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COVER: Differences in plumage color and pattern, bill color and shape, song, habitat, and migration distinguish the Patagonian Forest Earthcreeper (*Upucerthia saturator*) from the Scale-throated Earthcreeper (*U. dumetaria*) and indicate that it should be considered a species rather than a subspecies, as previously classified (Areta and Pearman, pp. 135–149). This adult was photographed at Lagunas de Epulauquen, Neuquén, Argentina. Note the distinctive short black bill, dark dorsal coloration, and indistinct breast markings. Photograph by Juan I. Areta, esporofila@yahoo.com.ar.

NATURAL HISTORY, MORPHOLOGY, EVOLUTION, AND TAXONOMIC STATUS OF THE EARTHCREEPER *UPUCERTHIA SATURATIONIOR* (FURNARIIDAE) FROM THE PATAGONIAN FORESTS OF SOUTH AMERICA

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Abstract The Patagonian Forest Earthcreeper (*Upucerthia saturationior*) is a distinctive furnariid that inhabits the Patagonian forests of central-western Argentina and adjacent Chile within the *Nothofagus* Center of Endemism. After its description as a species in 1900, *U. saturationior* was quickly subsumed, without comment or study, as a subspecies of the Scale-throated Earthcreeper (*U. dumetaria*), a treatment followed by most subsequent authors. On the basis of an apparent geographical cline within *U. dumetaria* and a reanalysis of the morphology and plumage of reported intergrades between *U. dumetaria* and *U. saturationior*, there is no evidence of intergradation between these taxa. *Upucerthia saturationior* differs from *U. dumetaria* by its song (“p-p-tirik-tirik-tirik-tirik-tirik-tirik” vs. “pli-pli-pli-pli- . . .”), which is also three times faster in *dumetaria*, call (“pep” vs. “keep”), morphology (smaller and darker with a short black bill vs. larger and paler with a long brown bill), distinctive tail pattern, breeding habitat (forest borders vs. shrubby steppe and open highland habitats), and migration patterns (trans-Andean vs. north–south). These differences exceed those between *U. jelskii* and *U. albigula* and are far greater than those between *U. jelskii* and *U. validirostris*; they overwhelmingly support ranking *U. saturationior* as a full species. The existence of a forest-dwelling species of *Upucerthia* parapatric to an open-country *Upucerthia* provides an opportunity for testing the role of habitat shift between dry exposed habitats and forest habitats (and vice versa) during speciation.

Key words: Andes, evolution, natural history, Nothofagus forest, Patagonian Forest Earthcreeper, systematics, taxonomy, *Upucerthia saturationior*.

Historia Natural, Morfología, Evolución, y Estatus Taxonómico de la Bandurrita *Upucerthia saturationior* de los Bosques Patagónicos de América del Sur

Resumen. *Upucerthia saturationior* es un furnarido bien diferenciado que habita los bosques patagónicos del centro-oeste de Argentina y Chile, dentro del área de endemismo de *Nothofagus*. Inicialmente descrita como una especie distinta en 1900, *U. saturationior* fue rápidamente incluida dentro de *U. dumetaria* sin una explicación o estudio que lo avalaran; este tratamiento ha sido seguido por la mayoría de los autores posteriores. Basados en la variación geográfica aparentemente clinal de *U. dumetaria* y en un re-análisis de la morfología y plumaje de individuos que se suponía representaban gradación entre *U. dumetaria* y *U. saturationior*, concluimos que no hay evidencia de gradación entre estos taxones. *Upucerthia saturationior* difiere de *U. dumetaria* en canto (“p-p-tirik-tirik-tirik-tirik-tirik-tirik” vs. “pli-pli-pli-pli- . . .”) y llamados (“pep” vs. “kiip”), morfología (más pequeña y oscura, con pico negro y corto vs. más grande y pálida, con pico largo y marrón) y patrón de la cola, hábitat reproductivo (bordes de bosque vs. estepa arbustiva y habitats abiertos de altura) y patrón migratorio (trans-andino vs. norte–sur). Estas diferencias son mayores a las que se encuentran entre *U. jelskii* y *U. albigula*, y son mucho mayores que las que encontramos entre *U. jelskii* y *U. validirostris*. Nuestros datos apoyan decididamente el estatus de especie plena para *U. saturationior*. La existencia de una *Upucerthia* de bosque en parapatría con una especie de ambientes abiertos provee de una oportunidad para poner a prueba el papel de los cambios de hábitat entre ambientes áridos abiertos y ambientes boscosos durante la especiación.

INTRODUCTION

The ground-dwelling and curve-billed earthcreepers of the genus *Upucerthia* have recently been the focus of two phylogenetic studies (Chesser et al. 2007, Fjeldså et al. 2007). Both

studies consistently showed that *Upucerthia* is the sister group of *Cinclodes* and that the four species that should belong to *Upucerthia* are the Scale-throated Earthcreeper (*U. dumetaria*, type species of *Upucerthia*), Buff-breasted Earthcreeper (*U. validirostris*), Plain-breasted Earthcreeper (*U. jelskii*), and

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FIGURE 1. A, Adult Patagonian Forest Earthcreeper (*Upucerthia saturator*) photographed at Lagunas de Epulauquen, Neuquén, Argentina. Note the distinctive short black bill, dark dorsal coloration, and indistinct breast markings. Photo: Juan I. Areta. B, Adult Scale-throated Earthcreeper (*Upucerthia dumetaria*) photographed at Sierra Baguales, Santa Cruz, Argentina. Note the distinctive long bill, lighter dorsal coloration, large undertail markings, and distinct breast markings. Photo: Santiago Imberti.

White-throated Earthcreeper (*U. albigula*). Additionally, the Striated Earthcreeper (*U. serrana*) was found to be basal to the monophyletic group of *Upucerthia* plus *Cinclodes* in one of the studies (Fjeldså et al. 2007), whereas it was found to be distantly related to all of these furnariids in a phylogeny sampling a broader range of taxa (Chesser et al. 2007). This pattern is consistent with the lack of close relatives shared by other bird species with the same relictual distribution of *U. serrana* in Peru (Fjeldså et al. 2007) and suggests that the position of *U. serrana* close to *Upucerthia* and *Cinclodes* reported by Fjeldså et al. (2007) should be interpreted as an artifact of insufficient taxon sampling. For the present, *U. serrana* is provisionally retained in *Upucerthia*.

The species-level taxonomy of *Upucerthia sensu stricto* remains confusing, leading to differing treatments (Zotta 1938, Esteban 1951, Meyer de Schauensee 1966, Vaurie 1980, Remsen et al. 2008). Geographical variation in *U. dumetaria* is not clearly understood. Historically, eight taxa (some of them originally described as species) have been included within *U. dumetaria* (Geoffroy Saint-Hilaire 1832, Reichenbach 1853, Scott 1900, Chubb 1911, Chapman 1919, Zimmer 1954), and between two and five subspecies have been recognized by various authors (Hellmayr 1932, Navas 1971, Vaurie 1980, Fjeldså and Krabbe 1990, Remsen 2003). Modern treatments acknowledge four subspecies, *dumetaria*, *hypoleuca*, *saturator*, and *peruana* (Remsen 2003). The distinction between *dumetaria* and *hypoleuca*, however, frequently proves difficult both with specimens and in the field (Navas 1971), and *peruana* is known from only two specimens (Zimmer 1954). By far the most distinctive subspecies within *U. dumetaria* is *saturator* (Fig. 1), originally described as a species (Scott 1900) and so treated occasionally (Chubb 1911, Esteban

1951). Nevertheless, this treatment has not been followed by most authors, who have classified *saturator* as a subspecies of *U. dumetaria* (e.g., Chapman 1919, Hellmayr 1935, Navas 1971, Vaurie 1980, Remsen 2003, Remsen et al. 2008). Evidence for either taxonomic treatment is weak, and more data for a convincing rationale are necessary.

Despite its uniqueness and *Cinclodes*-like aspect, *saturator* was not explicitly included in the recent molecular phylogenetic studies of *Upucerthia* (Chesser et al. 2007, Fjeldså et al. 2007), hampering our understanding of the phylogenetic relationships, biogeography, evolution, and alpha taxonomy of *Upucerthia*.

In this article we provide newly obtained data on the distribution, seasonal movements, morphology, habitat use, vocalizations, and behavior of the little-known *saturator* from the province of Neuquén (Argentina), and we analyze previously published data on morphology and distribution. These data overwhelmingly suggest that *saturator* should be elevated to the rank of species. We also discuss the evolutionary and biogeographic importance of the existence of a Patagonian forest-dwelling *Upucerthia*.

