DISPLAY FLIGHT AND MECHANICAL SOUNDS OF THE ANDEAN NEGRITO (*LESSONIA OREAS*), WITH COMMENTS ON THE BASIC STRUCTURE OF FLIGHT DISPLAYS IN FLUVICOLINE FLYCATCHERS

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Resumen. – Despliegue aéreo y sonidos mecánicos en el Sobrepuesto Andino (*Lessonia oreas*), con comentarios sobre la estructura básica de los despliegues aéreos de los Fluvicolinae. – Describimos el despliegue aéreo de *Lessonia oreas*. El despliegue aéreo posee tres partes: notas en percha *tsi*, vuelo diagonal con notas *tic* y giro y descenso con matraqueo de alas *trrrrrrrrrr* y nota *psie*. El matraqueo de alas parece ser un sonido fuerte de naturaleza mecánica previamente desconocido en la especie pero consistente con su posición filogenética en el clado *Lessonia-Knipolegus-Hymenops*. Los despliegues en vuelo están ampliamente distribuidos en los tiránidos. Los despliegues más conspicuos ocurren en los Fluvicolinae, especialmente en Fluvicolini y Xolmini. Los despliegues de algunas *Knipolegus* (al menos *striaticeps*, *aterrimus* y *hudsoni*) y *Lessonia* (al menos *oreas*) parecen compartir sonidos vocales y mecánicos homólogos (notas en percha; notas en vuelo; descenso con sonido mecánico y nota vocal tajante). La inferencia de pérdidas de despliegues en algunas *Knipolegus* en trabajos previos puede ser al menos en parte un artefacto de muestreo. Si *Lessonia* es hermano de *Knipolegus+Hymenops*, los despliegues en vuelo con sonidos mecánicos serían la condición ancestral del grupo. Homologías comportamentales profundas en los Xolmini son sugeridas por observaciones en la Monjita Castaña (*Neoxolmis rubetra*) y el reemplazo de sonidos mecánicos por la elevación y congelamiento ritualizados de alas en el despliegue de la Dormilona Chica (*Muscisaxicola maculirostris*). La porción sub-apical del vexilo interno de las primarias octava y novena es más cóncava en *L. oreas* que en *L. rufa*, y el perfil de la pluma es levemente más cóncavo en el primero y levemente recto o apenas cóncavo en el último. Estas diferencias sugieren que estos taxa difieren en sus despliegues en vuelo y potenciales sonidos mecánicos y son por lo tanto correctamente considerados especies distintas.

Abstract. – We describe the display flight of the Andean Negrito (*Lessonia oreas*). The display flight consists of three parts: perched *tsi* notes, diagonal flight with *tic* notes, and turn and descent with *trrrrrrrrrr* wing-whirr and *psie* note. The wing-whirr appears to be a loud mechanical sound heretofore unknown in the species but consistent with the species' phylogenetic position in the *Lessonia-Knipolegus-Hymenops* clade. Flight displays are widespread in the tyrant flycatchers. The most conspicuous displays occur in the Fluvicolinae, especially in Fluvicolini and Xolmini. The display flights of some *Knipolegus* (at least *striaticeps*, *aterrimus* and *hudsoni*) and *Lessonia* (at least *oreas*) appear to share homologous vocal and mechanical sounds (perched notes; flight notes; descent with mechanical sound and sharp vocal note). The inferred loss of display in some *Knipolegus* species in previous works may partly be a sampling artifact. If *Lessonia* is sister to *Knipolegus+Hymenops*, flight displays with mechanical sounds would be the ancestral condition for the group. Deep behavioral homologies in the Xolmini are suggested by observations on the Rusty-backed Monjita (*Neoxolmis rubetra*) and replacement of mechanical sounds by ritual-

ized elevation and freezing of wings in the display of the Spot-billed Ground-tyrant (*Muscisaxicola maculirostris*). The sub-apical portion of inner vanes of the eighth and ninth primaries are more concave in the Andean Negrito than in the Austral Negrito (*L. rufa*) and feather profile is slightly concave in the former and slightly straight or convex in the latter. These differences suggest that these taxa differ in flight displays and potentially in mechanical sounds and are thus correctly considered as different species. *Accepted 30 May 2014.*

