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Paraphyly of *Cinclodes fuscus* (Aves: Passeriformes: Furnariidae): Implications for taxonomy and biogeography

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ABSTRACT

The Andes are a hotspot of global avian diversity, but studies on the historical diversification of Andean birds remain relatively scarce. Evolutionary studies on avian lineages with Andean–Patagonian distributions have focused on reconstructing species-level phylogenies, whereas no detailed phylogeographic studies on widespread species have been conducted. Here, we describe phylogeographic patterns in the Bar-winged Cinclodes (*Cinclodes fuscus*), a widespread and common species of ovenbird (Furnariidae) that breeds from Tierra del Fuego to the northern Andes. Traditionally, *C. fuscus* has been considered a single species composed of nine subspecies, but its long and narrow range suggests the possibility of considerable genetic variation among populations. Sequences of two mitochondrial genes revealed three discrete and geographically coherent groups of *C. fuscus*, occupying the southern, central, and northern Andes. Surprisingly, phylogenetic analyses indicated that these groups were more closely related to other species of *Cinclodes* than to each other. Relationships of the southern and northern *C. fuscus* clades to other species of *Cinclodes* were straightforward; in combination with available information on plumage, behavioral, and vocal variation, this suggests that each should be recognized as a distinct biological species. The central Andean group was paraphyletic with respect to *C. oustaleti*, and relationships among these taxa and *C. olrogi* were poorly resolved. We suggest that the central Andean *C. fuscus* should also be considered a different species, pending new information to clarify species limits in this group. These new phylogenetic data, along with recently developed methods, allowed us to review the biogeography of the genus, confirming southern South America and the central Andes as important areas for the diversification of these birds.

1. Introduction

The monophyletic passerine genus *Cinclodes* (Furnariidae) consists of thirteen species found in the highlands of South America and the coastal lowlands of Chile, Peru, and southern Argentina (Remsen, 2003; Chesser, 2004). The species in this genus occur in a variety of environments, but are closely associated with water sources (Vaurie, 1980; Sabat, 2000). Some species have independently adapted to marine environments (Chesser, 2004) and tolerate salty conditions either permanently or seasonally, a pattern that appears to represent a case of adaptive radiation in osmoregulatory function (Sabat et al., 2006).

Two main biogeographic hypotheses have been postulated to account for the historical diversification of *Cinclodes* and other codistributed lineages. Chapman (1917) suggested that species occurring in the páramo regions of the northern Andes may have originated in the temperate zone of southern South America and then dispersed north. This hypothesis was applied to *Cinclodes* by Vaurie (1980) and Fjeldså (1992), who proposed that diversification in this genus took place in the south with subsequent dispersal north into the Andes. The second hypothesis proposes that the genus *Cinclodes* originated in highland areas of South America and secondarily invaded the Pacific coast and perhaps Patagonia (Vuilleumier, 1986).

The Bar-winged Cinclodes (*Cinclodes fuscus*) is by far the most widespread species in the genus; it is a common terrestrial bird

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that breeds, primarily in and along the Andes, from Tierra del Fuego to northern Colombia and Venezuela (Remsen, 2003). Phylogenetic work on other groups of birds with similar distributions has revealed diverse systematic and historical biogeographic patterns (García-Moreno et al., 1998; Chesser, 2000, 2004; Cheviron et al., 2005; Chesser et al., 2007). However, none of these studies included extensive sampling within a single species. Here, we investigate the phylogeography of *C. fuscus* to examine patterns of genetic variation within a widespread Andean–Patagonian species.

Cinclodes fuscus has traditionally been considered a single species (Sclater, 1890; Cory and Hellmayr, 1925; Peters, 1951), with nine subspecies currently recognized (Remsen, 2003; Fig. 1A). Four subspecies (*C. f. fuscus*, *C. f. albiventris*, *C. f. albidiventris* and *C. f. oreobates*) have relatively wide geographical ranges, whereas the others (*C. f. tucumanus*, *C. f. yzurietae*, *C. f. riojanus*, *C. f. rufus* and *C. f. heterurus*) are endemic to isolated highlands in Argentina or to the Venezuelan Andes. Although these subspecies (and their synonyms) have remained part of *C. fuscus* since their merger into a single species by Sclater (1890), several additional taxa, including Olrog's Cinclodes (*C. olrogi*), Cordoba Cinclodes (*C. comechingonus*), and Long-tailed Cinclodes (*C. pabsti*), have at times also been considered subspecies of *C. fuscus* (reviewed in Chesser, 2004). On the other hand, differences in plumage, song, and migratory behavior suggest that the southern subspecies *C. f. fuscus* and the central Andean subspecies *C. f. albiventris* may be different species (Jaramillo, 2003). This is supported by recent genetic data showing substantial mtDNA divergence between populations of these subspecies in Argentina (Kerr et al., 2009).

A recent molecular phylogenetic study on the systematics of the genus (Chesser, 2004) found that *C. fuscus* is sister to the Blackish Cinclodes (*C. antarcticus*), a marine species from extreme southern Argentina and Chile. The two *C. fuscus* samples included in that study formed a monophyletic group. However, because both individuals belonged to the nominate subspecies (*C. f. fuscus*) and representatives of *C. f. albiventris* and the northern forms were not sequenced, relationships between nominate *fuscus* and the other subspecies could not be assessed. Including additional populations of *C. fuscus* in phylogeographic analyses is of particular interest because its long and narrow range may restrict gene flow among populations, which may promote differentiation along the Andes (Graves, 1985, 1988). Moreover, polytypic species with wide distributions, such as *C. fuscus*, are often reported to be paraphyletic (Funk and Omland, 2003). Thus, geographically diverse sampling is needed to understand genetic variation in *C. fuscus* and the relationship of it to other *Cinclodes* species.

In this study, we use sequences of two mitochondrial genes to infer relationships among individuals of *C. fuscus* from much of its geographic range, and the relationships of populations of *C. fuscus* to other species in the genus. Specifically, we address the following questions: (1) What is the extent of genetic variation across the range of *C. fuscus*? (2) Is *C. fuscus* a monophyletic group with respect to other species of *Cinclodes*? (3) What are the implications of a more complete assessment of phylogenetic relationships within *Cinclodes* for our understanding of the biogeography of the genus?