METHODS

We studied *Upucerthia saturator* as follows: 2–8 December 1999, 6–14 March 2000, 2–6 January 2007, 11–15 January 2008, and 6–16 March 2008 at La Fragua, Arroyo Ranquileo, Reserva Turístico Forestal Lagunas de Epulauquén, Laguna Vaca Lauquén, Paso Pichachén, Pino Hachado, 20 km west of Rahue, and 10 km west of San Martín de los Andes, all in western Neuquén province, west-central Argentina (see Fig. 2). For each field observation we took notes on behavior,

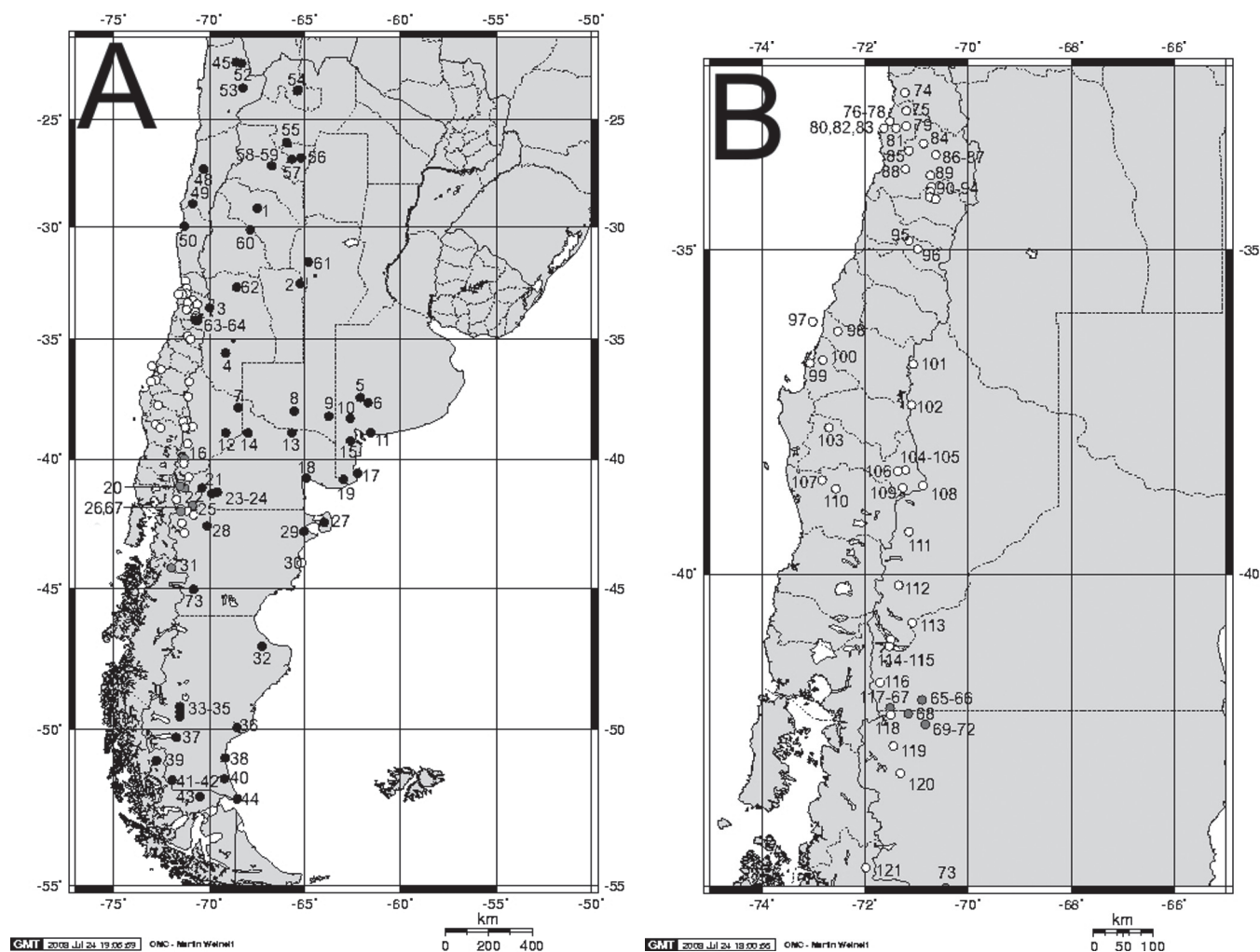


FIGURE 2. Distribution and migration patterns of the Patagonian Forest Earthcreeper (*Upucerthia saturator*) and Scale-throated Earthcreeper (*U. dumetaria*) in Argentina and Chile. A, Distribution of *Upucerthia dumetaria* and *U. saturator* in Argentina and Chile. White circles, *U. saturator*; black circles, *U. dumetaria*; gray circles, possible areas of breeding parapatry of *dumetaria/saturator* based on specimens [16/112, 20–22/114–115, 26/118, 31/121, 67/117]. Numbers: *dumetaria*, 1–44; *hypoleuca*, 45–64; *saturator*, no numbers, see B for details. B, Details of the distribution of *U. saturator* in Argentina and Chile. White circles, *U. saturator*; gray circles, dark specimens of *U. dumetaria* presumed to be intergrades *dumetaria/saturator* by Navas (1971). Numbers: *saturator*, 74–121; dark *dumetaria*, 65–73. See Appendix 3 for names and coordinates of localities. In nominate *dumetaria*, southern populations migrate to the pampas of Argentina during winter. In *saturator*, while most northern and some coastal Chilean records fall from April to September, some southern Chilean and most Argentine records fall from September to March. These highly divergent migration routes of *U. saturator* and *U. d. dumetaria* enhance their spatial segregation and argue for species status of both forms.

habitat, plumage, and the color, shape, and size of the bill. We recorded vocalizations with a Sennheiser ME-62 microphone in a Telinga Universal parabola and a Sony TCD5-ProII tape recorder and with a Sennheiser ME-67 microphone and a Sony TCM 5000 tape recorder. Recordings made by Areta are deposited at the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology), those by Pearman will be deposited in the British Library (National Sound Archive). To determine qualitative differences in the vocalizations of *saturator* from those of other species of *Upucerthia*, we examined our recordings aurally and then visually with the aid of spectrograms

built with Syrinx 2.6h (www.syrinxpc.com, John Burt). We examined 49 recordings of all the currently recognized species of *Upucerthia* (including *serrana*) and of three of the four currently recognized subspecies of *U. dumetaria* (nominate *dumetaria*, *hypoleuca*, and *saturator*; there are no known recordings of subspecies *peruana*; Appendix 2).

We carried out eight playback experiments between late September and mid October 2008 (early breeding season): three in El Chocón (Río Negro, Argentina), three in El Porvenir (Tierra del Fuego, Chile), and two in Farellones (Región Metropolitana, Chile). All the experiments tested the

response of *U. d. dumetaria/hypoleuca* to voices of *U. d. dumetaria/hypoleuca* and *saturator* during the breeding season (the response of *saturator* to voices of *dumetaria/hypoleuca* was not tested by this method). Each experimental individual of *U. d. dumetaria* was exposed to three stimuli: one song of *U. d. dumetaria*, one song of *hypoleuca*, and one song of *saturator*. The order of stimuli was randomized to avoid sequence effects, and the songs were sampled from our database (see Appendix 2) to avoid pseudoreplication (Kroodsma 1986, 1989a). We categorized the results of each experiment as silent approach, vocalization without approach, and approach with vocalization.

We examined and measured 35 specimens of *U. d. dumetaria*, 21 specimens of *hypoleuca*, and 45 specimens of *saturator* deposited at the Fundación Miguel Lillo, Tucumán (FML), Museo Argentino de Ciencias Naturales, Buenos Aires (MACN), and Museo de La Plata, La Plata (MLP) (Appendix 1). Bill length (exposed culmen) and tarsus length were measured to the nearest 0.05 mm with digital calipers, and flattened wing and tail length were measured with a metal ruler to the nearest 0.5 mm. We also used distributional information from specimens at the Field Museum of Natural History, Chicago (FMNH), Louisiana State University, Baton Rouge (LSU), and Yale Peabody Museum, New Haven (YPM) (Appendix 3).

RESULTS

DISTRIBUTION AND MOVEMENTS

Distribution. In Argentina, *U. d. saturator* is known from northwestern Neuquén, western Río Negro, and northwestern Chubut provinces (Zotta 1938, Esteban 1951, Navas 1971, Fig. 2). Specimen and sight records range from 250 to 1800 m above sea level and are restricted to Patagonian forest borders in the Andes of central Chile and central-western Argentina (this Andean form is unknown from the Patagonian steppe, see *Habitat* below). We recorded *U. d. saturator* at 10 localities in western Neuquén province (Fig. 2). The closest distance from *U. d. saturator* at which we could find *U. d. dumetaria/hypoleuca* was ca. 25 km (*saturator* at Epulauquen and *dumetaria/hypoleuca* at Las Ovejas). However, *U. d. dumetaria* has been also reported at Epulauquen (Veiga et al. 2005), an identification which, if correct, would indicate that both *U. d. saturator* and *U. d. dumetaria* can be found at the same locality. Additionally, Navas (1971) reported specimens of *U. d. saturator* and *U. d. dumetaria* collected as close as 4 km apart, and specimens of both subspecies have been collected at Nahuel Huapi (*saturator* MACN-8389 67a–e and *dumetaria* MACN-8389). Their geographic ranges may be parapatric or with minor overlap on a wide geographic scale (see Esteban 1951 and Navas 1971, Fig. 2, and Appendix 3 for other localities of possible overlap). Sympatry, however, does not imply syntopy (see *Habitat* below).

The absence of *U. d. saturator* from seemingly suitable habitat further south of its known restricted distribution in Argentina and Chile is remarkable and remains a mystery. This area is poorly studied, however, and possibly *saturator* has been overlooked there. From minimal data Navas (1971) estimated the breeding season of *saturator* in Argentina as September to February; the breeding season could extend into March (pers. obs.). Hellmayr (1932) reported recently fledged birds in central Chile in March; however, Zimmer (1954) clearly demonstrated that Pässler's observations of *saturator* breeding on the coast of Chile, quoted by Hellmayr (1932), were based on misidentifications (very likely of the coastal *Cinclodes nigrofumosus*). The lack of definite breeding records of *U. d. saturator* in Chile and the abundance of records during the nonbreeding period could suggest that *saturator* breeds exclusively in Argentina and not in Chile. Some records from the Andes of Chile, however, might refer to breeding birds (see Fig. 2, Appendix 3).

