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CLARIFYING THE NEST ARCHITECTURE OF THE *SILVICULTRIX* CLADE OF *OCHTHOECA* CHAT-TYRANTS (TYRANNIDAE)

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Resumen. – Una aclaración de la arquitectura del nido del grupo *Silvicultrix* de *Ochthoeca* (Tyrannidae). – *Ochthoeca* es un género de Tyrannidae de los Andes. Un análisis filogenético reciente confirmó la existencia de un grupo monofilético dentro del género *Ochthoeca* de aves que habitan bosques. Este grupo de aves se distinguía previamente por el género *Silvicultrix*. Este género difería de *Ochthoeca* por la arquitectura de nidos y la morfología de la siringe. Sin embargo, las diferencias en la arquitectura de nidos fueron mal documentadas para dos especies de los cuatro *Silvicultrix*, pues no se conocían nada de los otros dos. En este estudio presentamos una descripción completa y detallada de la arquitectura de los nidos del antiguo *Silvicultrix*: *Ochthoeca jelskii*, *O. diadema*, y *O. frontalis*. También presentamos datos sobre el cuidado en el nido de los pichones de *O. jelskii*. Mostramos que éstas tres especies construyen nidos distintos al resto de las especies de *Ochthoeca*. Las otras especies de *Ochthoeca* construyen nidos de copas abiertas en el suelo o rocas, mientras que las antiguas *Silvicultrix* construyen nidos semi-globulares y colgantes entre musgos.

Abstract. – *Ochthoeca* is a genus of tyrant-flycatchers distributed throughout the Andes. A recent molecular phylogeny confirmed the existence of a monophyletic clade of forest-dwelling species within the *Ochthoeca* genus. This clade, *Silvicultrix*, was previously split from other *Ochthoeca* species based on characters of syringeal morphology and nest architecture. These nest characteristics, however, were poorly documented for two of the four species of the *Silvicultrix* clade, and completely unknown for the other two. Here we present complete descriptions of the nests of three of the *Silvicultrix* clade species: the Jelski's (*Ochthoeca jelskii*), Yellow-bellied (*O. diadema*), and Crowned (*O. frontalis*) chat-tyrants. In addition, we provide data on the nestling care of Jelski's Chat-Tyrant. We show that these species have departed from the ancestral nest state of an open cup built on the ground or into a cliff face, and build partially domed cups suspended in hanging moss. *Accepted 15 April 2008*.

Key words: Ecuador, Andes, phylogeny, cloud forest, *Ochthoeca*, *Silvicultrix*.

INTRODUCTION

Ochthoeca is a genus of small to mid-sized tyrant-flycatchers found in the Andes from Venezuela and Colombia to northwestern Argentina (Ridgely & Tudor 1994). They occupy a variety of habitats, from open, grassy páramo to the interior of montane and premontane cloud forests, but all forage fairly low to the ground and perch erectly (García-Moreno *et al.* 1998, Ridgely & Greenfield 2001). Though generally inconspicuous, once observed, their active foraging habits, usual presence of a strong superciliary, and often obvious wingbars draw attention. Multiple species may be sympatric (Traylor 1985), but as each inhabits a characteristic ecological zone, they segregate their distributions by ele-