2. Materials and methods

2.1. Taxonomic and geographic sampling

Tissue samples of 55 individuals of *Cinclodes fuscus* were obtained from eight frozen tissue collections (Table 1 and Fig. 1). These individuals include multiple representatives of the four more wide-ranging subspecies, and cover a geographic area extending from southern Argentina to Colombia. In addition, we included samples collected in the province of Tucumán (Argentina), which correspond to either the widespread *C. f. albiventris* or to the restricted-range *C. f. tucumanus*. Because of

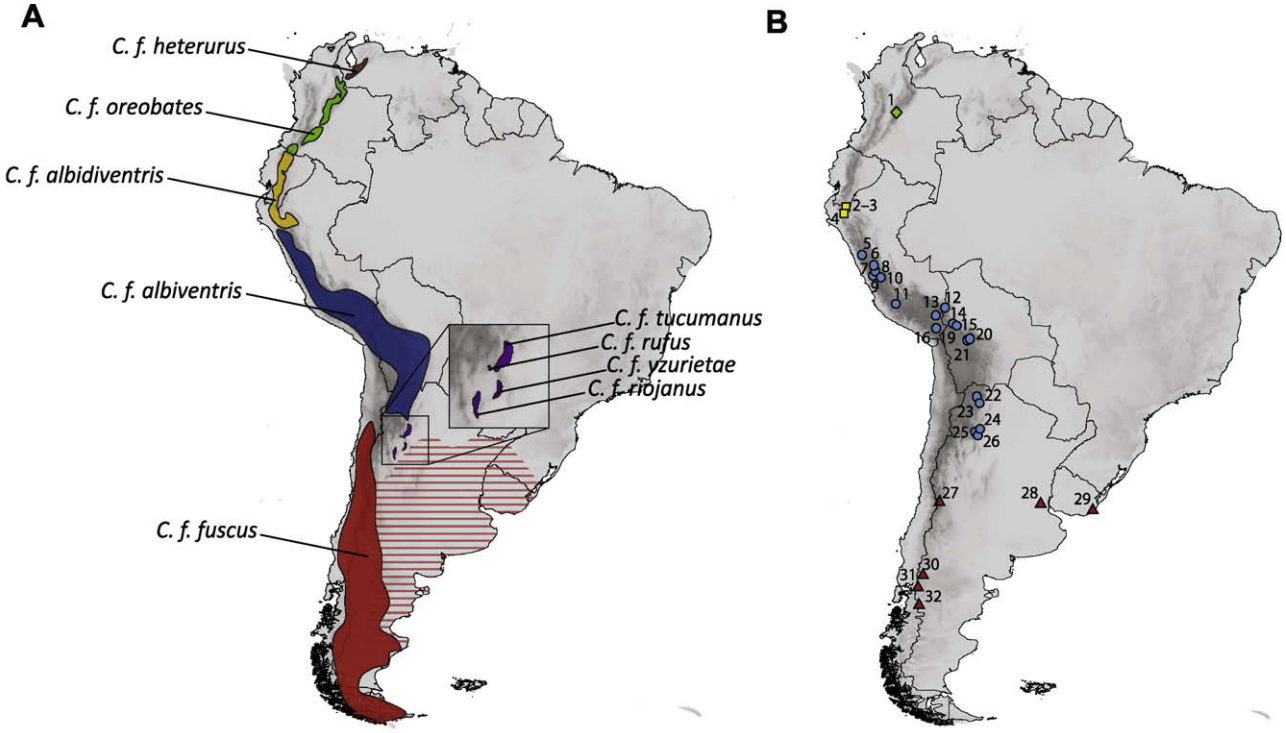

Fig. 1. (A) Distribution of the nine subspecies of *C. fuscus*. The lined distribution represents the winter range of the migratory form *C. f. fuscus*. (B) Sampling localities for this study. Symbols are colored and shaped according to subspecies designation. Green circles: *C. fuscus oreobates*, Yellow squares = *C. fuscus albidiventris*, Blue triangles = *C. fuscus albiventris*, and *C. fuscus tucumanus*, Red diamonds = C. *fuscus fuscus*. (For interpretation of color mentioned in this figure legend the reader is referred to the web version of the article.)

Table 1
List of haplotypes, tissue reference numbers, subspecies and collecting localities for sequenced individuals of *C. fuscus*. Locality numbers as shown in Fig. 1B are in parentheses.