INTRODUCTION

Vocalizations of tyrant flycatchers are innate: they have a strong genetic basis with little room for experience-based changes in structure or pattern (Kroodsma 1984, Kroodsma & Konishi 1991). For this reason vocalizations have long proven valuable and easy to use in systematic studies of Tyrannidae (Reynard *et al.* 1993, Rheindt *et al.* 2008, Abalos & Areta 2009, McCallum & Pieplow 2010). Mechanical sounds also are known for some tyrannids with attenuated primary feathers, and the presence of attenuated primary feathers in other species suggests that mechanical sounds may be widespread but understudied in the group (Wetmore 1926, Vuilleumier 1971, Straneck & Carrizo 1983). The genetic and developmental basis of mechanical sounds are unknown; hence it is not known whether these species-specific signals are developmentally closed, as are vocalizations.

The Austral Negrito (*Lessonia rufa*) has been frequently treated as a single species with two distinctively marked subspecies (*rufa* and *oreas*). However the latter is now generally considered to be a separate species, the Andean Negrito (*Lessonia oreas*) (Traylor 1977, Fitzpatrick 2004, Remsen *et al.* 2013). The vocal repertoire of both species has been described as small and simple, and mostly composed of isolated notes that are uttered only occasionally (Fjeldså & Krabbe 1990, Jaramillo 2003, Fitzpatrick 2004). However, vocalizations of these species have not been analyzed in detail. It is possible that both spe-

cies produce mechanical sounds as well, because the eighth and ninth primaries of adult males of the Austral Negrito are narrowed distally, whereas males in 'first winter' (first basic) plumage and females throughout their lives have unmodified feathers (Wetmore 1926): adult males therefore may produce mechanical sounds with the modified flight feathers during displays.

Mechanical sounds may be produced during display flights in which males of both species flutter upwards to ~ 10–15 m; however, sounds during such displays have not been reported (Fitzpatrick 2004), except for an overlooked entry in Canevari *et al.* (1991), where R. Straneck reports a fast ascending flight followed by a short descending soaring while uttering a high pitched 'Zip…zip… zrriinh' for *Lessonia rufa* (including *oreas*, and without explaining to which taxon this display belongs). Males of *L. rufa* have a flight display (details not studied critically) in which they give a distinctive, very high, thin "tssiu" call, suggesting the flight call of the Red-throated Pipit (*Anthus cervinus*) (S.N.G. Howell *in litt.*). Analyses of these displays are informative for phylogenetic studies; for example, *Lessonia* is apparently closely related to *Hymenops* and *Knipolegus* (Ohlson *et al.* 2008, 2013; Tello *et al.* 2009), two genera known for flight displays with both mechanical and vocal sounds (Straneck & Carrizo 1983, Vides Almonacid & Márquez 1990). In their analyses, Hosner & Moyle (2012:162) considered *Lessonia* flight displays to be silent, but we here report on both vocal and apparently mechanical sounds

in flight displays of male *L. oreas* observed during fieldwork in the Puna of northern Chile.

In this paper, we (1) describe the flight display and mechanical sounds of male Andean Negritos, (2) explore structural features of their feathers that may be related to mechanical sound production, and (3) discuss these findings in the broader context of display flights in tyrant flycatchers.

METHODS

We observed Andean Negritos *ad libitum* and made analyzable vocal recordings of two individuals at 24 bit and 48 kHz with a Marantz PMD-661 digital recorder and a Sennheiser ME–62 microphone with a Telinga Universal Parabola. The recordings have been deposited at the Macaulay Library of Natural Sounds (MLNS, Cornell Lab of Ornithology, Ithaca; catalogue numbers: 171103, 171116, 171128). Both individuals were recorded in the XV Región, Chile (GMT-4), one at Parcohaylla (18°52'40.7''S, 69°12'30.2''W, 4010 m a.s.l.) on 22 and 23 October 2011, and the other one at Parinacota (18°12'33.31''S, 69°16'33.25''W, 4400 m a.s.l.) on 25 and 26 October 2011.

To characterize display flight structure, we recognized and counted three types of vocally produced notes plus apparently non-vocal wing-whirr notes in each display, measured minimal and maximal frequency and duration of vocal notes, and duration of complete display bouts and wing-whirrs. We calculated wing-whirr rate by dividing average number of wing-whirr notes/average wing-whirr duration. All measurements were made with Raven Pro 1.4 (http://www.birds.cornell.edu/raven) using default spectrogram parameters (Window–Type: Hann, Size: 256 samples (=5.33 ms), 3dB Filter Bandwith: 270 Hz; Time grid–Overlap: 50 %, Hop size: 128 samples (=2.67 ms); Frequency grid–DFT size: 256 samples, Grid spacing: 188 Hz).