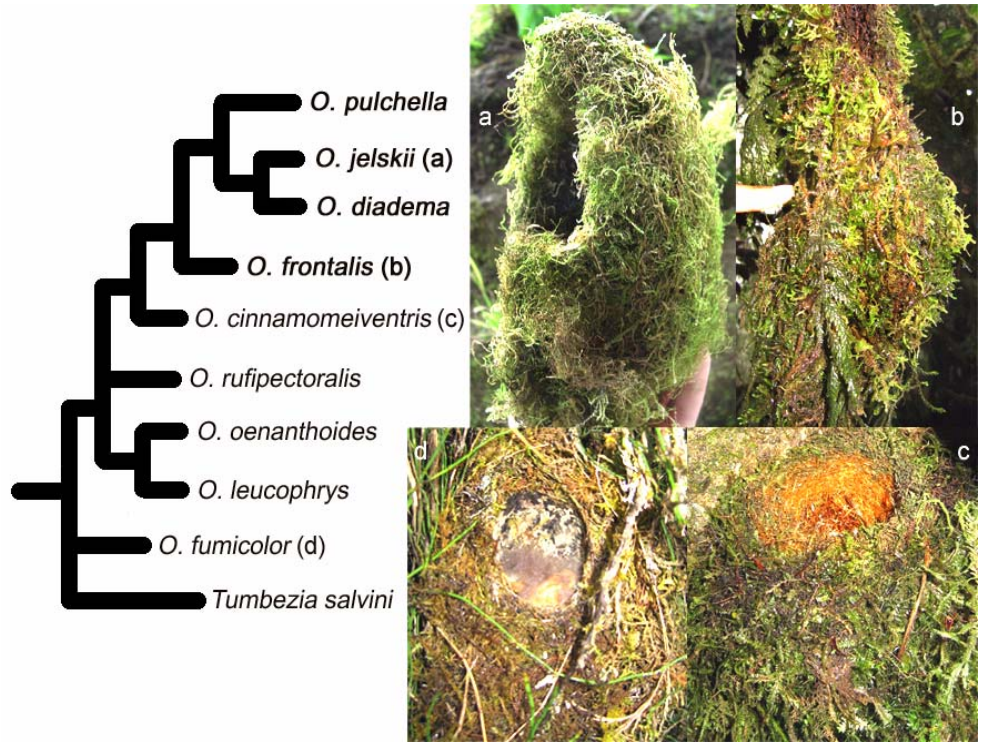

FIG. 1. *Ochthoeca* phylogeny adapted from García-Moreno *et al.* (1998). Branch lengths do not reflect genetic distance. Members of the *Silvicultrix* clade are noted in bold. Inset photos: (a) Jelski's Chat-Tyrant (*O. jelskii*), nest no longer *in situ*; (b) Crowned Chat-Tyrant (*O. frontalis*), view from side of nest, finger points into entrance; (c) Slaty-backed Chat-Tyrant (*O. cinnamomeiventris*); (d) Brown-backed Chat-Tyrant (*O. fumicolor*). Photos by authors.

vation or by occupying different habitats (García-Moreno *et al.* 1998).

Based on an analysis of mtDNA sequences, García-Moreno *et al.* (1998) propose an adaptive radiation of *Ochthoeca* in the Andes, beginning with a lowland, riparian-inhabiting ancestor. The uplift history of the Andes is one of complex regional variation in rate and form. The central Andean plateau appears to have been uplifted earlier than the northern Andes, reaching no more than half its modern elevation by 10.7 million years ago (Gregory-Wodzicki 2000). Species representing deep branches in the phylogeny, *O. fumicolor, O. oenanthoides, and O. leucophrys*, are associated with the dry, brushy, rocky habitats characteristic of this plateau; the latter two species, indeed, still range only on these drier, central Andean slopes, while the former has presumably expanded its range as the northern Andes were uplifted (Ridgely & Tudor 1994, J. Fjeldså pers. com.). The northern cordillera underwent a period of rapid uplift between two and five million years ago (Gregory-Wodzicki 2000). The cloud forests that now blanket much of these slopes would have developed during this time (Graham *et al.* 2001).