Haplotype	Tissue Number	Subspecies	Locality
Hap1	ANDESBT765	C. f oreobates	Colombia: Cundinamarca, PNN Sumapaz, Laguna Los Tunjos (1)
Hap2	ANSP 16993	C. f albidiventris	Ecuador: Zamora Chinchipe, 20 km road, Jimbura to Zumba (2)
Hap3	ANSP 19537	C. f albidiventris	Ecuador: Zamora Chinchipe, 25 km SSE Jimbura; E slope Cord. Lagunillas (3)
Hap4	LSUMZ 169792	C. f albidiventris	Peru: Cajamarca Department, Quebrada Lanchal, ca 8 km ESE Sallique (4)
Hap5	LSUMZ B-32706	C. f albidiventris	Peru: Cajamarca Department, Quebrada Lanchal, ca 8 km ESE Sallique (4)
Hap6	FMNH 391867	C. f albiventris	Peru: Ancash, Ishinca (5)
	LSUMZ 128410	C. f albiventris	Peru: Pasco Department, Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail (6)
	NMNH B23126	C. f albiventris	Peru: Junin, Ondores (8)
Hap7	LSUMZ B-48277	C. f albiventris	Peru: Pasco Department, Vicco area, ca 39.5 km NW Junin city (7)
	LSUMZ B-61346	C. f albiventris	Peru: Junin Department, Laguna Ancacocha, ca 5 km N Marcapomacocha (9)
Hap8	LSUMZ B-61335	C. f albiventris	Peru: Junin Department, ca 9 km SSE Marcapomacocha (9)
	NMNH-B05838	C. f albiventris/tucumanus	Argentina: Tucumán, Tucumán (26)
Hap9	LSUMZ B-7686	C. f albiventris	Peru: Huánuco Department, Unchog Pass NNW Acomayo (10)
Hap10	AMNH CBFMH13	C. f albiventris	Bolivia: La Paz, Tojoloque, near Queara (12)
	AMNH MOA39	C. f albiventris	Bolivia: La Paz, Tojoloque, near Queara (12)
	NMNH B23038	C. f albiventris	Peru: Puno, Km54 Puno-Moquegua road (17)
Hap11	AMNH RPC1	C. f albiventris	Bolivia: La Paz, Tojoloque, near Queara (12)
	FMNH 334439	C. f albiventris	Bolivia: Cochacamba, Km80 Cochacamba-Oruro road (21)
	FMNH 394414	C. f albiventris	Bolivia: Cochacamba, Km80 Cochacamba-Oruro road (21)
Hap12	LSUMZ 114118	C. f albiventris	Peru: Ayacucho Department, Pampa Galeras, 25 km WNW of Puquio (11)
Hap13	LSUMZ 114119	C. f albiventris	Peru: Puno Department, Isla Estaves, ca 5 km E. Puno. (13)
	LSUMZ B-22572	C. f albiventris	Bolivia: La Paz Department, Zongo Valley, 7 km by road N. of Summit (14)
Hap14	NMNH B23074	C. f albiventris	Peru: Puno, Km50 Puno-Moquegua road (16)
Hap15	NMNH B23039	C. f albiventris	Peru: Puno, Km54 Puno-Moquegua road (17)
Hap16	LSUMZ 101931	C. f albiventris	Bolivia: La Paz Department, ca 1km S Chuspipata (15)
Hap17	NMNH B23078	C. f albiventris	Peru: Puno, Km90 Puno-Moquegua road (18)
Hap18	NMNH B23070	C. f albiventris	Peru: Puno, Km251 Moquegua-Desaguadero road (19)
	NMNH B05802	C. f albiventris/tucumanus	Argentina: Tucumán, Tucumán (26)
Hap19	LSUMZ 123949	C. f albiventris	Bolivia: Cochabamba Department, 6.6 km NW Lopez Mendoza (20)
Hap20	MACN 1076	C. f albiventris	Argentina: Jujuy, Quebraleña (22)
Hap21	MACN 1027	C. f albiventris	Argentina: Jujuy, Volcán (23)
	UWBM DAB809	C. f albiventris/tucumanus	Argentina: Tucumán, San Miguel de Tucumán, El Infiernillo (24)
	UWBM DAB792	C. f albiventris/tucumanus	Argentina: Tucumán, San Miguel de Tucumán, El Infiernillo (24)
	UWBM DAB793	C. f albiventris/tucumanus	Argentina: Tucumán, San Miguel de Tucumán, El Infiernillo (24)
	UWBM DAB794	C. f albiventris/tucumanus	Argentina: Tucumán, San Miguel de Tucumán, El Infiernillo (24)
	UWBM JAG1780	C. f albiventris/tucumanus	Argentina: Tucumán, San Miguel de Tucumán, El Infiernillo (24)
	NMNH B05853	C. f albiventris/tucumanus	Argentina: Tucumán, Tucumán (26)
	NMNH B05794	C. f albiventris/tucumanus	Argentina: Tucumán, Tucumán (26)
Hap22	MACN 836	C. f albiventris	Argentina: Jujuy, Volcán (23)
Hap23	MACN 843	C. f albiventris	Argentina: Jujuy, Volcán (23)
Hap24	UWBM JAG1781	C. f albiventris/tucumanus	Argentina: Tucumán, San Miguel de Tucumán, El Infiernillo (24)
	LSUMZ B-17171	C. f albiventris/tucumanus	Argentina: Tucumán, Amaicha del Valle, 12 km S, 12 km E, along Ruta 307 near km 90 (25)
Hap25	AMNH RTC437	C. f fuscus	Chile: Region Metropolitana, 2 km ENE Embalse el Yeso (27)
	MACN 2181	C. f fuscus	Argentina: Buenos Aires, San Pedro (28)
	MACN 2186	C. f fuscus	Argentina: Buenos Aires, San Pedro (28)
	LSUMZ B-51986	C. f fuscus	Uruguay: Rocha Department, Barra de la Laguna de Rocha (29)
	AMNH PRS1133	C. f fuscus	Argentina: Rio Negro, Cerro Perito Moreno, ca. 20 km N El Bolsón (30)
	AMNH RTC360	C. f fuscus	Argentina: Rio Negro, Cerro Perito Moreno, ca. 20 km N El Bolsón (30)
	MACN 2594	C. f fuscus	Argentina: Rio Negro, Cerro Perito Moreno, NW El Bolsón (31)
	MACN 2649	C. f fuscus	Argentina: Rio Negro, Cerro Perito Moreno, NW El Bolsón (31)
	MACN 3020	C. f fuscus	Argentina: Chubut, Estancia "Tres Valles" (32)
Hap26	AMNH RTC418	C. f fuscus	Chile: Region Metropolitana, 2km ENE Embalse el Yeso (27)
Hap27	MACN 2158	C. f fuscus	Argentina: Buenos Aires, San Pedro (28)
Hap28	AMNH PRS1132	C. f fuscus	Argentina: Rio Negro, Cerro Perito Moreno, ca. 20 km N El Bolsón (30)
Hap29	AMNH RTC361	C. f fuscus	Argentina: Rio Negro, Cerro Perito Moreno, ca. 20 km N El Bolsón (30)

ambiguities in the geographical range and in the identification of individuals of these taxa (compare Chapman, 1919 and Fjeldså and Krabbe, 1990), samples from Tucumán were designated *C. f. albiventris/tucumanus*. Tissue samples of *C. f. heterurus*, *C. f. riojanus*, *C. f. yzurietae* and *C. f. rufus*, which are restricted to the Venezuelan Andes or to isolated highlands in Argentina, were not available for study.

2.2. Laboratory procedures

DNA was isolated from tissue samples using a DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) following the manufacturer's protocol. Two mitochondrial genes (ND3 and COII) were amplified by standard polymerase chain reaction (PCR) using locus-specific primers (Table 2) and conditions described previously (Chesser, 2004). These genes were chosen so that our data could be integrated with sequence data from other species of *Cinclodes* (from Chesser, 2004). This was important owing to the substantial genet-

Table 2
Primers used for the PCR amplification of the ND3 and COII mitochondrial genes.