We examined primary feathers in 10 adult male specimens of both *Lessonia* species in the Museo de La Plata, La Plata, Argentina (MLP) and in the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN).

RESULTS

Display flight. We observed and recorded sounds of three displaying adult male Andean Negritos in two widely separated localities in northern Chile (Región XV). Acoustic measurements of sounds during the following display descriptions are presented in Table 1.

Parcohaylla. At dusk (19:45 h) on 22 October we saw an adult male foraging on the ground with a female. He subsequently flew overhead while making a loud rattle (*trrrrrrrrrr*). It soon became dark and so no further observations were possible. At dawn on 23 October we again heard the rattle as this male was in a display flight. The bird displayed over a small (10 x 20 m) patch of sand and small rocks that was surrounded by a wet bog flowing into a small river ~ 30 m away. The specific display spot was a slightly more open area where the dominant tola (*Lepidophyllum tola*) bushes were sparse, creating a 5x5 m gap. The display had three clearly defined parts (Figs 1, 2).

1) Perched notes. Between display flights, the bird uttered brief (~ 60 ms) *tsi* notes (frequency descending-frequency ascending) ~ rhythmically at a rate of ~ 1/3 s (Fig. 2A). Each note spanned ~ 6.5–8 kHz and had a weak harmonic (Fig. 2B, Table 1). The bird called while perched atop the very tip of a 1.5–m high tola bush that was slightly taller than surrounding bushes, from a 0.8–m tall llareta (*Azorella compacta*) cushion-plant about 2 m away, and from the ground. Occasionally, the display ended after a series of *tsi* notes with the bird flying away, but once it was followed by a leap to the ground with a different

TABLE 1. Summary of quantitative traits of sounds during flight displays of two adult male Andean Negritos (*Lessonia oreas*). Data are shown as the mean values for two males with range and sample size in parentheses. Descriptive statistics of individuals from Parcohaylla/Parinacota respectively, in square brackets.

	Display component			
	tsi notes	*pic* notes	*trrrrrrrrrr* wing-whirr	*psie* terminal note
Number of notes	15.1 (4–20; 6) [18.2 ± 1.3 (17–20; 4)/ 12.0 ± 11.3 (4–20; 2)]	5.4 (4–8; 11) [4.6 ± 0.5 (4–5; 7)/ 5.8 ± 1.5 (5–8; 4)]	13.6 (12–15; 12) [12.6 ± 0.8 (12–14; 7)/ 14.6 ± 0.5 (14–15; 5)]	1 (6) [1 (5)/1 (1)]
Frequency minimum (Hz)	6640 (6408–6832; 30) [6597 ± 142 (6408–6815; 20)/6683 ± 92 (6565-6832; 10)]	2795 (2548–3011; 20) [2819 ± 100 (2649–3011; 15)/2771 ± 140 (2584–2928; 5)]	1486 (1268–1646; 27) [1444 ± 114 (1268–1646; 21)/1527 ± 84 (1462–1637; 6)]	6480 (6324–6586; 6) [6446 ± 119 (6324–6586; 5)/6515 (1)]
Frequency maximum (Hz)	7875 (7656–8332; 30) [7905 ± 138 (7743–8332; 20)/7845 ± 82 (7656–7923; 10)]	3635 (3569–3758; 20) [3648 ± 43 (3569–3758; 15)/3621 ± 25 (3598–3656; 5)]	2661 (2332–3050; 27) [2701 ± 218 (2332–3050; 21)/2620 ± 192 (2391–2867; 6)]	7554 (7152–8206; 6) [7956 ± 187 (7777–8206; 5)/7152 (1)]
Duration (ms)	54 (36–63; 30) [57.3 ± 4.1 (50–63; 20)/ 50 ± 8.2 (36–61; 10)]	16 (14-18; 20) [15.7±1.2 (14-18; 15)/ 16.2±0.4 (16-17; 5)]	10 (5–16; 27) [9.5 ± 2.2 (5–13; 21)/ 9.8 ± 3.3 (7–16; 6)]	71 (60–85; 6) [80.8 ± 4.1 (75–85; 5)/ 60 (1)]

sounding note (not recorded). Most of the time, the display was continued by a diagonal flight (described next).