Movements. It has been suggested that *U. d. saturator* could migrate north in Argentina and Chile during winter (Hellmayr 1932, Goodall et al. 1946, Johnson 1967, Vaurie 1980). All specimens and sight records from Argentina, however, are from September to March, and most specimens from Chile are from late March to August (Hellmayr 1932, Navas 1971, Fig. 2, Appendix 1, Appendix 3). We suspect, as did Navas (1971), that *U. d. saturator* is a trans-Andean migrant because of (1) the geographic and temporal distribution of specimens, (2) the mapping by Jaramillo (2003) of an exclusive winter range (unspecified to subspecies), north of the regular Chilean range of *saturator*, in dry deciduous forest and matorral along the coast of central Chile between the lake district and Valparaíso. Furthermore, Hellmayr (1932) mentioned *saturator* as only a winter visitor in the Angol and Nilahué valleys of Chile, at the same latitude at which birds can be found breeding in Argentina but across the Andes. Despite this, Jaramillo (2003) mapped the Angol Valley as part of the resident range of *U. d. saturator*. This trans-Andean migration pattern is shared by other species (e.g., *Phytotoma rara*) and differs strongly from the well-known migration undertaken by nominate *dumetaria*, from the arid Patagonian steppe north and northeast principally to the pampas region (Fig. 2, Navas 1971, Fjeldså and Krabbe 1990). Outside of the breeding season, *saturator* and *dumetaria* are segregated for at least five months, since there is no overlap in Chile.

HABITAT USE

In the province of Neuquén we found *U. d. saturator* at forest borders, primarily close to bodies of water but also away from them, both during the breeding season and at the onset of fall migration. All our observations were at the edges of both large and small patches of *Nothofagus* forest, at a clearing at least 1.5 km inside *Nothofagus* forest, or at the edge of a densely wooded mosaic of rivers and pools with introduced *Salix* and

other trees (some possibly native) but without *Nothofagus*. Although surrounding vegetation was almost always *Nothofagus* forest, the birds were never found inside the forest. At the same time, during the breeding season, we found several territories of *U. d. dumetaria/hypoleuca* (e.g., one pair singing and holding territory at Laguna Varvarco Campos on 14 January 2008), and during mid-March 2008 (probably just prior to migration), we noted ten individuals (five pairs) of *U. d. dumetaria/hypoleuca*, all in dry areas, without surrounding forest, in habitats of Monte desert and Patagonian steppe in western Neuquén.

Navas (1971) mentioned the collection, in February, of a nominate *dumetaria* at Confluencia Trafal Limay and of a typical *saturation* in Valle Encantado del Río Limay. These two localities are only 4 km apart and have the same mixed habitat dominated by subantarctic forest intermixed with Patagonian steppe. Although syntopy of the two forms while breeding is possible, it has yet to be confirmed. In the Patagonian Andean forest region open habitats are always close to forests. Therefore, it is almost impossible to determine the precise habitat in which specimens of *U. dumetaria* were collected from locality data on older specimen labels only. Thus, for example, birds collected “around San Martín de los Andes” cannot be safely attributed to either steppe or forested habitats.

MORPHOLOGY

General morphology. The most detailed description of *saturation* in the literature is by Hellmayr (1932:165), who wrote, “*U. d. saturation* differs at a glance from the other races by very much darker, olive or sepia brown, upper parts and middle tail feathers without paler tips to the wing coverts; tawny rather than cinnamonaceous basal portion of remiges; generally wider, deeper cinnamon rufous tips to lateral rectrices; much duller, avellaneous rather than buffy, under parts with the blackish margins on foreneck and chest much more pronounced, and the flanks dark buffy brown or olive-brown. Besides, the bill is shorter, stouter, and more blackish.” This description is an accurate synthesis, although we contest the suggestion that *saturation* has breast scaling more pronounced than in the other races (Fig. 1, Table 2). To the contrary, *saturation* shows broader, often brown (not black) scaling, usually restricted to the upper breast, creating a more diffuse and less conspicuous scaled pattern than in *U. d. dumetaria/hypoleuca* (Fig. 1). *Upucerthia d. saturation* is therefore distinctly darker. It is also smaller with a shorter (distinctly black, not brown) bill than in other subspecies of *U. dumetaria*, and its tail is also proportionately shorter, with a distinct pattern (Fig. 1, Tables 1 and 2, Hellmayr 1925, 1932, Zotta 1938, Esteban 1951, Zimmer 1954, Navas 1971, Vaurie 1980). These differences are easily noticed in the field. At first glance, *U. d. saturation* looks intermediate between *U. d. dumetaria* and one of the dark species of *Cinclodes* of Patagonia (e.g., *C. patagonicus*) in overall shape, size, and plumage. For example, a foraging

U. d. saturation seen facing away could easily be mistaken for a *Cinclodes*, a scenario most unlikely with any other species of *Upucerthia*. This similarity is interesting (although not unexpected) given the close relationship between *Cinclodes* and *Upucerthia* (Chesser et al. 2007, Fjeldså et al. 2007, see *Behavioral notes* below).

We assume, from the examination of numerous specimens, that juveniles of both *U. dumetaria/hypoleuca* and *U. d. saturation* have whitish shaft streaks on the nape and upper back, are more extensively scaled on the breast, and show broken brown barring on the lower abdomen, especially at the sides. Likewise, immatures may retain a few pale nuchal streaks but always show some barring on the lower abdomen, which is lacking in adults. In all of these plumages, *saturation* maintains its distinct tail pattern (as mentioned by Hellmayr 1932; see above), which allowed us to immediately distinguish young specimens of *saturation* from *U. dumetaria/hypoleuca* (see *Evidence of Intergradation* below). It is noteworthy that juveniles of *U. d. dumetaria/hypoleuca*, like adults of *saturation*, have black bills. Measurements of juvenile *dumetaria* average larger than those of juvenile *saturation* and are similar to those of adult *saturation* (Table 1).

Ecomorphological variation and clines. Most species of *Upucerthia* are believed to fit Gloger’s rule (i.e., birds inhabiting more humid regions have darker pigmentation; Remsen 2003). The northern subspecies *U. dumetaria hallinani* was synonymized with the more southern *U. dumetaria hypoleuca* on the basis of weak morphological differentiation, local variation in color intensity, and the presence of paler individuals toward drier areas (Hellmayr 1932, Esteban 1951, Johnson 1967). All authors agree that *U. d. dumetaria* and *U. d. hypoleuca* are very similar (Navas 1971, Remsen 2003, Jaramillo 2003). Pigmentation varies greatly, regardless of sex, in a series of nine adult specimens of *hypoleuca* taken in August 1898 (one probably in 1897) at an unspecified location in San Luis province (MLP-425 through 433). Although some individuals appear indistinguishable from nominate *dumetaria*, others show a slightly paler and more rufescent dorsal coloration and paler ventral coloration suggesting *U. d. hypoleuca*. A specimen from Río Seco, Concarán (also from San Luis province), taken in mid-May is referable to nominate *dumetaria* (MLP-10734). Zotta (1938) argued that *hypoleuca* was the form intermediate between *hallinani* and *dumetaria*, and Hellmayr (1932) suggested that *hallinani* should probably be merged with *hypoleuca*. Both authors indirectly argued that the variation is clinal. We suspect that this clinal variation, combined with strong individual variation, might have been the basis for Vaurie’s (1980) decision to merge all subspecies of *dumetaria* (except *saturation*) under nominate *dumetaria* (see Table 2). The darker individuals of *dumetaria* close to the Andes add another dimension of complexity to the variation within *dumetaria* (see *Evidence of intergradation* below). Also, the large, dark subspecies *peruana*, known only

TABLE 1. Measurements of bill length, tail length, and wing chord of the Scale-throated Earthcreeper (*Upucerthia dumetaria dumetaria*, *U. d. hypoleuca*) and Patagonian Forest Earthcreeper (*Upucerthia saturator*) according to various authors and specimens listed in Appendix 1. Values are given in mm as mean \pm SD with sample size in parentheses and range in brackets, if available. Measurements of specimens suggested by Navas (1971) to be intergrades appear under "dark adults." The measurements support full species status for *U. saturator* and lack of evidence of intergradation between *U. saturator* and *U. dumetaria*. Note the consistent size differences between juvenile and adults of both forms.