Primer	Locus	Sequence (5′–3′)	Source
L10755	ND3	GACTTCCAATCTTTAAAATCTGG	Chesser (1999)
H11151	ND3	GATTTGTTGAGCCGAAATCAAC	Chesser (1999)
L8302	COII	GCCTTGTCAAGACTAAATCGCAGG	Chesser (2004)
H9036-A	COII	CTTTCTCTAGCTTAAAAGGCTAGTGC	Chesser (2004)
NF3COII[a]	COII	GCCTTGTCAAGACTAAATYGCAGG	This study
GLYPHRCOII[a]	COII	CATGGGTTGGGATTTAATTGTGGCAT	This study

[a] Samples from LSUMZ were amplified and sequenced using these primers, designed by JMM.

ic divergence noted between individuals of two subspecies of *C. fuscus* in Argentina (Kerr et al., 2009) and the possibility that this species might not be monophyletic. Sequencing of PCR products was performed on a 3130×l Genetic Analyzer (Applied Biosystems, Foster City, CA) using the BigDye Terminator Kit.

2.3. Alignment and phylogenetic analyses

Sequences (1035 bp) were assembled and edited using Sequencher 4.7 (GeneCodes Corporation, Ann Arbor, Michigan) or Geneious 4.0 (Drummond et al., 2008). We used MacClade 4.08 (Maddison and Maddison, 2000) to reduce our sequences to a data set of unique *C. fuscus* haplotypes and combined these data with previously published sequences for other *Cinclodes* species (Chesser, 2004) to establish the relationships of the groups of *C. fuscus* within the genus. A maximum parsimony (MP) analysis and 1000 bootstrap replicates were conducted using the program MEGA 4.0 (Tamura et al., 2007). We also analyzed the data using maximum likelihood (ML) and evaluated nodal support using 1000 bootstrap replicates in RaxML (Stamatakis et al., 2008) run from the CIPRES online portal (http://www.phylo.org). Finally, we ran a Bayesian analysis for 1×10^7 generations using the relaxed molecular clock approach implemented in BEAST (Drummond and Rambaut, 2007). Both the ML and Bayesian analyses were run under the GTR + G + I model, which was selected as the best fit to the data according to the Akaike Information Criterion in ModelTest 3.7 (Posada and Crandall, 1998). For all phylogenetic analyses, *Upucerthia dumetaria*, *U. validirostris*, *Furnarius rufus*, *Synallaxis spixii*, and *Geositta cunicularia* were used as outgroups, following Chesser (2004).

We tested whether the observed topologies (see below) were significantly more parsimonious and likely than a topology enforcing the monophyly of *C. fuscus* haplotypes; for this, we performed a Kishino–Hasegawa test (KH test) (Kishino and Hasegawa, 1989) for the MP analysis, and a likelihood ratio test (LRT) for the ML analysis in PAUP* 4.0 (Swofford, 2003). Subsequently, we built a median-joining haplotype network using Network 4.502 (Bandelt et al., 1999) to visualize relationships within the clade formed by *C. fuscus albiventris/tucumanus*, *C. oustaleti*, and *C. olrogi*, three taxa that were weakly differentiated (see below). We calculated the genetic divergence (uncorrected p-distance) between selected lineages using MEGA 4.0.

2.4. Ancestral area analysis and reconstruction

Using the resulting Bayesian inference tree, we reconstructed ancestral areas for *Cinclodes* using several methods. First, we followed Chesser (2004) and performed ancestral area (AA) (Bremer,