2) Diagonal ascending flight. – From the tip of the tola bush, the male flew upward at ~ 45° while uttering a series of 5 brief (~ 16 ms) *pic* notes (frequency ascending-frequency descending) at an accelerating pace, spanning ~ 2.8–3.6 kHz with a weak upper harmonic (Fig. 2C, Table 1), until the bird was ~ 6 m high and ~ 6 m away from its starting point (Figs 1, 2C).

3) Turn and descent. – After the last *pic* note, the bird turned abruptly laterally in the air almost 180° and began descending diagonally roughly in the same plane toward the starting point of the display; soon thereafter a loud mechanical wing-whirr rattling sound (*trrrrrrrrrr*) was produced by rapidly shaking the outstretched

wings with the body held horizontally as the bird descended, which was followed by a sibilant, trembling inverse chevron-shaped but mostly frequency-descending and very soft *psie* note (Figs 1, 2D). Wing notes spanned ~ 1.5–2.8 kHz and lasted ~ 10 ms each (produced at a rate of ~ 30 Hz), while the descending note ranged over ~ 6.5–8 kHz and was ~ 80 ms long (Fig. 2D, Table 1). The descending trajectory of the male deviated slightly from the original take-off point as a slight final turn was made and the bird landed on the llareta or on the ground behind it, returning to the first stage of the display (Fig. 1). When landing on the ground, it jumped from the ground behind the llareta to the llareta and from there to the tip of the taller branch in the tola, never jumping directly from the ground to the tola.
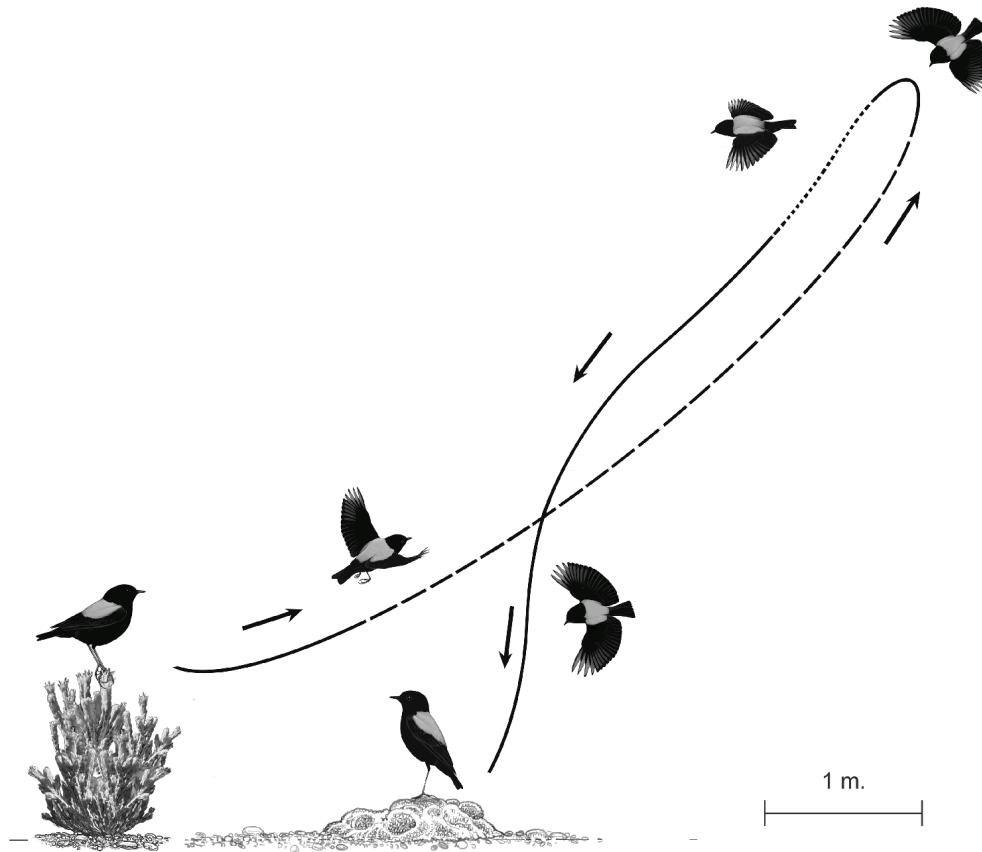
FIG. 1. Schematic representation of the display flight of an dult male Andean Negrito (*Lessonia oreas*). An entire display bout can be broken into three parts: perched notes, diagonal flight and turn and descent, the last portion of which includes mechanical sounds heretofore unknown in the species but consistent with its phylogenetic position in the *Lessonia-Knipolegus* clade. Continuous line = silent flight, dashed line = *pic* notes during diagonal flight, pointed line = *trrrrrrr* wing-whirr during turn and descent. See Fig. 2 for illustration of accompanying sounds. Illustration by Aldo Chiappe.

