonidos Animales of the Inst. Alexander von Humboldt (BSA) (Supplementary material Appendix 1). These recordings represented 82 individuals in the red-legged tinamou complex and related forms: *C. e. erythropus* (71), *C. e. idoneus* (3), *C. e. saltuarius* (2), *C. kerriae* (2) and *C. boucardi* (4). We included recordings of *C. kerriae* and *C. boucardi* in analyses because both species have been considered to be allied to the red-legged group. For *C. obsoletus*, we analyzed recordings from 42 individuals of the following taxa: *griseiventris* (5), *obsoletus* (13), *ochraceiventris* (10, we here include subspecies *traylori* due to its uncertain elevational distribution and to marked vocal similarity with *ochraceiventris*), *punensis* (8) and *castaneus* (6). *Crypturellus*

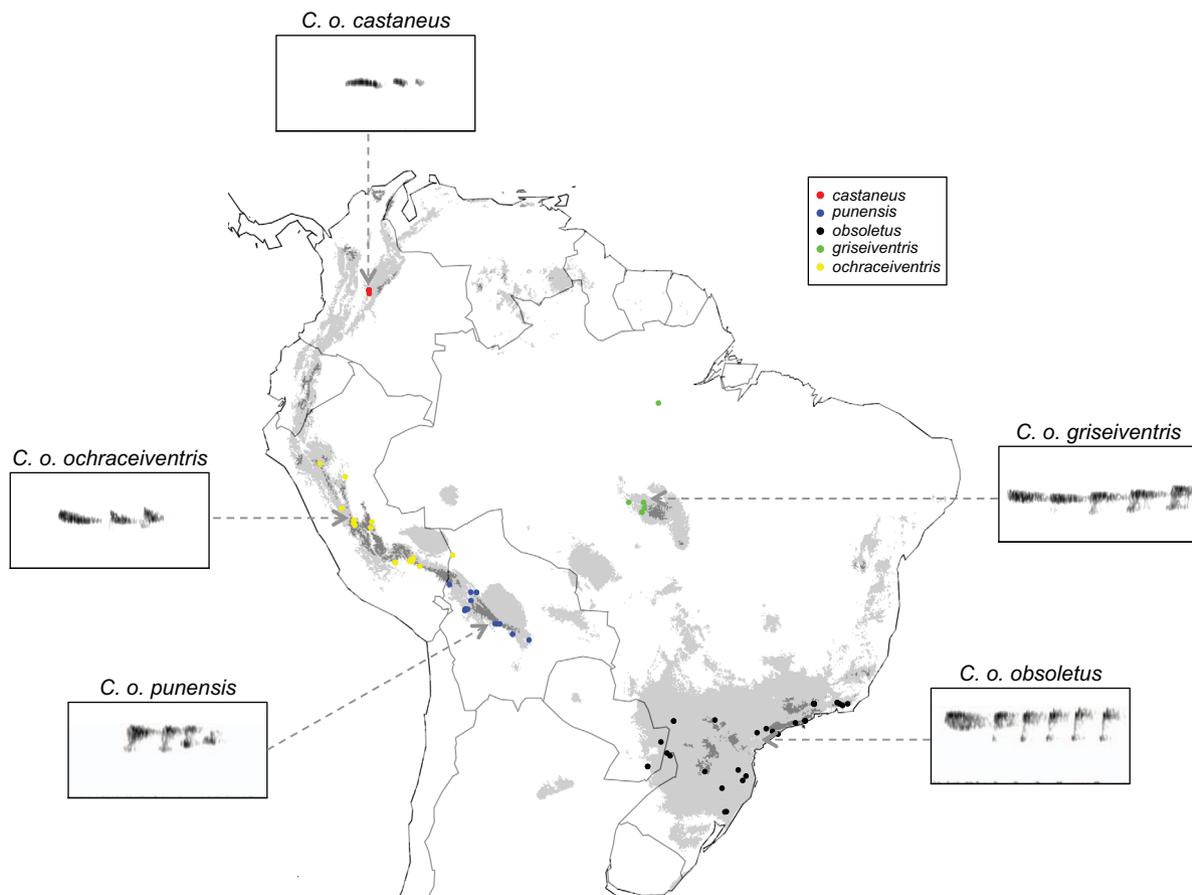


Figure 2. Geographic distribution and vocal variation of the brown tinamou complex in South America. Circles represent the location of recordings used in acoustic analyses. A potential distribution map is shown in grayscale, with darker tones indicating greater probability of presence. The map was constructed using the maximum entropy method implemented in package DISMO for R (Hijmans et al. 2011) based on the localities from which recordings were available and using 19 climate surfaces obtained from WORLDCLIM, ver. 1.2 (Hijmans et al. 2005). Representative sonograms of two-second songs of each form are depicted; the horizontal axis indicates time and the vertical axis indicates frequency (range 0–2 kHz).

erythropus has one type of vocalization emitted constantly, its song. In *C. obsoletus*, long vocalizations are rarely produced and short vocalizations are commonly used; we chose short vocalizations for analyses. We assume homology between the vocalizations selected for analyses and refer to them as songs, defined as loud vocalizations functioning to establish and defend territories and to attract mates (Kroodsma 2007).

We selected a single song from each recording for analysis. Songs were analyzed with the RAVEN bioacoustics program ver. 1.4 (Cornell Lab of Ornithology, Ithaca, New York) using default settings: FFT window = 512, window overlap = hann method. Song structure was quantified on sonograms using on-screen cursors to measure time and frequency characteristics. Sonograms for publication were built using the Seewave library (Sueur et al. 2008) for R (R Core Team).