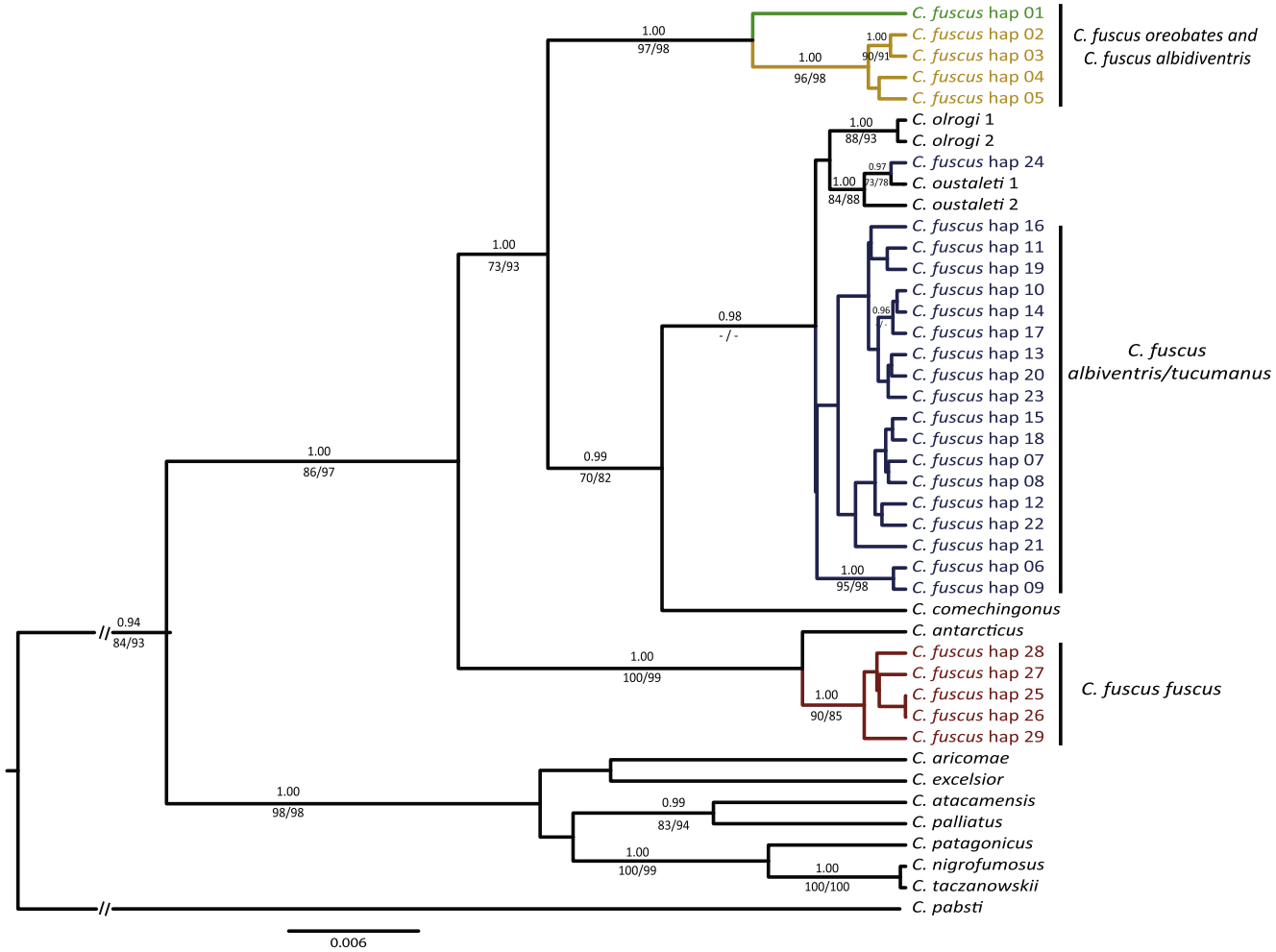

Fig. 2. Maximum clade credibility tree for ND3 and COII haplotypes of *C. fuscus* and the other *Cinclodes* species, inferred using Bayesian analysis as implemented in BEAST (Drummond and Rambaut, 2007). Outgroups are not shown. Posterior probabilities (>0.95) are listed above the branches and bootstrap support (>70) for parsimony and maximum likelihood analyses are listed beneath the branches (MP/ML). Taxa and branches are colored according to the subspecies assignments. Green: *C. fuscus oreobates,* Yellow = *C. fuscus albidiventris*, Blue = *C. fuscus albiventris*, and *C. fuscus tucumanus*, Red = C. *fuscus fuscus*. Note that BEAST estimates depth for nodes uniting even identical haplotypes (e.g. the identical haplotypes of *C. fuscus 24* and *C. oustaleti 1*). (For interpretation of color mentioned in this figure legend the reader is referred to the web version of the article.)

1992), and weighted AA (Hausdorf, 1998) analyses. Both of these analyses assume that a group's original distribution was more restricted than its current one. In addition, we used a likelihood-based method for inference of geographic range evolution by dispersal, local extinction, and cladogenesis (DEC) implemented in the program Lagrange 2.0.1 (Ree et al., 2005; Ree and Smith, 2008) using default settings with no prior constraints.

For these analyses, taxa were coded using one or more categorical characters representing the continental breeding range of each species, following Chesser (2004): southern Andes–Patagonia (SP), central Andes (CA), northern Andes (NA), highlands of central Argentina (AR), highlands of southeastern Brazil (BR), and Pacific coast of Chile and Peru (PC). We then divided the genus (excluding *C. pabsti*, which occurs in southeast Brazil) into the two main clades recovered in phylogenetic analyses: one formed by *C. fuscus*, *C. oustaleti*, *C. olrogi*, *C. comechingonus*, and *C. antarcticus* (Clade 1), and a separate one formed by *C. aricomae*, *C. excelsior*, *C. atacamensis*, *C. palliatus*, *C. patagonicus*, *C. nigrofumosus*, and C. *taczanowskii* (Clade 2). Ancestral areas were estimated for these two clades using AA and weighted AA analyses, and for each node in the Bayesian tree using DEC.

3. Results

3.1. Phylogeography of *Cinclodes fuscus*

Complete sequences (1035 bp) were obtained for all individuals of *C. fuscus* (GenBank Accession Nos. FJ799361–FJ799413 and AY613379–AY613380 for COII sequences; FJ799414–FJ799466 and AY613359–AY613360 for ND3 sequences). Twenty-nine unique haplotypes were represented among the 55 sequences. All methods of phylogenetic inference consistently recovered three distinct groups of *C. fuscus* (Fig. 2). Group 1 consisted of birds from Colombia, Ecuador, and northern Peru (subspecies *C. f. oreobates* and *C. f. albidiventris*); Group 2 of birds from central–southern Peru, Bolivia, and northwestern Argentina (subspecies *C. f. albiventris/tucumanus*); and Group 3 of birds from central and southern Argentina and Chile (subspecies *C. f. fuscus*). The average genetic distances among these groups (range 1.5–3.6%) were an order of magnitude greater than the average distances between individuals within each group (range 0.2–0.4%; Table 3).

The three groups of *C. fuscus* were not sister taxa, but instead formed clades with other *Cinclodes* species (Fig. 2). Consistent with previous work (Chesser, 2004), individuals of the nominate subspecies formed a clade sister to *C. antarcticus* (posterior probability: 1.00, ML bootstrap: 99%. MP bootstrap: 100%). The northernmost subspecies (*C. f. albidiventris* and *C. f. oreobates*) formed a well-supported clade (1.00, 98%, 97%) that was sister to a clade including *C. comechingonus*, *C. oustaleti*, *C. olrogi*, and the remaining *C. fuscus* subspecies, *C. fuscus albiventris/tucumanus* (1.00, 93%, 73%). The topologies we obtained, in which *C. fuscus* is not monophyletic, are significantly more likely and parsimonious than topologies enforcing a monophyletic *C. fuscus* (LRT: $p < 0.0001$; KH test: $p < 0.0001$).

Most haplotypes of the central subspecies *C. f. albiventris/tucumanus* formed a weakly supported clade (0.59, 28%, 24%), which grouped with *C. olrogi* and *C. oustaleti* (0.93, 40%, 42%). However, one haplotype, observed in two individuals from Tucumán, Argentina, was identical to one of the two haplotypes of *C. oustaleti* reported by Chesser (2004). In the Bayesian analysis, *C. f. albiventris/tucumanus* was sister to a clade formed by *C. olrogi* and *C. oustaleti* (posterior probability: 0.98), whereas in the MP and ML trees *C. oustaleti* was weakly supported (<20%) as sister to a clade formed by *C. olrogi* and *C. f. albiventris/tucumanus*. Divergence of some haploypes within *C. fuscus albiventris/tucumanus* (range 0.09–1.06%) was greater than the divergence of haplotypes between *C. f. albiventris/tucumanus* and *C. oustaleti* (range 0. 38–0.96%, without considering the shared haplotype between them)

Table 3
Average uncorrected p-distance within (diagonal) and between subspecies (under diagonal). Only one individual of *C. f. oreobates* was available; therefore, no intraspecific distance is provided for this subspecies.