The male displayed ~ 15–18 times from 06:41 to 07:04 h, beginning when it was completely dark so it was not possible to see the bird, until soon after there was enough light to observe it in detail. When perched on the tola bush (unusual behavior in this species which spends most of the time on the ground) the overall shape of the male recalled that of other displaying tyrants like Spectacled Tyrant (*Hymenops perspicillata*) and several black

tyrants (*Knipolegus* spp.). Soon after its last display, we observed the bird running on slippery ice of the bog with plumage fluffed, and foraging occasionally.

Parinacota. On 25 October, we heard two males displaying simultaneously at ~ 06:40 h when it was still completely dark. Displays (~ 8–10) continued until 06:52 h, by which time birds were visible. One adult male was sound-
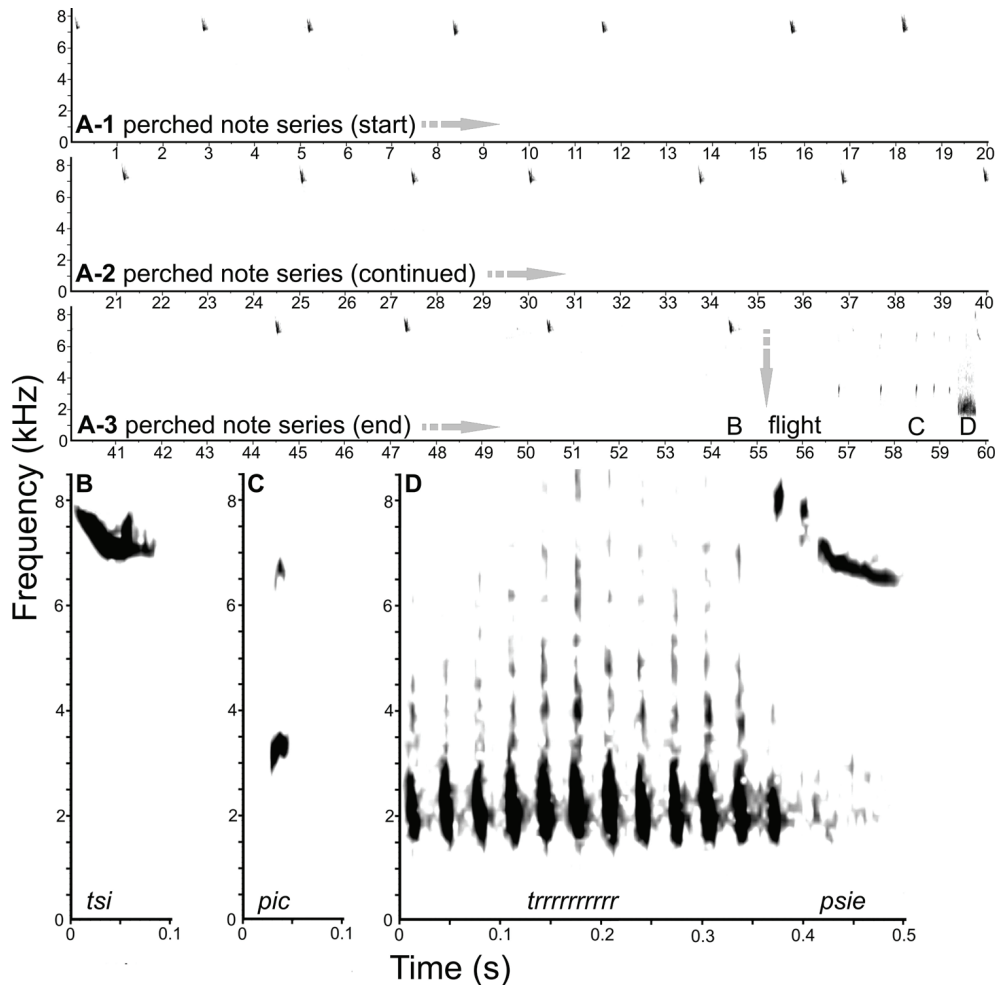
FIG. 2. Spectrogram of an entire display bout of an adult male Andean Negrito (*Lessonia oreas*). A-1–A-3) Entire display lasting 60 seconds consisting of 18 *tsi* notes, 5 *pic* notes, *trrrrrrrrrr* wing-whirr and *psie* note, B) *tsi* note in display context (above) and detail (below), C) *pic* note in display context during diagonal flight (above) and detail (below), and d) *trrrrrrrrrr* wing-whirr during turn and descent and *psie* note (above) and detail (below). Horizontal gray arrows indicate initiation and continuation of perched notes, vertical gray arrow indicates approximate flight start. See Fig. 1 for illustration of accompanying behavior and Table 1 for acoustic characterization. Recorded at Parcohaylla, Región XV, Chile, 23 October 2011 (MLNS-171103; http://macaulaylibrary.org/audio/171103).