	<i>U. saturator</i>	<i>U. d. dumetaria</i>	<i>U. d. hypoleuca</i>	<i>U. d. peruana</i>	Source
Bill length	29.1 \pm 0.9 (17)	—	35.7 \pm 1.6 (15)		Hellmayr 1932 ^a
	[28–31]		[34–37.5]		
	33.05	35.55	38.2		Esteban 1951
	[30.8–35.4]	[33–38.6]	[34.4–41.5]		
	27.9 (22)	31.8 (34)	32.95 (16)		Navas 1971
	[25–29]	[29–35]	[29–35]		
	34 (10)	38.5 (10)	lumped with		Vaurie 1980
	[31–37]	[35–43]	<i>dumetaria</i>		
	30.5 \pm 1.3 (12)	—	35.8 \pm 2.8 (5)		Zotta 1938 ^b
	[28.5–31]		[31–38.5]		
	—	—	—	35	Zimmer 1954
	<i>Adults</i>	<i>Adults</i>	<i>Adults</i>		Appendix 1
	28.37 \pm 1.08	31.57 \pm 1.49	32.98 \pm 2.15		
	(33)	(17)	(17)		
[26.82–30.56]	[30.41–34.7]	[27.52–34.48]			
<i>Juveniles</i>	<i>Juveniles</i>				
23.77 \pm 3.13 (4)	30.8 \pm 1.1 (5)				
[19.45–26.38]	[29.24–30.95]				
	<i>Dark adults</i>				
	33.9 \pm 2.1 (3)				
	[32.29–36.19]				
	<i>Dark juveniles</i>				
	28.6 \pm 2.5 (6)				
	[24.91–30.37]				
Tail length	79.9 \pm 2.3 (17)	—	83.0 \pm 3.0 (15)		Hellmayr 1932 ^a
	[77–84]		[77–88]		
	74.85	79.65	83.6		Esteban 1951
	[69.5–78.7]	[75.5–86.2]	[76.9–87.9]		
	78.2 (23)	83.4 (35)	83.8 (20)		Navas 1971
	[73–81]	[80–93]	[79–90]		
	83.6 \pm 4.6 (12)	—	88.2 \pm 3.5 (5)		Zotta 1938 ^b
	[77–86]		[84–93]		
	—	—	—	85	Zimmer 1954
	<i>Adults</i>	<i>Adults</i>	<i>Adults</i>		Appendix 1
	72.25 \pm 3.02	79.37 \pm 3.74	78.03 \pm 4.11		
	(38)	(19)	(20)		
	[66–77.5]	[73–84.5]	[67.5–83]		
	<i>Juveniles</i>	<i>Juveniles</i>			
69.38 \pm 3.44 (7)	75.8 \pm 2.6 (6)				
[68.5–78.5]	[73–80]				
	<i>Dark adults</i>				
	79.7 \pm 6.1 (3)				
	[73–85]				
	<i>Dark juveniles</i>				
	75.8 \pm 3.0 (6)				
	[70.5–78.5]				

(continued)

TABLE 1. (Continued).

	<i>U. saturator</i>	<i>U. d. dumetaria</i>	<i>U. d. hypoleuca</i>	<i>U. d. peruana</i>	Source
Wing chord	99.6 ± 3.4 (17) [95–106] 97.45 [92.2–104.9] 99.7 (23) [95–106] 95.6 ± 2.7 (12) [91–101] — <i>Adults</i> 96.82 ± 3.47 (32) [92.5–103.5] <i>Juveniles</i> 91.90 ± 3.30 (7) [91.5–100]	— 99.85 [94.4–109.2] 101.4 (35) [95–109] — — <i>Adults</i> 101.23 ± 4.37 (20) [93–111] <i>Juveniles</i> 99.2 ± 1.8 (6) [96.5–101] <i>Dark adults</i> 100.0 ± 0.5 (3) [99.5–100.5] <i>Dark juveniles</i> 97.0 ± 3.0 (6) [94–101.5]	101.0 ± 3.4 (15) [95–106] 100.85 [96.2–108.5] 102.5 (20) [96–110] 101.3 ± 3.5 (5) [98–106.5] — <i>Adults</i> 101.48 ± 4.51 (21) [92–110.5]	108	Hellmayr 1932 ^a Esteban 1951 Navas 1971 Zotta 1938 ^b Zimmer 1954 Appendix 1
Tarsus length	— <i>Adults</i> 24.42 ± 0.68 (6) [23.41–25.31]	— <i>Adults</i> 26.02 ± 0.96 (8) [24.44–27.4]	— <i>Adults</i> 25.96 ± 0.93 (10) [24.57–27.71]	26.5	Zimmer 1954 Appendix 1

^aHellmayr (1932) referred these measurements to *hallinani*, but we include them with *hypoleuca*.

^bZotta (1938) measured *hallinani* and *hypoleuca* separately, here measurements are pooled according to modern taxonomic use. See text for discussion of clinal variation.

from two specimens, seems to fit the pattern of ecomorphological variation with humidity (Table 1). Clearly, more study is needed to ascertain whether *hypoleuca* and *peruana* are diagnosable subspecies and to elucidate patterns of genetic and morphological geographical variation in the *U. dumetaria* complex.

The comparatively dark color and small size of *U. d. saturator*, of forest borders, compared to the larger *U. d. dumetaria*,

of brushland, parallels the color differences between *U. albigula* and *U. jelskii* (Schulenberg 1987). In northern Chile *U. albigula* inhabits *Polylepis* woodlands and shrubbery along river courses, whereas the rather similar *U. jelskii* inhabits drier shrub-steppe and river beds with sparser and lower shrubs (pers. obs., Schulenberg 1987). The two can be found within 500 m of one another along the same river in Putre, Chile (pers. obs.), where *albigula* is slightly darker above, and their songs

TABLE 2. Summary of features distinguishing the Patagonian Forest Earthcreeper (*Upucerthia saturator*) and Scale-throated Earthcreeper (*Upucerthia dumetaria*).

	<i>U. saturator</i>	<i>U. dumetaria/hypoleuca</i>
Geographic variation	None or minor	Apparent north-to-south cline
Breast scaling	Mild	Strong
Dorsal color	Very dark brown	Variable, from ferruginous (N) to light brown (S), and dark brown (indiscriminate distribution)
Tail pattern	Reduced chestnut terminal markings	Large light terminal markings
Measurements (Table 1)	Smaller	Larger
Habitat	Forest borders	Open steppe
Fall/winter migration	Trans-Andean (Argentina to Chile)	South to northeast
Song	Syncopated series of couplets or triplets	Continuous series of single notes
Playback experiments	Not tested	Ignores voice of <i>saturator</i> , strong response to own voice

differ in pitch and speed. A cline involving both plumage and measurements has been suggested to link *U. validirostris* and *U. jelskii* (Vaurie 1980, Mazar Barnett et al. 1998), although they are currently treated as separate species (Remsen 2003). Hellmayr (1925) suggested a similar explanation for increased pigmentation in relation to habitat humidity in *U. dumetaria* and in a number of other Chilean furnariids that inhabit dry and open areas, such as the Common Miner (*Geositta cunicularia*), Crag Chilia (*Chilia* [*Ochetorhynchus*] *melanura*), Plain-mantled Tit-Spintail (*Leptasthenura aegithaloides*), and Cordilleran Canastero (*Asthenes modesta*).

Evidence of intergradation. Although *U. d. hypoleuca* of northwestern Argentina ranges south to the steppe region of central Neuquén (Navas 1971; 3 MACN specimens), no intermediates between *U. d. hypoleuca* and *U. d. saturator* have been reported. The reference by Navas (1971) to supposedly intermediate individuals between *saturator* and *dumetaria* close to the Andean forests is confusing and inconclusive. On one hand, he mentioned widely scattered specimens from La Pampa, Buenos Aires (both far from the Andes), Río Negro, and Chubut that could be regarded as dark (toward sepia) individuals of *U. d. dumetaria*. On the other hand, he later considered that Andean specimens of three dark juveniles (two from Ñorquinco and one from El Bolsón in western Río Negro) and two dark adults from El Maitén (western Río Negro), whose bill measurements (34 and 35 mm) are well outside his range for *saturator*, provided evidence of intergradation between *saturator* and *dumetaria* (Fig. 2). Similarly, four dark Andean birds from Cushamen, northwestern Chubut (one adult and three juveniles), and one adult from Alto Río Senguerr, southwestern Chubut (both adults with bill lengths of 32 and 34 mm, typical of *dumetaria*) were also considered intergrades between *dumetaria* and *saturator* (Fig. 2). However, (1) dark individuals seem to occur in various parts of the range of *U. d. dumetaria* without *U. saturator* (e.g., widely scattered localities in Buenos Aires, La Pampa, and Río Negro provinces; *vide* Navas 1971, MACN specimens), and pale individuals of *U. d. dumetaria* also seem to occur without a consistent geographic pattern (e.g., several localities in Buenos Aires, La Pampa, San Luis, and Río Negro *vide* Navas 1971, MACN specimens). (2) No intermediate measurements have been reported for *U. d. dumetaria* closer to the Patagonian forests because bill measurements of juveniles cannot be directly compared to those of adults and measurements of purportedly intermediate individuals fall within the range of *U. d. dumetaria*, being larger than those of *U. d. saturator*. (3) There may be confusion regarding the significance of dark birds close to the Andean forests; these birds might exemplify variation according to Gloger's rule within a species (*U. dumetaria*) independent of the existence of a darker species (*U. saturator*), not necessarily intergradation with *U. saturator*. Additionally, Alto Río Senguerr (one of the localities with birds presumed intermediate between *U. d. saturator* and *U. d. dumetaria*) is

outside of, and a long distance from, the known distribution of *U. d. saturator* (Fig. 2). We examined the supposedly intermediate specimens mentioned by Navas (1971) and found that they are dark variants of *dumetaria*. Most are juveniles (with measurements larger than those of juvenile *saturator* but close to those of adult *saturator*, Table 1). Others are adults, referable to *dumetaria* because their measurements are well outside the range of *saturator* (Table 1). Although these individuals are indeed darker than some of *dumetaria*, others of *dumetaria* from distant locations are similarly dark, and all have the tail pattern typical of *dumetaria* and distinct from that of *saturator* (see *General morphology* above, see Table 2).