	C. f. oreobates	*C. f. albidiventris*	*C. f. albiventris*	*C. f. fuscus*
C. f. oreobates	–			
C. f. albidiventris	0.009	0.002		
C. f. albiventris	0.015	0.016	0.004	
C. f. fuscus	0.034	0.036	0.034	0.002

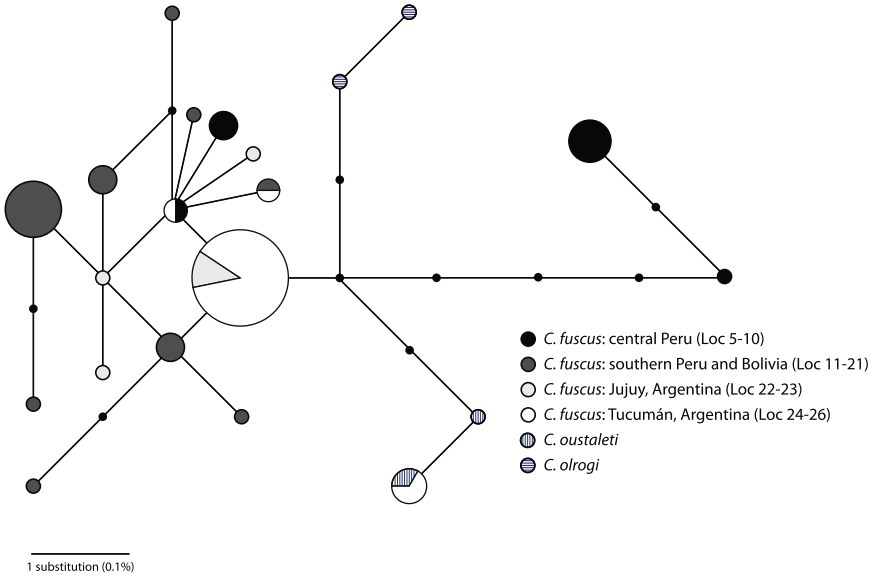

Fig. 3. Median-joining haplotype network showing relationships among *C. fuscus albiventris, C. oustaleti*, and *C. olrogi* haplotypes. Sizes of the circles are proportional to the number of individuals sampled with that haplotype. Connection lengths are proportional to the number of mutations between two haplotypes. Shadings and patterns correspond to different regions or species. Small black vertices represent unsampled or extinct haplotypes.

or *C. olrogi* (range 0.29–0.87%). The haplotype network (Fig. 3) provided a different perspective on relationships among these taxa. Although most *C. f. albiventris/tucumanus* haplotypes clustered together, two haplotypes from central Peru were distant from the rest. The two haplotypes of *C. olrogi* formed a cluster, as did those of *C. oustaleti* (including the *fuscus* individuals that share the haplotype), but these two clusters did not form a distinct unit. These clusters were separated from the rest of the network by only two mutations each, whereas the separate *C. f. albiventris/tucumanus* haplotype cluster was four steps removed.

3.2. Biogeography of the genus Cinclodes

The AA analysis (Table 4) designated the southern Andes and Patagonia, the central Andes, and the Argentinean highlands as the most likely distribution for the ancestor of Clade 1. In this clade, the weighted ancestral area analysis identified the southern Andes and Patagonia as the most likely distribution. For the ancestors of Clade 2 and of Clades 1 + 2, both the AA analysis and the weighted AA analysis agreed that the most likely distribution was the central Andes.

The DEC biogeographic reconstruction (Fig. 4) is relatively ambiguous because alternative ancestral areas were within two log-likelihood units of the most likely reconstructions for most of the nodes (11 out of 14). However, the Andes are the most likely ancestral areas towards the root: the southern Andes and Patagonia for Clade 1 and the central Andes for Clade 2. These are also the two most likely areas for the ancestor of Clades 1 + 2. The central highlands of Argentina, followed by the southern Andes and Patagonia, are the most likely ancestral distribution for the clade formed by *C. f albiventris*, *C. olrogi*, *C. oustaleti*, and *C. comechingonus*. The distribution on the Pacific coast of Chile and Peru was most likely derived on the branch leading to the species currently distributed in those areas.

4. Discussion

4.1. Phylogenetics

Cinclodes fuscus exhibits substantial geographic variation in song, migratory behavior, and some plumage characteristics. In some cases, variation is clinal; for example, plumage in *C. f. albidiventris* becomes generally paler and duller as one moves north into the range of *C. f. oreobates* (Vaurie, 1980). In other cases, no intermediate forms between adjacent subspecies exist; for example, *C. f. fuscus* and *C. f. albiventris* appear to be diagnosably distinct in several traits (Jaramillo, 2003). These patterns suggest that *C. f. albidiventris* and *C. f. oreobates* are likely members of the same clade, whereas *C. f. fuscus* and *C. f. albiventris* may form genetically distinct lineages. Both of these predictions are supported by our molecular data. Moreover, our analyses reveal that the species traditionally recognized as *C. fuscus* is actually composed of three independent and unrelated lineages.

We found *C. f. fuscus* to be sister to *C. antarcticus*, in keeping with previous work (Chesser, 2004). This subspecies migrates north in the winter and is the only subspecies of *C. fuscus* with partial marine behavior. Thus, the phylogenetic position of this taxon is congruent with the hypothesis that strict coastal habits evolved from an ancestor that shifted between freshwater and marine environments (Sabat et al., 2006). The other two groups of *C. fuscus* (*C. f. albiventris/tucumanus* and *C. f. albidiventris-C. f. oreobates*) formed a clade with *C. comechingonus*, *C. olrogi*, and *C. oustaleti*. Based on their morphological characteristics and geographical distribution, *C. f. heterurus* and the unsampled subspecies from the highlands of Argentina are also presumably part of this clade. This is not entirely unexpected considering all these forms are very similar morphologically (Vaurie, 1980).