For each recording, we selected a single song for analysis, in which we measured the following variables: 1) total length of song; 2) length of the first, middle and final note; 3) highest frequency of the first, middle and final note; 4) lowest frequency of the first, middle and final note; 5) maximum frequency of the first, middle and final note; 6) bandwidth of the first, middle and final note, and 7) average entropy of the first, middle and final note. Peak frequency was defined as the frequency at which most energy in the note selected is found (Charif et al. 2010). The average entropy measurement describes the amount of disorder for a selected spectrum; high entropy values correspond to sounds with greater disorder whereas zero entropy would characterize a pure tone with energy in only one frequency bin (Charif et al. 2010). When the song selected on a given recording had an even number of notes (e.g. 4, 6), we measured the first of the two middle notes.

Statistical analysis

We first examined overall patterns of variation in songs within each species complex (red-legged and brown tinamou) using principal component analyses (PCA) based on the correlation matrices derived from acoustic variables. Prior to PCA, variables not normally distributed were log-transformed. Coefficients of variation were used to compare the extent of intra-taxon vocal variation between *C. obsoletus* and *C. erythropus*.

We tested whether taxa could be distinguished in multivariate vocal space using discriminant analysis (DA), combining all measurements of songs of: five subspecies of *C. obsoletus* (*castaneus*, *griseiventris*, *ochraceiventris*, *obsoletus* and *punensis*), the three forms of *C. erythropus* (*erythropus*, *idoneus* and *saltuarius*), *C. kerriae* and *C. boucardi*. We conducted three separate discriminant analyses to examine the sensitivity of results to establishing different sets of taxa as groupings. These sets were defined based on 1) existing hypotheses about species limits (Hellmayr and Conover 1942, Cabot 1992, Clements et al. 2010) and 2) our preliminary inspections of vocal variation based on PCA, which revealed the existence of taxa with apparently distinct vocalizations. First, we treated all ten taxa as independent entities. Second, we lumped *C. e. erythropus*, *C. e. idoneus*, *C. e. saltuarius* and *C. kerriae* into one entity (i.e. broad-sense *C. erythropus*), and then tested for discrimination

between this entity, *C. obsoletus* (including *C. o. castaneus*, *C. o. griseiventris*, *C. o. ochraceiventris*, *C. o. obsoletus* and *C. o. punensis*), and *C. boucardi*; in this scheme, we grouped *C. erythropus* and *C. kerriae* due to their remarkably similar songs (see below). Finally, we examined discrimination between *C. boucardi*, broad-sense *C. erythropus* as defined above, *C. obsoletus* (including *C. o. griseiventris*, *C. o. ochraceiventris*, *C. o. obsoletus* and *C. o. punensis* and excluding *C. o. castaneus*) and *C. o. castaneus*; we left *C. o. castaneus* apart from the rest of *C. obsoletus* due to its strikingly different songs (see below).