Thus, from the lowland riparian ancestor, *Ochthoeca* accordingly radiated into a number

of habitats, from open, brushy areas, to the shady forest edges along ravines, then the dark interior of montane forests, and ultimately, the interior of lower montane and submontane forests (García-Moreno *et al.* 1998). Historically, syringeal morphology data has been used to segregate this final radiation of *Ochthoeca* into the genus *Silvicultrix* (Lanyon 1986), and the results of García-Moreno *et al.* (1998) support the monophyly of the *Silvicultrix* clade. They found it, however, to be a radiation within *Ochthoeca* (Fig. 1), and subsumed it to avoid paraphylly. It is worth noting here that three species previously considered to be members of the genus *Myiophobus*, *M. flavicans*, *M. phoenicomitra*, and *M. roraimae*, were recently found to belong to the *Ochthoeca* clade (Ohlson *et al.* 2008). These taxa represent more recent branches in the clade and, notably, continue the down slope trend manifested in successive branches along the phylogeny, inhabiting middle elevation, humid forest interior (Farnsworth & Langworth 2004).

In this paper we present nest descriptions and additional data for three of the four species of the *Silvicultrix* radiation, the Jelski's (*O. jelskii*), Yellow-bellied (*O. diadema)*, and Crowned (*O. frontalis*) chat-tyrants. The information that we provide for Jelski's Chat-Tyrant is the first of any breeding data published on the species; for the latter two, we clarify previously conflicting nest descriptions.

STUDY SPECIES

Jelski's Chat-Tyrant is the first of the species we discuss in the *Silvicultrix* clade. Following Traylor (1985), it was raised to species status, formerly being considered conspecific with the Golden-browed Chat-Tyrant (*O. pulchella*). Uncommon in the undergrowth of montane forest borders along the West slope of the Andes (Ridgely & Tudor 1994), Jelski's Chat-Tyrant differs from many of its congeners in its completely (so far as is known) allopatric distribution (Traylor 1985). In Ecuador, known only from Loja Province in the far southwest, it ranges from there to Northwest Peru, occurring at higher elevations in the South of its range (Traylor 1985). The breeding habits of Jelski's Chat-Tyrant are unknown and its nest is undescribed.

The Yellow-bellied Chat-Tyrant also belongs to the *Silvicultrix* clade, and like its closest congeners (*sensu* García Moreno *et al.* 1998), inhabits the undergrowth of montane forest (Ridgely & Tudor 1994). The nest of the Yellow-bellied Chat-Tyrant was first described in 1879 in two separate articles published in the same volume of the Proceedings of the Zoological Society of London (Sclater & Salvin 1879, Taczanowski 1879). Sclater & Salvin (1879) presented the English description of T.K. Solomon's as "made entirely of moss lined with a few feathers and built in a bank, generally into a mass of growing moss." Taczanowski (1879, 1884), however, offered in French the description of M. Stolzmann in which he described the nest as having "the shape of an elongated pear; the entrance is on the underside, slightly to one side…constructed entirely of moss…lined with feathers" (translation from Lanyon 1986). Taczanowski (1879) also remarked that the "nest was suspended on vertical lianas" (authors' translation). Subsequent publications (e.g., Hilty & Brown 1986, Hilty 2003, Farnsworth & Langham 2004) have noted this discrepancy (though the description of Solomon's does not preclude the nest shape discussed by Stolzmann) and, to date, no reliable description of the nest has been published.

The Crowned Chat-Tyrant is the third species in the *Silvicultrix* clade for which we present data. It looks much like Jelski's Chat-Tyrant, except that the relevant subspecies (*O. f. frontalis*) of the Crowned Chat-Tyrant that

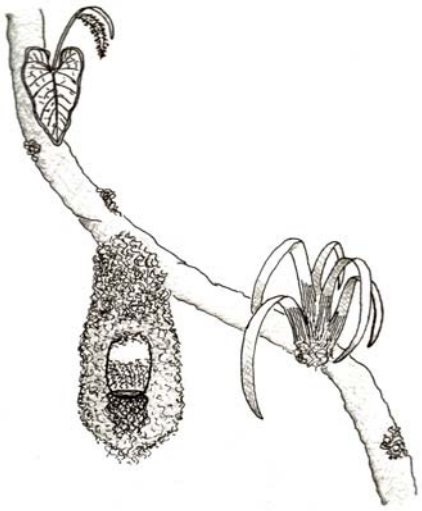

FIG. 2. A Jelski's Chat-Tyrant (*Ochthoeca jelskii*) nest *in situ*. Note that the partially domed cup, which hangs down from below a liana, is built into hanging moss to give the appearance of a pendulum with side entrance. Illustration by ETM.