recorded and observed; the second male was distant and could not be seen but we made some distant sound recordings. The area was an open dry bog composed of a mosaic of tunneled chunks of earth in which water was frozen; no bushes or rocks were within ~ 50 m from the displaying bird. The display was similar to that described above except: the display began and ended on the ground (altitude ~ 6 m; horizontal movement ~ 6–8 m in

the diagonal flight); the bird returned to the same location between display flights; and the *tsi* notes were occasionally uttered as doublets. We recorded two complete displays by this individual, one of which included only four *tsi* notes and eight *pic* notes. On 26 October we recorded only *tsi* notes of the same adult male plus further low-quality recordings of the more distant individual.

Males differed in wing-whirr duration and number of notes but not in rate of wing-whirr notes which was ~ 33 in both individuals (Table 1). Total display duration in seconds expressed as mean ± SD (range; *N*) for males at Parcohaylla and Parinacota were respectively: 70.0 ± 18.6 (57–97; 4) and 45.6 ± 14.0 (36–56; 2).

Despite our extensive experience with high-Andean birds in Argentina, Bolivia and Chile, we have never observed *L. oreas* displaying during the day. During a 15-day field trip to the area in which our observations of display flights took place, we only found them displaying at dawn, and seldom at dusk.

Feather shape. The shape of primary feathers differs between *L. rufa* and *L. oreas*. In both species, the apical and sub-apical portions of the outer vane from the seventh to the ninth primary are slightly attenuated and in the tenth are normal (i.e., not attenuated) (Fig. 3). In *L. oreas*, the sub-apical portion of the inner vanes of the eighth and ninth primaries has a marked concavity (deeper in the eighth), which continues as a convexity that turns into a slight concavity toward apex of the feather, giving the feather a slightly concave profile (Fig. 3A). In *L. rufa*, the sub-apical portion of the inner vanes of the eighth and ninth primaries has a shallow inward inflection (occasionally becoming a very shallow concavity in the eighth), which continues as a slightly curving line, giving the feather a slightly straight or convex profile (Fig. 3B).

DISCUSSION

Flight displays are widespread in the tyrant flycatchers (Traylor & Fitzpatrick 1982, Fitzpatrick 2004). The most conspicuous displays occur in the Fluvicolinae, especially in Fluvicolini (e.g., *Alectrurus*, *Pyrocephalus*) and Xolmini (e.g., *Muscisaxicola*, *Hymenops*, *Lessonia*, *Knipolegus*). The flight displays of *Knipolegus* (at least *striaticeps*, *aterrimus* and *hudsoni*; JIA unpubl.) and *Lessonia* (at least *oreas*) appear to share homologous vocal and mechanical sounds (perched notes; flight notes; descent with mechanical sound and sharp vocal note), based on the traditional criteria of similarity of position and special quality (Wenzel 1992). Additionally, flight-pursuit vocalizations are known in *Knipolegus* and *Lessonia* (JIA unpubl.). More extensive and detailed field observations across *Lessonia* and *Knipolegus* species are necessary to correctly work out the evolution of display behavior in the clade. Hosner & Moyle (2012) considered the displays of *Lessonia* and of the Blue-billed Black-tyrant (*K. cyanirostris*) to be silent, however we have here shown that *L. oreas* has a complex flight display involving four different sound types, whilst the display flight of *K. cyanirostris* includes at least one sound type (M. Repenning *in litt.*). Thus, the inferred loss of display forms in some species by Hosner & Moyle (2012) may partly be a sampling artifact and, if *Lessonia* is sister to *Knipolegus+Hymenops* (Tello *et al.* 2009), the presence of a shared flight display with mechanical sounds further indicates that this is the ancestral condition for the group.