Results

A visual inspection of sonograms reveals very similar songs among members of the red-legged tinamou complex (Fig. 1) but considerable variation in songs among members of the brown tinamou complex (Fig. 2). Songs of members of the red-legged tinamou complex are stereotyped, low-paced tremulous whistles comprising two to three pure tones, with unmodulated frequency. Brown tinamou songs are highly variable among populations, consisting of one to nine notes, with greater frequency modulation and variable note shape between forms. The songs of *C. o. castaneus* stand out as especially divergent from those of other populations because they only show three unmodulated pure tones whereas other taxa show longer and tremulous songs with more modulated frequencies.

The first principal component (PC1) accounted for 40% of the variation in song measurements in *C. erythropus* and allies (Fig. 3) and is associated largely with duration of the middle note (loading coefficient 0.68) and total length of song (0.32). PC2 accounted for 30% of the variation and correlated most with length of first note (0.62). In the acoustic space described by the first two PCA axes, songs of *C. e. idoneus*, *C. e. saltuarius* and even of *C. kerriae* exhibit characteristics within the range of variation existing in songs of *C. e. erythropus* (see also sonograms in Fig. 1).

PC1 accounted for 46% of the variation in song measurements in *C. obsoletus* (Fig. 4), with frequency bandwidth of the first, middle and final note loading heavily on this axis (loadings 0.45, 0.53, and 0.38, respectively). PC2 accounted for 31% of the variation, with total length of songs and length of middle and final notes loading heavily on it (loadings 0.58, 0.28, and 0.38, respectively). Songs of *C. o. castaneus* stand out as distinct from those of other taxa; they tend to have notes with narrower bandwidth, and shorter songs and notes relative to others members of *C. obsoletus* group (Fig. 2, 4). Coefficients of variation of most song characteristics were considerably larger in *C. obsoletus* than in *C. erythropus* (Table 2).

Discriminant function analysis of song measurements for all 10 taxa combined revealed significant differences among centroids (Wilks' L = 0.001, DF = 117, $p < 0.0001$, Fig. 5, Table 1). This analysis classified correctly 83.8% of individuals to their respective population designation, with most of the misclassified songs corresponding to members of the red-legged group. When we treated *C. e. erythropus*, *C. e. idoneus*, *C. e. saltuarius* and *C. kerriae* as one entity (i.e. broad-sense *C. erythropus*) separate from