VOCALIZATIONS

We tape-recorded three different vocalizations of *U. d. saturator* ($n = 8$ individuals): the song (and subsongs = partial songs), a continuous song, and one contact call. The song of *U. d. saturator* differs structurally from the apparently homologous song of *U. d. dumetaria*. The complete song of *U. d. saturator* consists of one or two sharp, short, and lower-pitched initial notes followed by either a syncopated or a continuously delivered series of triplets, at three per second, each of which starts with one fast metallic, abrupt, and almost vertical note followed by two shorter, flatter, longer variably v-shaped or shallowly u-shaped notes (only the latter two distinguished by the human ear). Occasionally, it ends with a distinct triplet including a lower-pitched final note (Fig. 3A). A complete version of the song of *U. d. saturator* can be described as “p-p-tirik-tirik-tirik-tirik-tirik-tirik” (Figs. 3A, B). Both the soft introductory “p’s” and the disyllabic “tiriks” (triplets) vary in number. After playback, the song is faster, and an extra u-shaped note may be added to the triplets (Fig. 3C). Birds heard along forest borders around San Martín de los Andes, towards Paso Hua-Hum, were not tape-recorded but sounded identical to birds in other localities of western Neuquén province. In contrast ($n = 13$ individuals), the song of *U. d. dumetaria* is a series of fairly homogeneous similarly shaped notes delivered in rapid succession (Figs. 4A, B), with nine notes per second (i.e., three times faster than in *saturator*), and again the precise number of notes is highly variable. The song of *hypoleuca* ($n = 7$ individuals) appears indistinguishable from that of nominate *dumetaria* (Fig. 4C). A complete version of the song of *U. d. dumetaria/hypoleuca* can be described as “pli-pli-pli-pli-pli . . .” which increases slightly in pitch, sometimes descending toward the end (Figs. 4A–C). Both *saturator* and *dumetaria/hypoleuca* also sing a form of “continuous song” in which successive songs are linked by many rapidly delivered notes that gradually change in pitch (Figs. 3D, 4D). The continuous song of *U. d. dumetaria/hypoleuca* and *U. d. saturator* was given by agitated birds, either naturally excited during territorial encounters or after playback (this type of continuous song is present at least also in *U. jelskii* and *U. validirostris*). Both, the song and the continuous

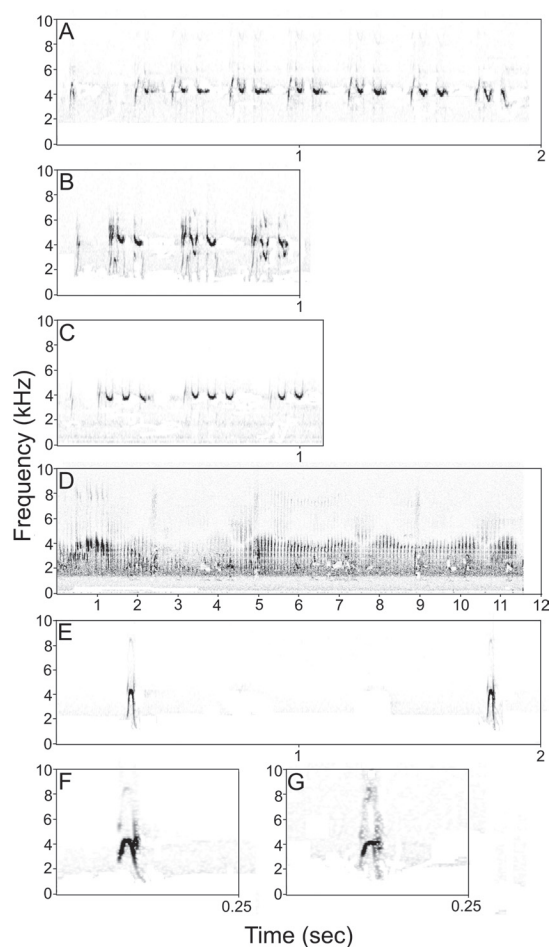


FIGURE 3. Spectrograms of songs and calls of the Patagonian Forest Earthcreeper (*Upucerthia saturator*). A, Song of *U. saturator* (13 March 2008, Epulauquen, Neuquén, JIA 1); B, song of *U. saturator* (13 March 2008, Epulauquen, Neuquén, JIA 2); C, song of *U. saturator* after playback (January 2007, west of Rahue, Neuquén, MS/MP A6); D, continuous song of *U. saturator* after playback (8 December 1999, Pino Hachado, Neuquén, MP B38/39); E, calls of *U. saturator* (8 December 1999, west of Pino Hachado, Neuquén, MP B34/35); F, call of *U. saturator* (7 December 1999, Pino Hachado, Neuquén, MP B29); G, call of *U. saturator* (13 March 2008, Epulauquen, Neuquén, JIA 3). Time scale reduced by 6 in Fig. 3D and augmented by 3 in Figs. 3F and 3G to show details. Voices of *U. saturator* differ markedly from those of *U. dumetaria* and support full species status for *U. saturator*.

song, can be performed in conjunction with the wing-raising display. The contact call of *U. d. saturator* is a hollow “pep,” peaking at just over 4 kHz, uttered alone or as a series of notes spaced with intervals of ca. 1.5 to 3 sec between successive notes (Figs. 3E–G). The contact call of *U. d. dumetaria* is a softer and squeaky sounding “keep,” peaking at just over 6 kHz (Fig. 4E).

Previously published descriptions of the voice of *U. dumetaria* have not specified the subspecies or locality on which

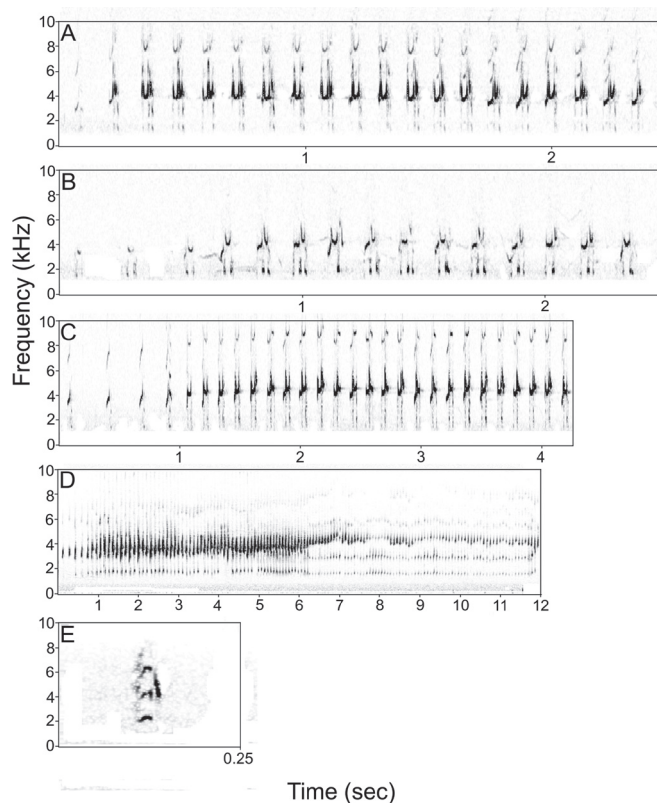


FIGURE 4. Spectrograms of songs and calls of the Scale-throated Earthcreeper (*Upucerthia dumetaria/hypoleuca*). A, Song of *U. d. dumetaria* (November, Península Valdés, Chubut, from Straneck 1990); B, song of *U. d. dumetaria* (22 October 2004, Ea. La Querencia, Santa Cruz, S. Imberti); C, song of *U. d. hypoleuca* after playback (1 October 2001, El Infiernillo, Tucumán, L. Macaulay, MLNS 115989); D, continuous song of *U. dumetaria* after playback (28 September 2008, El Chocón, Río Negro, JIA); E, call of *U. d. dumetaria* (5 February 1984, Laguna Los Escarchados, Santa Cruz, N. Krabbe, XC 15997). Time scale reduced by 2 in Fig. 4C and by 6 in Fig. 4D to show overall pattern, and augmented by 3 in Fig. 4E to show details. Voices of *U. dumetaria* differ markedly from those of *U. saturator* and support full species status for *U. saturator*.

they were based and do little to aid our understanding of vocalizations in the complex. For example, Fjeldså and Krabbe (1990) wrote, “Song a rapid *chippy chippy chippy chip*. Call a wheezy, abrupt *keet*” (p. 331), to which Remsen (2003:247) added a “sharp, dry ‘dzit.’” Jaramillo (2003:158) wrote, “A series (1.5–3 sec) of scolding, ringing, syncopated notes given at a speed just fast enough to be uncountable. Usually rises in pitch in middle and trails off at end: *chwip chwip chwip chwip chwip chwip chwip chwip chwip chwip chp chp*,” none of which we are able to identify to a taxon. Ridgely and Tudor (1994:31) stated, “The song in cen. Chile is a spritely, rather musical ‘tr, tr, trretrretrretrritritritri’ with a slightly ascending effect,” and Canevari et al. (1991:301) described “a harsh voice which is emitted while perching in bushes ‘Cli cli cli cli . . .,’” which undoubtedly refers to *U. d. dumetaria/hypoleuca*.

Songs and calls of nominate *dumetaria* and *hypoleuca* differ from those of *saturation* in note shape, pattern, and pace and are consistently distinctive to the human ear (Figs. 3, 4). Our data on the vocalizations of *U. d. saturation* span most of its known distribution in Argentina and are not limited to a small geographic area (see Remsen 2005). Geographic variation in voice within a species is relatively small in the Furnariidae (e.g., Zimmer 1997, 2008), and we do not expect voices of *U. d. saturation* at other localities outside Neuquén to differ substantially from our recordings.