The display flight of the Crested Black-tyrant (*K. lophotes*) seems equivalent to those of other *Knipolegus* (listen to the display sounds and display description in MLNS-113417–113419). However, Hosner & Moyle (2012: 163) indicated the presence of an exclusive "spectacular flight song of *K. lophotes*—a long, arcing flight over an open area
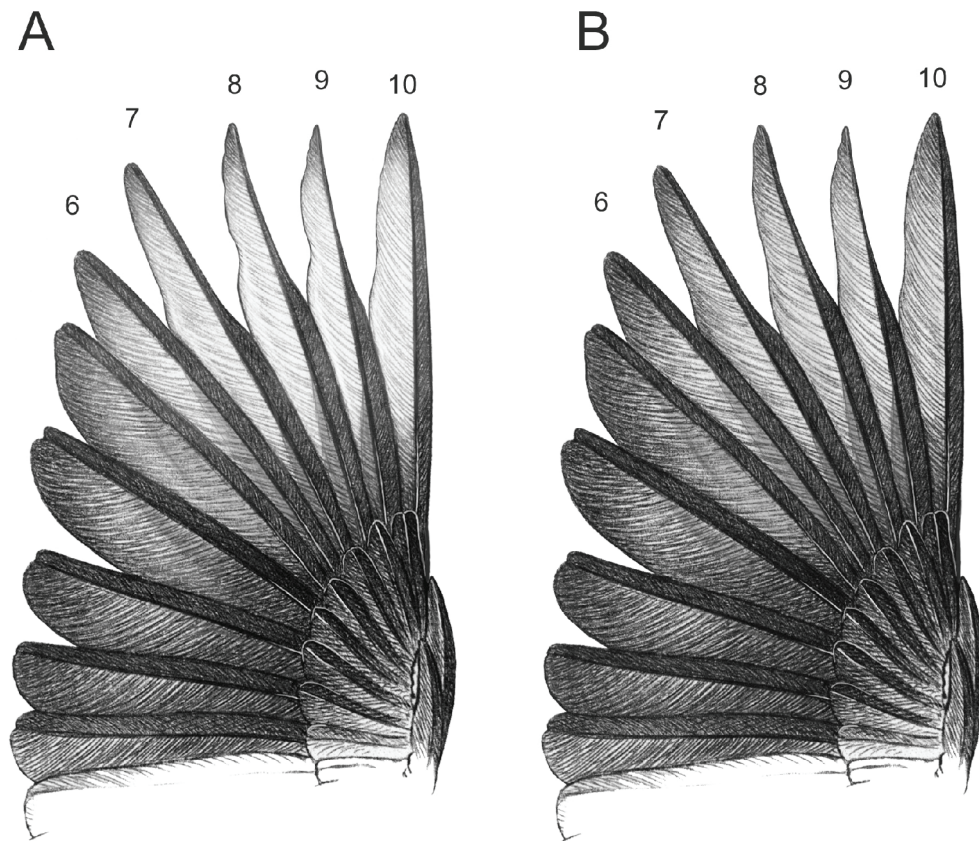
A

B

FIG. 3. Differences in shape of primary feathers in A) adult male Andean Negrito (*Lessonia oreas*) and B) adult male Austral Negrito (*L. rufa*) suggest that these taxa will differ in flight displays and mechanical sounds and that are thus correctly considered as different species. The sub-apical portion of inner vanes of the eighth and ninth primaries are more concave in *L. oreas* than in *L. rufa* and feather profile is slight concave in *L. oreas* and slight straight or convex in *L. rufa*. Note also whiter primaries in *L. oreas*. Illustration by Aldo Chiappe.

with a loud, complex song at the peak (the only true song of any *Knipolegus*)." Flight notes (different from those used during the display flight) are also emitted by at least *K. aterrimus* during fairly circular horizontal flights on slow wing-beats and with raised crest (perhaps homologous to the "flight song" of *K. lophotes*?; JIA pers. observ.). We contend that phylogenetic reconstruction of display evolution should be based on thorough field studies. A literature review as that of Hosner & Moyle (2012) is likely to miss important behaviors and references, resulting in turn in inaccurate descriptions of display flights and in spurious evolutionary patterns.