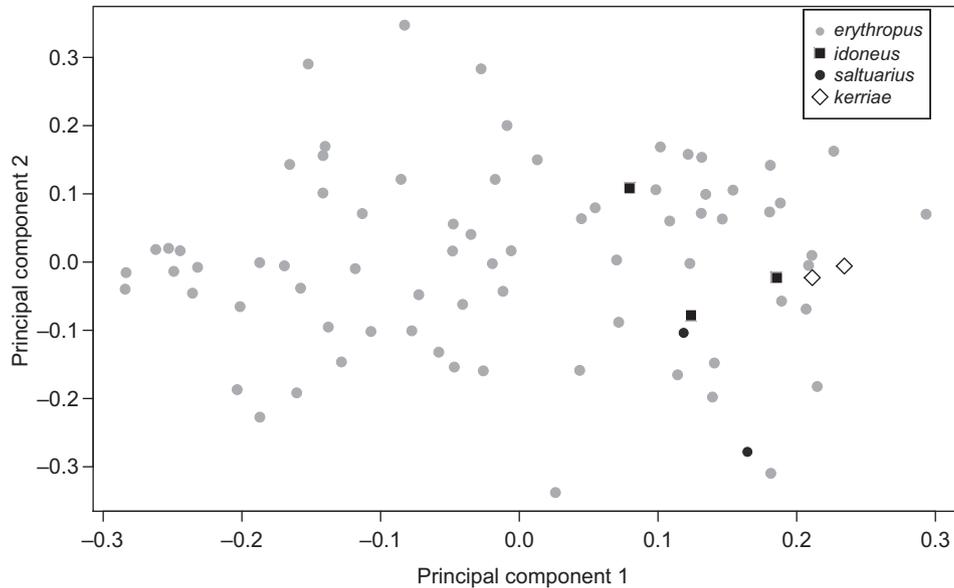


Figure 3. Principal component analysis of measurements taken on recordings of songs of red-legged tinamou and allies. Note the marked variation existing in songs of *C. erythropus*, which overlap with those of *saltuarius*, considered by some to represent a different species, and even with those of *C. kerriae*.

C. obsoletus and *C. boucardi*, 96.9% of individuals were classified correctly in their respective taxon designation (Wilks' L = 0.0006, DF = 117, $p < 0.0001$, Fig. 5, Table 1). Finally, when we tested for discrimination between *C. boucardi*, broad-sense *erythropus*, *C. obsoletus*, and *C. o. castaneus*, 100% of individuals were classified correctly (Wilks' L = 0.0005, DF = 117, $p < 0.0001$, Fig. 5, Table 1).

Discussion

Much uncertainty exists regarding species limits in the red-legged tinamou group and about the taxonomic status of related forms. *Crypturellus e. columbianus*, *C. e. saltuarius* and *C. e. idoneus* have all been recognized as full species or as

varieties of species different from *C. erythropus* (Blake 1977, Cabot 1992). For instance, Meyer de Schauensee (1970) considered *saltuarius* to be a distinct species rather than a subspecies of *C. erythropus*, but Blake (1977) proposed that this taxon might instead be a subspecies of *C. kerriae*. Hilty (2003) indicated that forms of *erythropus* are all rather similar, with variation within each subspecies almost as great as variation between them. In keeping with this suggestion, our vocal analyses show that *C. e. idoneus*, *C. e. erythropus*, *C. e. saltuarius* and even *C. kerriae* (sometimes considered conspecific with *C. boucardi*, Cabot 1992) have very similar songs. Unfortunately, we were unable to obtain confirmed recordings of *C. e. columbianus*, but assuming this population is in contact with *idoneus* and *saltuarius*, we expect its song to fall within the variation existing in *C. erythropus*.

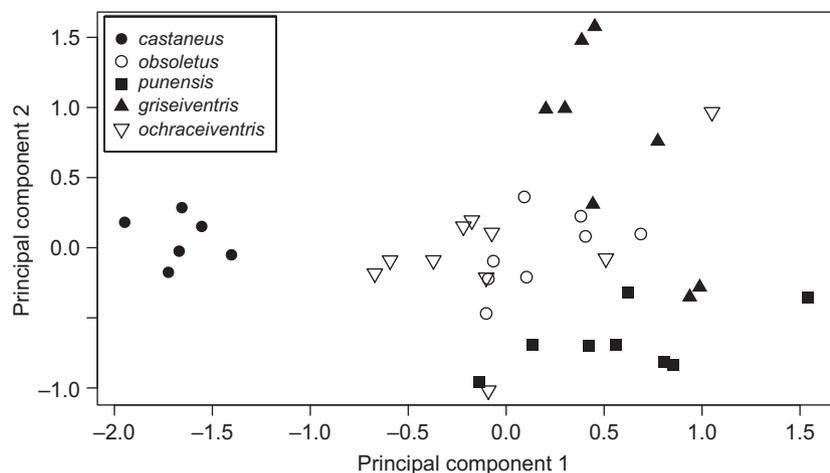


Figure 4. Principal component analysis of measurements taken on recordings of brown tinamou songs. Note that songs of each taxon tend to cluster together and the marked separation of songs of *castaneus*.