For all eight playback experiments the response was identical: individuals of *U. d. dumetaria/hypoleuca* answered strongly to voices of *U. d. dumetaria* and *U. d. hypoleuca*, approaching and vocalizing to the sound source, regardless of the order of stimuli. Likewise, all individuals of *U. d. dumetaria/hypoleuca* tested ignored the voices of *U. d. saturation*. On the other hand, our uncontrolled experiments with *U. d. saturation* demonstrate that they answer to the playback of their own voices, unlike *U. d. dumetaria/hypoleuca*.

BEHAVIORAL OBSERVATIONS

Upucerthia dumetaria saturation foraged exclusively on the ground near tall trees, around small bushes in sandy soils, on boggy ground close to forest edge, and in forest clearings by vigorously and rapidly probing its bill into the ground obliquely (video available at ibc.lynxeds.com). Occasionally, it removed large clumps of earth and stones with the aid of the feet or pushed them aside with lateral bill movements. After some minutes of foraging, the ground was furrowed, the birds leaving several small holes with mounds around their borders. While foraging, members of a pair frequently gave their contact call (Figs. 3E–G).

Between foraging bouts, *U. d. saturation* commonly perches in trees, unlike other forms of *U. dumetaria*, to preen and to sing (thus making important use of an element not present in the habitat of *U. dumetaria*; pers. obs., Johnson 1967). A territorial pair of *U. d. saturation* studied in a clearing 1.5 km inside Patagonian forest dominated by Lenga (*Nothofagus pumilio*), Pehuén (*Araucaria araucana*), and Ñire (*Nothofagus antarctica*) spent much of their time perching in two dead trees of *N. antarctica*, where they preened and rested, with one bird (presumably the male) singing 2–4 m up, sometimes accompanied by a wing-rotating display, usually from the extremity of dead branches. Most prey was consumed on the ground, although on one occasion a bird returned to one of the favored trees to consume a large grub. When delivering contact calls, the birds shifted its tail from side to side or flicked it up and down.

Once, a single bird also used a large unidentified dead tree over marshy ground with some standing water for resting and preening before and after terrestrial foraging. This individual sang and displayed 7 m up in a live *N. antarctica* tree, but also from nearby fence posts. In contrast, the song

of *U. d. dumetaria/hypoleuca* is delivered from bushtops. In the height of the breeding season birds begin singing from a bush and then launch themselves downslope while singing in flight.

Another *U. d. saturation* was observed foraging on the ground when an immature Chilean Hawk (*Accipiter chilensis*) landed noisily in a Roble Pellín (*Nothofagus obliqua*) tree ca. 30 m from the bird, upon which two White-throated Tree-runners (*Pygarrhichas albogularis*) started calling excitedly. The *U. d. saturation* immediately adopted a frozen posture, positioning its legs to the side of the body and flattening its body toward the ground. At this moment we could approach the bird to ca. 1.5 m while it remained frozen before eventually flying off (video available at ibc.lynxeds.com).

In flight, *U. d. saturation* exhibits fast wingbeats, fast turns, lateral movements of the body, and abrupt takeoffs that are characteristic of the true *Upucerthia* and *Cinclodes*, supporting its placement in this group. Wing-raising and wing-rotating displays in *Upucerthia* and *Cinclodes* are also similar but are not present in any other furnariid genus of which we are aware.

DISCUSSION

TAXONOMIC REMARKS

Upucerthia dumetaria saturation was originally described as *Upucerthia saturation* by Scott (1900). Soon after, Chapman (1919) listed *saturation* as a subspecies of *U. dumetaria*, under the misspelled name *Upucerthia dumetoria saturation*, without providing any rationale. Most subsequent authors (Hellmayr 1925, 1932, Wetmore 1926, Peters 1951, Meyer de Schauensee 1966) have followed Chapman's classification without providing an explicit explanation for adopting the modified taxonomy. It is of interest to note that *Upucerthia tamucoensis* Chubb, 1911 (presumably a typographical error in the original description for *temucoensis*), was also described as a full species, although thereafter Hellmayr (1925) and Wetmore (1926) considered it a synonym of *U. dumetaria saturation* (i.e., both Scott and Chubb ascribed species status to *saturation*). Since then, even the most conservative approaches have retained *saturation* as a subspecies within *U. dumetaria* (e.g., Hellmayr 1932, Vaurie 1980). Notwithstanding, various works (e.g., Fjeldså and Krabbe 1990, Remsen 2003, Jaramillo 2003, Kovacs et al. 2006) have illustrated *saturation*, desirable in aiding its field identification, given its striking differences from *U. d. dumetaria*.

Zotta (1938:55–56), who treated *U. (jelskii) pallida* as a subspecies of *U. validirostris*, wrote, “The differences offered by *saturation* compared to the rest of the *dumetaria* subspecies are so noteworthy that they make one suspect it is a distinct species” and went on to say “the established trinomial division does not appear to be very justified.” Reflecting his opinion, Zotta (1938, 1944) twice referred to the

form as *Upucerthia (dumetaria?) saturator*. Esteban (1951) was the first to argue in favor of full species status for *U. saturator* on the basis of its diagnostic morphology (plumage and measurements) and the supposed geographical overlap of *U. d. dumetaria* and *saturator* during the breeding season in Chile. This second argument was later invalidated, because Navas (1971) interpreted the birds in question to belong to *hypoleuca*, not to *dumetaria*. However, there is no modern evidence or confirmation of former coexistence of any two forms of *dumetaria* in Chile, and *saturator* and *dumetaria/hypoleuca* are apparently allopatric in Chile (Jaramillo 2003).

Only Navas (1971) tried to justify, from available museum specimens, considering *saturator* as a subspecies of *U. dumetaria*. Nonetheless, his argument is not convincing (see *Morphology*). Despite Navas' (1971) proposal to consider dark individuals of *dumetaria* close to the Andes as intergrades between *dumetaria* and *saturator*, no cline in plumage, measurements, or voices between *U. d. dumetaria* and *saturator* are known (see *Morphology* above). The small *U. saturator* is encapsulated in its restricted distribution and habitat within the range of the larger, wide-ranging *U. dumetaria*, which has larger forms to the north and south of *U. saturator*. Thus *U. saturator* does not easily conform to any general biogeographical rule of geographic variation. The divergent migration patterns also provide strong evidence for considering *saturator* as a species different from *dumetaria*, since, besides the different habitats that they use during the breeding season, the two forms are segregated for at least five months of the year. Moreover, it is striking that although *saturator* and *dumetaria* breed in close vicinity to one another, they winter in completely different areas.

Voices are presumed innate in most suboscines (Lanyon 1978, Kroodsma 1984, 1989b, Kroodsma and Konishi 1991), and are thought to be innate in the Furnariidae (Zimmer 2002, 2008, Remsen 2003, Robbins and Zimmer 2005). Differences in voices have been repeatedly shown to be species-specific cues of importance to species recognition in the Furnariidae (Zimmer 2002, 2008). The differences between the vocalizations of *U. d. dumetaria* and *saturator* provide perhaps the strongest evidence for raising *saturator* to species rank. Similar levels of differences in voices between populations have been considered as evidence for species rank for various furnariids (Vaurie and Schwartz 1972, Kratter and Parker 1997, Robbins and Zimmer 2005, Areta 2007, Zimmer 2008) and have yielded consistent species-specific responses to playback experiments in various phylogenetically distant ovenbird taxa (e.g., Zimmer and Whitaker 2000, Zimmer 1997, 2002, 2008). Similarly, in our playback experiments, *U. d. dumetaria/hypoleuca* responded strongly to voices of widely distant populations of the same species while ignoring the voices of closer populations of *saturator*. Although we did not conduct formal playback experiments to assess the

response of *saturator*, the aural and visual differences in the voices of *U. d. dumetaria/hypoleuca* and *saturator* are striking. Thus we strongly suspect that such playback experiments will yield results similar to those found in the *U. d. dumetaria/hypoleuca* complex, with *saturator* answering only to its own song and ignoring songs of *U. d. dumetaria/hypoleuca*. Moreover, the near if not actual parapatry of the two forms (although in different habitats) further supports the idea that both forms already ignore each other's vocalizations and are not in reproductive contact. Differences in the presumably innate vocalizations of *Upucerthia* can be used as a surrogate of genetic similarity between *U. dumetaria* and *saturator* and tentatively argue against the existence of an intergradation zone or significant genetic introgression between the forms (see *Vocalizations*).

The differences we report between between *U. d. dumetaria* and *saturator* in morphology, plumage, habitat use, migration patterns, and voice are in agreement with currently accepted species-level differences in *Upucerthia*. We suggest that *U. saturator* is best treated as a full species, as originally described by Scott (1900) and later supported by Esteban (1951). The differences support species status for *U. saturator* under any species concept. In the absence of an adequate English vernacular name for *U. saturator*, we propose "Patagonian Forest Earthcreeper," to highlight one of its most distinctive ecological features that instantly distinguishes it from the parapatric *U. dumetaria*. We also propose the Spanish vernacular name "Bandurrita de los Bosques Patagónicos." The name *saturator*, from Latin, simply means "more richly colored" (Jobling 1991).