Deep behavioral homologies in the Xolmini are suggested by observations on the Rusty-backed Monjita (*Neoxolmis rubetra*), in which the two outermost primaries are attenuated in adult males (Wetmore 1926, Vuil-

leumier 1971). Wetmore (1926: 302) described their display flight: "Males at intervals flew up to make a metallic rattle with their wings as they turned abruptly and dropped to the ground." The display flight of the Spot-billed Ground-tyrant (*Muscisaxicola maculirostris*) also appears to share the same three elements as in Andean Negritos, but here the mechanical sound is apparently replaced by a ritualized elevation and freezing of wings in the aerial display (Smith 1971; see Ohlson *et al.* 2008, 2013 and Tello *et al.* 2009 for phylogenetic placement of *Neoxolmis* and *Muscisaxicola*). Substitution of vocal sounds by mechanical sounds has been proposed for the Elaeninae, where bill snaps of the Crested Doradito (*Pseudocolopteryx sclateri*) may be homologous to introductory notes given by other members of the genus (Bostwick & Zyskowski 2001, Abalos & Areta 2009). In this subfamily, modified primaries have been reported in various species but their function is not known (Hellmayr 1927, Bostwick & Zyskowski 2001). However, the display of Bearded Tachuri (*Polystictus pectoralis*) includes loud mechanical sounds: typically a whistle is followed by a rapid series of ascending notes that finish in a bow display, where the male thrusts its body forward and makes very rapid wing movements to generate a harsh trilled sound. This display is performed perched and in flight (JIA unpubl.).

Osteological and syringeal characteristics place *Lessonia* close to *Pyrocephalus* within the 'Knipolegus group' (including also *Knipolegus* and *Hymenops*; Lanyon 1986). However, molecular data do not support this arrangement, since *Pyrocephalus* belongs to the Fluvicolini (Tello *et al.* 2009, Ohlson et al. 2013). Both *Knipolegus* and *Hymenops* perform aerial displays with mixed vocal and mechanical sounds (Straneck & Carrizo 1983, JIA pers. obs.). The phylogenetic position of *Lessonia* needs clarification, since perch calls, wing-raising displays and wing-whirr in *Hymenops* (JIA pers. observ., see

Straneck & Carrizo 1983), anatomy (Lanyon 1986) and molecular data (Tello *et al.* 2009) suggest that it belongs to the *Hymenops-Knipolegus* clade.

Knipolegus and *Hymenops* display at dawn and dusk, but also during the day, unlike *Lessonia*, which apparently does not display in intense light. However, display intensity may be greater at dawn and dusk in the former genera. For example, the display of *Knipolegus a. aterrimus* usually includes a short upward leap during the day, but this may be replaced by a 10-15m upward flight early in the morning. Display time and duration of the flights may be severely constrained by winds, which tend to build up during the day and to decrease at dusk.

Mechanical sounds produced by specialized feather structures have evolved independently in many groups of birds (Delacour & Amadon 2004, Bostwick & Prum 2005, Bostwick 2006, Clark *et al.* 2011), including tyrant flycatchers (Bostwick & Zyskowski 2001). Without the aid of high-speed videography, we cannot assure that the *trrrrrrrrrr* wing-whirr notes are effectively mechanical. However, given the facts that (1) the sound was heard while the birds flapped their wings at a rhythm consistent with that of the sound and (2) the acoustic properties of the sound are unlike those of known vocal sounds and much like those of mechanical sounds, we feel that our consideration of this sound as mechanical is justified.

Species-specific patterns of primary feather attenuation have been reported in *Xolmis*, *Agriornis*, and *Neoxolmis* (Vuillumier 1971). The consistent (but subtle) differences in feather shape between adult males of *L. rufa* and *L. oreas* add more support for their species-level treatment and suggest that their display flights differ as well. However, these differences appear mild in comparison to those reported between present subspecies of Fork-tailed Flycatcher (*Tyrannus savana*)

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(Zimmer 1937). Description and sound recordings of the display flight of *L. rufa* are needed to test this hypothesis.

ACKNOWLEDGEMENTS

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