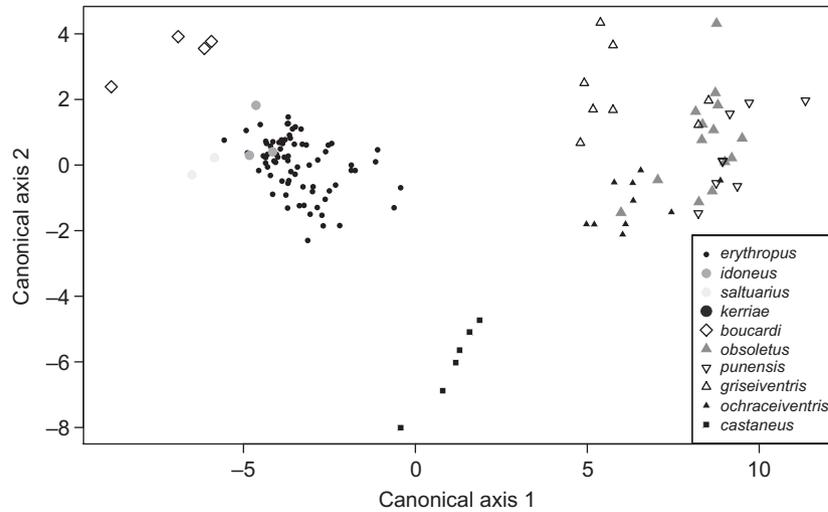


Figure 5. Call variation in 10 tinamou taxa summarized by the first two discriminant canonical functions derived from 13 acoustic variables. The first two canonical functions explained 89.4% of the variation in vocal variables (81.8 and 7.6%, respectively; Table 1). Note the marked discrimination in members of the brown tinamou group relative to discrimination among forms of the red-legged group.

In contrast to the situation of the red-legged tinamou group, there has been little debate with regard to species limits in the brown tinamou (Cabot 1992, Clements et al. 2010). The extensive variation in songs revealed by our analyses suggests that *C. obsoletus* likely comprises more than one species. Because only one species is recognized in the brown tinamou group, whereas as many as three species have been suggested to exist in the red-legged tinamou group, vocalizations suggest that current taxonomy may not adequately represent species-level diversity in these birds.

Populations of *C. erythropus* from east and west of the Andes are likely connected through the lowlands north of the Andes (Fig. 1). Such connection would facilitate gene flow (Brumfield and Capparella 1996) and could account for the lack of vocal differentiation we observed. In contrast, geographic distributions of populations of *C. obsoletus*

are not contiguous. Lowland subspecies are well isolated by distance and major rivers (Fig. 2): *C. o. obsoletus* of the southern Atlantic forest is isolated by more than 1000 km from *C. o. griseiventris* of north-central Brazil and *C. o. hypochraceus* is separated from *C. o. griseiventris* by the Madeira River. In turn, montane forms (*C. o. cerviniventris*, *C. o. knoxi*, *C. o. castaneus*, *C. o. ochraceiventris*, *C. o. traylori* and *C. o. punensis*) have seemingly disjunct distributions from Venezuela to Bolivia (Fig. 2, Cabot 1992). Finally, it appears that *C. o. castaneus* differs ecologically from other populations: its elevational range ($n = 6$ localities, 2650 ± 55 m, mean \pm standard deviation) does not overlap with that of *C. o. griseiventris* ($n = 34$, 270 ± 39 m) or *C. o. obsoletus* ($n = 23$, 647 ± 370 m), and only narrowly overlaps with the highland forms *C. o. punensis* ($n = 13$, 1750 ± 470 m) and *C. o. ochraceiventris* ($n = 13$, 1650 ± 680 m). Populations with contrasting elevational distributions and different voices have been shown to represent different species in recent studies in other Neotropical birds (Cadena and Cuervo 2010, Caro et al. 2013) including tinamous (Maijer 1996).