Relationships among *C. oustaleti, C. olrogi*, and *C. fuscus albiventris/tucumanus* were not clearly resolved. Support for most branches was poor and the internodes within this group were short. This may be a result of rapid diversification during the middle Pleistocene (assuming a molecular clock calibration for mtDNA of 2.1% per million years; Weir and Schluter, 2008), perhaps due to the narrowing of the mountain forest during the cyclic variations in this period (Hooghiemstra and van der Hammen, 1998) and to the isolation of individual Argentinean highlands as ecological islands (Nores, 1986). Patterns of Pleistocene lineage diversification have also been observed in frog lineages occurring in this same region (Koscinski et al., 2008).

We found *C. oustaleti* to be paraphyletic in our analysis: one haplotype of *C. fuscus,* found in two individuals, was identical to one of the two haplotypes of *C. oustaleti* reported by Chesser (2004). This pattern is consistent with incomplete lineage sorting or with hybridization between the two species (Funk and Omland, 2003). However, *C. oustaleti* does not occur in Tucumán, the area where the specimens of *C. fuscus* were collected, so hybrids are not likely to be found in that location, although it is possible that this pattern of genetic variation reflects historical introgression.

Table 4
Ancestral area (AA) analyses (Bremer, 1992, 1995) for the two major clades within the genus *Cinclodes*. Gains and losses are number of necessary gains and losses of areas under Camin–Sokal parsimony. G/L = number of gains divided by number of losses. AA scores = G/L scores rescaled to a maximum value of 1 within each of the three analyses. AA scores of 1 indicate the most likely ancestral area for each clade.

Proposed ancestral area	G	L	G/L	AA
Clade 1				
Northern Andes	1	2	0.50	1.00
Central Andes	2	4	0.50	1.00
Southern Andes–Patagonia[a]	2	4	0.50	1.00
Highlands of central Argentina	2	4	0.50	1.00
Clade 2				
Northern Andes	1	2	0.50	0.50
Central Andes[a]	2	2	1.00	1.00
Southern Andes–Patagonia	1	3	0.33	0.33
Highlands of central Argentina	1	3	0.33	0.33
Pacific coast	1	3	0.33	0.33
Clade 1 + 2				
Northern Andes	2	4	0.50	0.75
Central Andes[a]	4	6	0.67	1.00
Southern Andes–Patagonia	3	7	0.43	0.64
Highlands of central Argentina	3	7	0.43	0.64
Pacific coast	1	4	0.25	0.38

[a] These areas were designated as the most likely distribution for the ancestor by the weighted AA analysis.

4.2. Ancestral area reconstruction

Despite the observed paraphyly of *C. fuscus,* Chesser's (2004) two major clades within *Cinclodes* remain valid with our dataset. Our ancestral area and weighted ancestral area analyses provided similar results to those published previously (Chesser, 2004). According to the AA and weighted AA analyses, the most likely distribution for the ancestor of the genus (excluding *C. pabsti*) is the central Andes, whereas the DEC analysis suggests a wide distribution across the Andes. For the ancestor of Clade 1, the southern Andes and Patagonia were the most likely distribution across all analyses. This supports the hypothesis of diversification in the south and later colonization of the high Andes (Chapman, 1917; Vaurie, 1980; Fjeldså, 1992), which was also supported in biogeographic studies of additional lineages of birds (e.g. Chesser, 2000) and other organisms (e.g. McDaniel and Shaw, 2003). For the ancestor of Clade 2, all analyses found the central Andes to be the most likely ancestral distribution. The later dispersal of