From its morphology, behavior, plumage, and voices, *U. saturator* seems to belong to the true *Upucerthia* earthcreepers, as long recognised by its inclusion within *U. dumetaria*. From the agreement between plumages and phylogenetic affinity found in *Upucerthia* (Chesser et al. 2007), it seems reasonable to expect that *U. saturator* and *U. dumetaria* are each others closest relatives, although this remains to be demonstrated. The genus *Upucerthia* thus consists of six species (subspecies not listed):

- Scale-throated Earthcreeper (*U. dumetaria*)
- Patagonian Forest Earthcreeper (*U. saturator*)
- White-throated Earthcreeper (*U. albigula*)
- Plain-breasted Earthcreeper (*U. jelskii*)
- Buff-breasted Earthcreeper (*U. validirostris*)
- Striated Earthcreeper (*U. serrana*)

Genetic (Chesser et al. 2007) and vocal (Appendix 2) data strongly suggest that *U. serrana* does not belong in *Upucerthia* (see *Introduction*). Additionally, we suggest that *Upucerthia jelskii* may not deserve species rank, because it is indistinguishable from *U. validirostris* in our sample of vocalizations, and both might be best treated as variants within a morphocline (see Vaurie 1980, Remsen 2003).

BIOGEOGRAPHY AND EVOLUTION

The recognition of *U. saturator* as a distinct species provides insight into speciation patterns and endemic bird areas in the Patagonian forests. Cracraft (1985) did not include *U. d. saturator* among the endemic birds of the Nothofagus Center. The distributional pattern of *U. saturator*, however, is consistent with this center of endemism and should be considered as belonging to it (see Vuilleumier 1985, 1991 for mapping of Patagonian habitats). In his study of the ecological geography, speciation, and endemism of Patagonian forest birds, Vuilleumier (1985) did not include *U. d. saturator* as a forest form. This can be fully appreciated in his Appendix I (p. 289), where *U. dumetaria* is listed only as a nonforest species. He also did not mention *Upucerthia* in his survey of speciation in Patagonian birds (Vuilleumier 1991). Hence, no discussion is provided as to the evolutionary meaning of the presence of forms of forest (*saturator*) and dry open habitats (*dumetaria/hypoleuca*) within the species complex. *Pygarrhichas albogularis*, a Nothofagus Center forest endemic, has been found to be closely related and phylogenetically basal to a group of species living in dry open habitats, the Crag Chilia (*Chilia melanura*), Band-tailed Earthcreeper (*Eremobius phoenicurus*), and two species formerly classified in *Upucerthia*, the Straight-billed Earthcreeper (*Ochetorhynchus ruficauda*) and Rock Earthcreeper (*O. andaecola*) (Chesser et al. 2007, Fjeldså et al. 2007). This divergence has been associated with the creation of dry open habitats during the Andean uplift in the Miocene (Fjeldså et al. 2007). In the broader context of repeated shifts from forested to open habitats in the Furnariidae (Fjeldså et al. 2005, 2007), the existence of a forest-dwelling *Upucerthia* provides an opportunity for further testing of this hypothesis in closely related birds. We can only speculate as to the phylogenetic position of *U. saturator*, but if it proves to be basal to *U. dumetaria*, *jelskii*, *validirostris*, and *albigula*, the pattern would provide further support for a forest origin of another lineage that now occupies open habitats. Regardless of the direction of evolutionary change, the existence of the forest-based *U. saturator* implies a habitat shift during speciation at some point in the history of *Upucerthia*, but whether it originated following a secondary incursion into forest habitats by an ancestral open-habitat *Upucerthia* or the reverse can be tested only through complete taxon-sampling of the group in a formal phylogenetic analysis. Knowledge of the exact phylogenetic position of *U. saturator* might also prove instrumental in fully solving the relationships between *Cinclodes* and *Upucerthia*.

The voucher specimen of *U. dumetaria* used by Fjeldså et al. (2007) is from Meseta Strobel (900 m above sea level), Santa Cruz, Argentina (J. Fjeldså in litt., ZMUC 1984-02-14), and undoubtedly therefore refers to *U. d. dumetaria*. The voucher specimen used by Chesser et al. (2007) was collected at Cerro Perito Moreno (ca. 800 m above sea level), ca. 2 km below Refugio Perito Moreno, ca. 20 km NE of El Bolsón,

Dpto. Bariloche, Río Negro, in a “steppe like area within the forest,” but since it was later prepared as skeleton it is impossible to attach a subspecific designation to this specimen on the basis of current criteria (P. Sweet in litt., AMNH RTC 368). From the habitat description the specimen could be either *dumetaria* or *saturator*.

The lack of attention to the distinctive *U. saturator* in the literature is somewhat surprising given its unique aspect, ecology, and distribution, and its potential to contribute toward the understanding of evolution and biogeography of *Upucerthia* and *Cinclodes*. Further studies on the systematics of the *U. dumetaria/saturator* complex should focus on the integration of genetic, morphological, and vocal data in the ecotone between Andean forests and open steppe habitats. Until this issue is finally elucidated, the recognition of *U. saturator* as a distinct species is fully supported by our data.

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APPENDIX 1. List of specimens examined and measured for this study.

U. saturator: FML 4106, 4157, 4231, 4248, 4254, 7751, 7758. MACN nn, 65g, 1478a, 1478a, 2280-295a, 2282, 2285, 2331a, 3611, 4340a, 4483, 4626a, 4797, 4822, 4824, 4842, 4927, 4821, 5262, 5263, 5264, 5371, 8389-67a, 8389-67b, 8389-67c, 8389-67d, 8389-67e, 33414, 38056, 38058, 38059, 38075, 42461. MLP10162, 10163, 10164, 10165, 10166, 10167.

U. d. dumetaria: FML 1586, 8285, 12114, 12115, 12116, 12117, 12118, 12120, 12121. MACN 8339-65c, 8339-65e, 8339-65d, 8389, 31518, 49226, 49241, 51491, 52219. MLP 5730, 5731, 10734, 12412, 12455, 12873, 13015, 13530, 13656.

U. d. hypoleuca: FML 1570, 1571, 1572, 5451, 5614, 8202, 8203, 8204, 11314, 11315, 12119. MLP 425, 426, 427, 428, 429, 430, 431, 432, 433, 7917.

Specimens considered intermediates between *saturator* and *dumetaria* by Navas (1971). Adults: MACN 42765, 48572, 48575. Juveniles/immatures: MACN 40763, 40764, 42459, 48570, 48571, 48573.

List of specimens not examined but used to plot geographical distribution and migration patterns.

U. saturator: FMNH 61140, 61141, 61142, 61143, 61144, 61145, 61146, 61147, 61148, 61149, 61150, 61151, 61152, 61153, 62457, 316676. LSU 31036, 69968. YPM 21731, 21732, 21797, 21828, 22680, 82818, 82819, 82820, 82821, 82822, 82823, 82824, 82825, 82826, 82827, 82828, 82829, 82830, 82831, 82832, 82833, 82834, 82835, 82836, 82837, 82838, 112658, 112659, 112660.

U. d. dumetaria: FMNH 56810, 56811, 58944, 120658, 120659, 120660, 262641, 303506, 303507, 303508, 303509, 303510. LSU 63628, 69967, 178756, 178757. YPM 82790, 82791, 82792, 82793, 82794, 82795, 82796, 82797, 82798, 82799, 82800, 82801, 82802, 82803, 82804, 82805, 82806, 82807, 82808, 82809, 82810, 82811, 82812, 82813, 82814, 82815, 82816, 82817, 115046, 115047.

U. d. hypoleuca: FMNH 54124, 54125, 58945, 61154, 61155, 61156, 61157, 61158, 61159, 61160, 61161, 61162, 61163, 61164, 61165, 61166, 61167, 61168, 180034. LSU 37595. YPM 21730, 21794, 21795, 38925, 38926, 38927, 38928.

APPENDIX 2. List of recordings used for this study. Capitalized names refer to Argentine provinces, Chilean regions, and Bolivian or Peruvian departments. Each locality is followed by name of the recordist or catalogue number, and the number of individual birds recorded at each locality is in parentheses. Acronyms: MLNS, Macaulay Library of Natural Sounds, Cornell Lab of Ornithology; NSA, National Sound Archive, British Museum; XC, www.xeno-canto.org.

U. saturator: NEUQUÉN. Lagunas de Epulauquen (Areta 3, Roesler 1), Paso Pichachén (Pearman 1), Pino Hachado (Pearman 2), 20 km west of Rahue (Sokol/Pearman 1).

U. d. dumetaria: CHUBUT. Península Valdez (Straneck 1). RIO NEGRO. Embalse El Chocón (Areta 5). SANTA CRUZ. Estancia Las Buitreras [60 km from Río Gallegos] (Imberti 1), Estancia La Querencia [northern limit of Lago Argentino] (Imberti 1), Lago Cardiel (Pearman 1), Laguna Los Escarchados (Krabbe 1 [XC-15997, 16226]), Monumento Natural Bosque Petrificado (Imberti 1). XII REGION. El Porvenir (Areta 1), Sierra Baguales (Imberti 1).

U. d. hypoleuca: MENDOZA. Cuesta de los Terneros (Areta 1), San Rafael (Areta 1), Refugio San Antonio (Areta 2). SAN JUAN. Las Flores to La Serena road (Pearman 1). TUCUMÁN. El Infiernillo (Athanas 1, Macaulay 1 [MLNS-115989]). REGION METROPOLITANA. Farellones (Knapp 2 [XC-15774, 17124]).

U. albigula: AREQUIPA. 15 km e from Arequipa on road to Puno (Parker 2 [MLNS-33870, 33879]), ca 10 km w of Arequipa by road west of Chiguata (Schulenberg 1 [MLNS-36056]). I REGION. Putre (Whitney 2 [MLNS- 46451, 46452], N. Krabbe 1 [NSA 23462]).