The patterns uncovered by our analyses reveal greater vocal differentiation among populations of the brown tinamou group relative to the red-legged tinamou group, which contrasts with the patterns observed in plumage variation. Because traditional taxonomy of tinamous has

Table 1. Standardized canonical discriminant function coefficients of the discriminant function analysis of vocal variation in *C. erythropus*, *C. boucardi*, *C. castaneus* and *C. obsoletus* based on 13 measurements taken on songs. Bold numbers highlight the most important variables in the discriminant functions.

Variable	Function	
	1	2
Length of song	-0.061	0.148
Lower frequency first note	0.384	-0.380
Higher frequency first note	0.819	-0.411
Max frequency first note	0.691	-0.381
Bandwidth first note	0.444	0.096
Entropy first note	0.473	0.294
Length of the first note	-0.239	0.225
Lower frequency second note	0.447	-0.542
Higher frequency second note	0.812	-0.321
Max frequency second note	0.647	-0.292
Bandwidth second note	0.485	0.335
Entropy second note	0.484	0.412
Length of the second note	-0.196	0.380

Table 2. Coefficients of variation of song features in the red-legged and the brown tinamou groups. Note the greater variation in most measurements in the brown tinamou group.

	Red-legged group	Brown group
Number of notes	16.54	58.10
Song length (s)	16.80	63.20
Pace (notes/s)	23.29	21.99
Bandwidth (Hz)	16.89	46.89
Peak frequency (Hz)	12.41	16.57
Entropy	2.79	20.76

relied largely on plumage coloration (Hellmayr and Conover 1942, Blake 1977), the recognition of several species in the red-legged tinamou group is based on marked geographic variation in plumage coloration, especially of the crown and belly (Cabot 1992). Although plumage traits carry some phylogenetic signal in tinamous (Bertelli et al. 2002, Bertelli and Porzecanski 2004), we suggest they may not be reliable taxonomic markers for species delimitation. In particular, color intensity may be highly sensitive to the local environment and thus result in within-species geographic variation in association with humidity (i.e. Gloger's rule, Burt and Ichida 2004) and light availability in the environment (Gomez and Théry 2007). Consistent with such scenario, an examination of specimens and photographs of members of the red-legged tinamou group by F. G. Stiles revealed that all of the forms share a similar overall plumage pattern and differ mainly in intensity of coloration, with variation seemingly following Gloger's rule (i.e. darker plumages in more humid areas; Remsen et al. 2014). Thus, the phenotypic variation that led to recognition of several taxa in this group may reflect geographic variation over environmental gradients within a single lineage. In contrast, geographic variation in plumage in the brown tinamou group is much more subtle and this may explain why this group has been subject to far less debate concerning species delimitation.

If one follows the biological species concept (BSC), which focuses on reproductive isolation as a criterion for species delimitation (Mayr 1963), the taxonomic implications of the patterns of variation revealed by our study must necessarily be tentative in the absence of studies assessing the role of songs and plumage in species recognition (Uy et al. 2009), especially considering the allopatric distributions of most taxa. Pending such additional analyses and also examinations of genetic variation and phylogenetic relationships, however, it appears that, minimally, the montane Colombian form *castaneus* merits recognition as a distinct biological species based on its remarkably different song and distinct elevational distribution (Fig. 2, 4). The degree of vocal and ecological differentiation between *castaneus* and other populations is comparable to, or even greater than, variation existing among good (i.e. reproductively isolated) species of tinamous (Cabot 1992, Maijer 1996), a criterion often used to treat allopatric populations as different species under the BSC (reviewed by Remsen 2005). Alternatively, if one were to follow species concepts based on diagnosability (e.g. the phylogenetic species concept, Cracraft 1983), which are often used in ornithology (Sangster 2014), then it is likely that several species would need to be recognized in the brown tinamou group. In turn, vocal variation does not support the split of *C. erythropus* into more species than currently recognized (Remsen et al. 2014) as has been suggested by some authors (Collar 1992, Renjifo et al. 2002, BirdLife International 2008). Intriguingly, our analyses indicate that *C. kerriae*, which has never been considered part of this group, exhibits songs within the range of vocal variation existing in *C. erythropus*, suggesting these two taxa may well be conspecific and that their phenotypic distinctiveness should be recognized at the subspecies level. We refrain, however, from formally recommending lumping *C. kerriae* and *C. erythropus* given