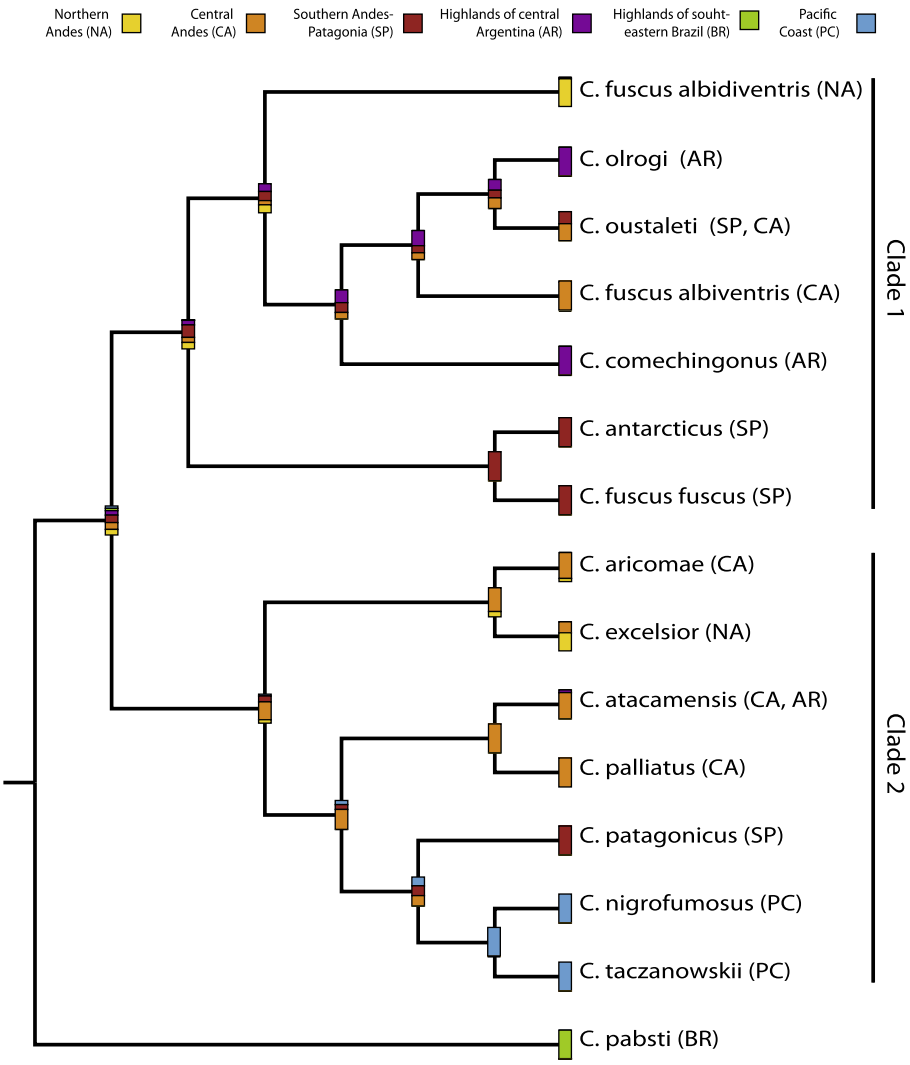

Fig. 4. Cladogram showing the reconstruction of ancestral areas based on the six-state analysis using the DEC method. Colors of the bars at each node are proportional to the likelihood that a given area was involved (either solely or as part of a wider distribution) in the split leading to that ancestor. Only scenarios that were not significantly different from the most likely were used for drawing the bars. (For interpretation of color mentioned in this figure legend the reader is referred to the web version of the article.)

members of this clade to the northern and southern Andes, the central highlands of Argentina, Patagonia, and the Pacific coast suggests the great importance of the central areas of the Andes for the diversification of the genus, which is concordant with Vuilleumier's (1986) hypothesis.

4.3. Taxonomy

The three *C. fuscus* groups recovered by our analysis represent three genetically diagnosable and independent lineages, and thus three phylogenetic (Nelson and Platnick, 1981; Cracraft, 1983) or evolutionary (Wiley, 1978) species. The nominate form *C. f. fuscus* is morphologically and behaviorally diagnosable from the other two. This is the only migratory subspecies (Vaurie, 1980; Jaramillo, 2003) and its vocalizations and plumage differ greatly from those of *C. f. albiventris,* with no intermediate forms, despite their close geographic proximity (Jaramillo, 2003). Given that these taxa are not closely related and that differences between them in voice and plumage are similar to those between *C. f. fuscus* and its sympatric congener *C. oustaleti*, it is likely that *C. f. fuscus* and *C. f. albiventris* are reproductively isolated and deserve status as distinct biological species.

Jaramillo (2003) suggested that the forms of *C. fuscus* restricted to the Ecuadorian, Colombian, and presumably Venezuelan Andes (*C. f. albidiventris*, *C. f. oreobates*, and *C. f. heterurus*) may also represent a species distinct from *C. f. albiventris*. This is congruent with our results: this group is distantly related to other forms of *C. fuscus*, and is 1.7% divergent from its sister group (*C. f. albiventris/tucumanus* + *C. olrogi* + *C. oustaleti*). However, little is known about the ecology and behavior of this clade and more studies are needed to establish its degree of divergence in relevant taxonomic characters, such as song, ecology, behavior, and plumage coloration.

Although *C. f. albiventris/tucumanus*, *C. olrogi,* and *C. oustaleti* form a moderately supported clade, relationships among these taxa remain unresolved. Nores (1986) suggested that *C. olrogi* was a form of *C. fuscus*, but most observers believe it to be more closely related to *C. oustaleti* than to *C. fuscus*. For example, Olrog (1979) included *C. olrogi* as a subspecies of *C. oustaleti*, and Ridgely and Tudor (1994) considered the two more closely related than either was to *C. fuscus*. Our genetic results provide weak support for a sister relationship between *C. olrogi* and *C. oustaleti*.

Several options are available for the taxonomic treatment of these taxa: *C. f. albiventris/tucumanus*, *C. olrogi,* and *C. oustaleti* could be considered as one, two, or three biological species.

Treatment as three species is closest to most current treatments, but current treatment is likely based in part on sympatry between *C. fuscus* and *C. oustaleti*. If *C. f. albiventris/tucumanus* is distinct from nominate *fuscus*, however, then the ranges of *C. f. albiventris/tucumanus*, *C. olrogi,* and *C. oustaleti* are entirely allopatric. Nevertheless, vocalizations of *C. f. albiventris* and *C. oustaleti*, as described by Jaramillo (2003), seem to be different enough to maintain these two as different species. Evidence for merging *C. olrogi* into either of these is equivocal. Given this, we recommend that *C. olrogi* continue to be considered specifically distinct, pending further data. Better sampling in the Argentinean highlands and more studies of potential barriers to gene flow among these three species should be conducted to clarify their relationships.

In conclusion, considering the evidence that *C. f. fuscus* and *C. f. albiventris* are most likely distinct biological species (this study; Jaramillo, 2003), a taxonomic revision of the group is required. Although relevant information on some groups is still lacking, we believe splitting *C. fuscus* into three species-level taxa is the most sensible and conservative (considering the taxonomic status quo; Remsen et al., 2009) alternative given available data. The southern form should be recognized as a monotypic species and would keep the name *C. fuscus*. Although the status of the forms occurring in the central Andes and Argentinean highlands is not entirely clear with respect to *C. olrogi* and *C. oustaleti*, we suggest they should be maintained separate and elevated to the species-level, taking the name *C. albiventris.* This species would provisionally comprise five subspecies: *C. a. albiventris*, *C. a. tucumanus*, *C. a. yzurietae*, *C. a. riojanus,* and *C. a. rufus*. Additional work will be necessary to determine whether these taxa are maintained as specifically distinct from *C. olrogi* and *C. oustaleti.* Finally, we recommend the northern forms to be treated as a single species *C. albidiventris*, provisionally composed of three subspecies: *C. a. albidiventris, C. a. oreobates*, and *C. a. heterurus*.

The conclusions of this study are based primarily on mitochondrial DNA. Confirmation using nuclear DNA would make an even stronger case for the existence of three distinct lineages of *C. fuscus*; however, in this instance additional evidence supporting their distinctiveness already existed in the form of vocal and plumage data (e.g. Jaramillo, 2003), providing independent lines of evidence that converge on the same result. Thus, we consider the possibility that the mtDNA data have led to erroneous conclusions to be remote. We also note that mtDNA has a higher mutation rate and shorter coalescence time than nuclear DNA, making it generally more informative than nuclear sequence data for studies of phylogeography (Zink and Barrowclough, 2008), especially when the clades under investigation have relatively recently diverged, as is the case in our study.

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