U. jelskii: JUJUY. Azul Pampa (Pearman 1). REGION I. Putre (Pearman 1, Areta 2). LA PAZ. Apolobamba National Park (Hennessey 1 [MLNS-110776]).

U. validirostris: TUCUMAN. El Infiernillo (Pearman 5, Macaulay 1 [MLNS-115979]).

U. serrana: ANCASH. Llanganuco (Parker 1 [MLNS-33953], Van den Berg 2 [MLNS-28713, 28717]). LA LIBERTAD. Tayabamaba outskirts (Parker 1 [MLNS-17462]).

APPENDIX 3. List of localities and dates used to build distribution maps in this study. Numbers of each locality refer to Figure 2. Latitude ($^{\circ}$ S) and longitude ($^{\circ}$ W) in parentheses; months in brackets.

U. d. dumetaria: 1, Chilecito (29° 10', 67° 30') [May]; 2, Río Seco, Concarán (32° 34', 65° 15') [May]; 3, Embalse El Yeso (33° 38', 70° 00') [Nov]; 4, Laguna Llanecanelo (35° 35', 69° 09') [Sep]; 5, Curamalán Chico (37° 28', 62° 06') [Aug]; 6, D'Orbigny (37° 41', 61° 43') [Aug]; 7, Sierra Auca Mahuida (37° 53', 68° 31') [Nov]; 8, Lihuel Calel (38° 02', 65° 33') [Jun]; 9, Caleu Caleu, Laguna Colorada (38° 15', 63° 45') [May]; 10, Chasico (38° 20', 62° 39') [Jul]; 11, Río Sauce Grande, Monte Hermoso (38° 55', 61° 33') [May]; 12, Plaza Huincul (38° 55', 69° 09') [?]; 13, 40 km N Choele Choele (38° 56', 65° 41') [Feb]; 14, Cipolletti (38° 56', 67° 59') [Sep]; 15, Mayor Buratovich (39° 15', 62° 37') [Aug]; 16, 18 km N San Martín de los Andes (39° 59', 71° 20') [Nov]; 17, Bahía San Blás (40° 33', 62° 15') [May]; 18, San Antonio Oeste (40° 44', 64° 56') [?]; 19, Carmen de Patagones (40° 48', 62° 59') [Apr]; 20, Nahuel Huapi (40° 58', 71° 30') [Apr]; 21, Departamento Pilcaniyeu, near Neneo Ruca (41° 09', 70° 24') [Nov–Jan]; 22, Departamento Bariloche (41° 09', 71° 18') [Feb]; 23, Ingeniero Jacobacci (41° 18', 69° 35') [Mar]; 24, Estancia Huanu-luan (41° 22', 69° 52') [Nov]; 25, Departamento Ñorquinco (imprecise locality) (41° 51', 70° 54') [Feb]; 26, El Hoyo (imprecise locality) (42° 04', 71° 30') [Sep]; 27, Península Valdez (42° 30', 64° 00') [Feb]; 28, 100 km ENE Esquel (42° 38', 70° 08') [?]; 29, 7 km S Puerto Madryn (42° 50', 65° 03') [Dec]; 30, Punta Tombo (44° 03', 65° 11') [?]; 31, Río Pico (44° 14', 71° 59') [Jan]; 32, 8 km S Fitzroy (47° 06', 67° 15') [Nov]; 33, 43 km N Tres Lagos (49° 13', 71° 32') [Jan]; 34, 21 km N Tres Lagos (49° 24', 71° 32') [Jan]; 35, 1 km N Tres Lagos (49° 34', 71° 32') [Jan]; 36, Río Chico (49° 56', 68° 32') [Apr]; 37, Estancia La Julia (50° 16', 71° 44') [Jan]; 38, Coy Inlet (50° 57', 69° 10') [Apr]; 39, Lago Sarmiento (51° 02', 72° 46') [Aug–Oct]; 40, Río Gallegos (51° 38', 69° 13') [Jul]; 41, Estancia Federica (51° 41', 71° 58') [Nov]; 42, between Estancia Punta Alta and Estancia Federica (51° 41', 71° 58') [Sep]; 43, Río Ciaike, near Argentine boundary (52° 13', 70° 29') [Dec]; 44, Estancia Monte Dinero (52° 17', 68° 32') [Dec].

U. d. hypoleuca: 45, Río Loa (22° 14', 68° 36') [Jul, Nov]; 46, Maimara, Lagunas del Cerro Colorado (23° 37', 65° 24') [Apr]; 47, Ramadilla Copiapó Valley (27° 21', 70° 18') [Nov]; 48, Monte Amargo (27° 21', 70° 19') [Aug]; 49, Domeyko (28° 57', 70° 53') [Jul]; 50, Romero (29° 58', 71° 18') [Feb–Jun]; 51, Baños del Toro (29° 58', 71° 18') [Feb–Mar]; 52, Aiquina (22° 17', 68° 20') [Jul]; 53, San Pedro de Atacama (23° 30', 68° 15') [Jul]; 54, Tilcara (23° 34', 65° 22') [Aug]; 55, Cafayate (26° 05', 65° 58') [Aug]; 56, Tucumán (26° 49', 65° 13') [May, Oct]; 57, Tafi del Valle (26° 52', 65° 41') [May]; 58, Los Nacimientos de Abajo, Hualfin (27° 11', 66° 44') [Sep]; 59, Gualfin (27° 14', 66° 50') [Aug]; 60, Ischigualasto, Valle de la Peña (30° 08', 67° 51') [Apr–May]; 61, Pampa de Achala (31° 35', 64° 50') [May]; 62, General Lavalle (32° 43', 68° 35') [Sep]; 63, Cordillera de La Punta (34° 00', 70° 38') [Sep–Oct]; 64, Manantiales (34° 10', 70° 43') [Jul].

U. d. dumetaria (dark specimens, intergrades *sensu* Navas [1971]): 65, 66, Ñorquinco (41° 51', 70° 54') [Feb]; 67, El Bolsón (41° 58', 71° 31') [Dec]; 68, El Maitén (42° 03', 71° 10') [Sep]; 69–72, Cushamen (42° 12', 70° 50') [Dec–Feb]; 73, Alto Río Senguerr (45° 02', 70° 50') [Feb].

U. saturation: 74, La Ligua (32° 27', 71° 14') [Apr]; 75, La Calera (32° 45', 71° 12') [Apr]; 76, 77, Concon (32° 55', 71° 31') [Jul]; 78, Río Aconcagua (32° 56', 71° 31') [?]; 79, Olmue (33° 00', 71° 12') [Aug]; 80, Costa Valparaíso (33° 01', 71° 33') [?]; 81, Quilpué (33° 02', 71° 24') [Jun]; 82, Aconcagua (33° 02', 71° 38') [Apr]; 83, Casablanca (33° 03', 71° 36') [?]; 84, Lampa (33° 17', 70° 52') [Jun]; 85, Cerros de Curacavi (33° 24', 71° 09') [Jun]; 86, Alrededores de Santiago (33° 28', 70° 38') [May]; 87, Santiago (33° 28', 70° 38') [Aug]; 88, Melipilla (33° 42', 71° 13') [Aug]; 89, Paine (33° 48', 70° 44') [Apr]; 90, San Francisco del Mostazal (33° 59', 70° 43') [May]; 91, Graneros (34° 04', 70° 44') [Aug]; 92, Rancagua (34° 09', 70° 44') [Jun]; 93, Peleuquen (34° 09', 70° 45') [Jan]; 94, Machali (34° 11', 70° 38') [Sep]; 95, Teno (34° 51', 71° 09') [Sep]; 96, Cordillera de Curicó (34° 59', 70° 59') [May]; 97, Concepción (36° 08', 73° 01') [Apr]; 98, Quirihue (36° 17', 72° 32') [Jan]; 99, Penco (36° 44', 72° 49') [Aug]; 100, Hacienda Gualpencillo (36° 47', 73° 04') [Aug–Feb]; 101, Lagunas de Epulauquen (36° 48', 71° 04') [Dec–Mar]; 102, Paso Pichachén (37° 26', 71° 06') [Dec]; 103, Angol (37° 47', 72° 42') [Oct]; 104, Lonquimay Pedregoso (38° 26', 71° 13') [Dec]; 105, Río Lolen, Lonquimai Valley (38° 26', 71° 14') [Aug–Oct]; 106, Villa Portales (38° 27', 71° 22') [Feb]; 107, Reñaco (38° 35', 72° 50') [Jul]; 108, Pino Hachado (38° 40', 70° 53') [Dec]; 109, Laguna Gualletue (38° 42', 71° 16') [Mar]; 110, Temuco (38° 43', 72° 34') [Jul]; 111, 20 km west of Rahue (39° 22', 71° 09') [Dec]; 112, Sierra de Pilpil, San Martín de los Andes (40° 10', 71° 21') [Dec]; 113, Valle Encantado del Río Limay (40° 43', 71° 05') [Feb]; 114, Nahuel Huapi (40° 58', 71° 30') [Sep–Jan]; 115, Lago Moreno (41° 04', 71° 32') [Mar]; 116, Lago Escondido on the Río Foyel (41° 36', 71° 43') [?]; 117, El Bolson (41° 58', 71° 31') [Feb]; 118, Laguna Espejo, El Hoyo (42° 04', 71° 30') [Oct]; 119, Cholila (42° 31', 71° 27') [May]; 120, Esquel (42° 54', 71° 19') [?]; 121, Río Pico (44° 14', 71° 59') [Jan].