their marked differences in plumage coloration and the lack of evidence about the importance of such differences as indicators of species limits in tinamous. Moreover, because a cladistic analysis based on 80 integumentary characters indicates that *C. erythropus* and *C. kerriae* are distant relatives within the Tinamidae (Bertelli et al. 2002), any proposal to lump these taxa in a single species should be based on additional data. In addition to analyses directed at establishing the function of plumage and vocal traits, molecular-based assessments of phylogenetic relationships and population-genetic differentiation are sorely needed. Another important priority for future analyses would be to acquire and analyze recordings of the songs of taxa not included in our analyses owing to lack of material, especially in the brown tinamou group (i.e. *C. o. cerviniventris*, *C. o. knoxi*, *C. o. hypochaceus*).

The uncertain taxonomic status of threatened bird populations is particularly evident among the Neotropical avifauna. On one hand, some Neotropical bird species of particular conservation concern (e.g. the critically endangered tumaco seedeater *Sporophila insulata* and Entre Ríos seedeater *S. zelichi*) have been shown to be invalid taxa (Stiles 2004, Areta 2008), whereas other populations that might merit species recognition are currently treated only as subspecies of more widespread species (e.g. *Pyrrhura picta subandina*, *Cistothorus apolinari apolinari*) are rapidly vanishing owing to a lack of formal protection (Joseph 2000, Cadena 2003). In addition, the existence of threatened species that only recently have been discovered or recognized (Krabbe and Schulenberg 1997, Krabbe et al. 1999, 2005, Cuervo et al. 2005, Carantón-Ayala and Certuche-Cubillos 2010, Lara et al. 2012), or whose validity as species has only been confirmed through recent work (Krabbe et al. 2005, Krabbe and Cadena 2010), highlights the importance of studies on species-level taxonomy to enable sound conservation of Neotropical birds.

Our study of two groups of tinamous highlights that incomplete knowledge of patterns of variation in relevant traits, in addition to adhering to the momentum carried by traditional taxonomy, may lead to potential pitfalls in conservation planning. On one hand, the red-legged tinamou group, in which much attention by conservationists has been devoted to threatened populations (BirdLife International 2008), may actually consist of a single lineage with a sufficiently large range and population sizes so as to be relatively safe from a conservation standpoint. In contrast, the brown tinamou, long considered of least concern by conservationists owing to its large geographical distribution, may actually comprise several species of uncertain, and likely worrisome conservation status. Our data indicate that taxon *castaneus* should be considered a species separate from the rest of *C. obsoletus*; this formerly unrecognized species is likely under risk. Its distribution range is quite small and largely deforested, and is known to occur only within a single small reserve (Parque Natural Chicaque; ca 250 ha). Other recent records west of Bogotá (La Aguadita and Subachoque) are from a region lacking protected areas; thus, this tinamou occurs in areas entirely lacking official protection (Franco et al. 2007, BirdLife International 2013).

More generally, our work serves to illustrate that conservation biologists and managers should bear in mind that taxonomy has the potential to influence, and even mislead, perceived priorities for conservation action, especially in groups and areas where taxonomic revisions of many groups are still required (e.g. many birds in the Neotropics). Conservation would clearly benefit from consultation with taxonomists and from consideration of alternative metrics of biodiversity in addition to a species-centered approach relying on prevailing (and possibly incorrect) taxonomy (Faith 1992, Moritz 2002, Cadena 2003).

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Supplementary material (Appendix JAV-00298 at <www.avianbiology.org/readers/appendix>). Appendix 1.