occurs parapatrically with Jelski's Chat-Tyrant (Traylor 1985) lacks the rufous wing bars of the latter (Ridgely & Tudor 1994). The Crowned Chat-Tyrant also generally occurs at higher elevations than either of the other two species, found in Ecuador mostly from 2800 to 4000 m (Ridgely & Greenfield 2001). Its nest is described as an open cup placed in a cavity on a cliff, among roots projecting from a bank, in an *Espeletia* shrub, or in a bush (*fide* Farnsworth & Langham 2004).

OCHTHOECA JELSKII

Nest site and nest architecture. On 17 April 2006, we found a nest of Jelski's Chat-Tyrant in the Utuana Reserve, Important Bird Area EC079 (Birdlife International 2006), a private reserve managed by the Fundación Jocotoco in the south of Loja Province, Ecuador, near the border with Peru (79°45'W, 4°22'S). The Utuana Reserve protects a small remnant of hill-top evergreen forest at 2600 m elevation, an important transitional zone between humid montane forests and the dry Tumbesian region. The reserve shelters a number of rare and endemic species and, although little of it appears to be primary forest, much of it is intact and contains many large epiphyte-laden trees.

The nest was situated in one such intact section of the reserve. The understory in the area was dense, and the surrounding forest was composed of small, moss-covered trees draped in vines and lianas, as well as a number of thick stands of *Chusquea* bamboo. The vegetation was not notably stratified; most was contained between the forest floor to approximately 8 m above it, but a few older trees stood above this at around 20 m.

The nest had a northern exposure and faced uphill towards a stand of *Chusquea*. As such, and due to the dense nature of the vegetation, it rarely received direct sunlight. The nest was suspended in a naturally occurring sheet of moss and epiphytes, 3.5 m up along an almost vertical liana (1 cm diameter). See Figure 2 for an illustration of nest placement. Aside from the sheet of moss into which it was built, no other vegetation was immediately adjacent to the nest, giving the adults an unobstructed view to and from the nest.

The nest (Fig. 1a) was a slightly pendulous, vertically oblong (19.5 cm tall), and partially domed cup (11 cm outside diameter at base). It was formed completely of green moss and lined with small pieces of black and white lichen pressed into the moss of the nest. This thin lining extended up from the cup to approximately three quarters the height of the partial dome. The inside of the cup had a diameter of 5.5 cm, was 3.4 cm deep, and did not have a lip. The chamber height above the rim of the cup was 7 cm. Because the sides of the partial dome only wrapped around half the circumference of the cup, the inside diameter of the cup and the

chamber height also describe the size of the nest "entrance."

The nest proper was indiscernible from the surrounding moss while *in situ*. When we first located it, it appeared to be a large, mossy, pendulous structure with a side entrance. Upon removing it, however, we determined that it had been built along the liana under a large piece of pre-existing moss. The sides and base of the nest had also been decorated with hanging strands of the same moss – particularly concentrated out from and below the entrance – which created the appearance of one large clump of dangling moss. This entire pendulous structure was 44 cm tall, with a 15 cm diameter base that tapered to approximately 10 cm at the top.

Parental care and behavior. When we discovered the nest at 11:00 h, it contained two nestlings. The adults were fairly confiding and not overly disturbed by human presence. We placed a video camera in an unobtrusive location approximately 4 m from the nest to better observe behavior of the nestlings and the adults. We recorded 2 h of video (11:30–13:30) that we later digitized and archived at the Yanayacu Natural History Video, Sound, and Image Library.

The adults made 24 trips to the nest during video observation. We believe we could differentiate the adults, and that both were indeed caring for the young. One of the adults had a stronger superciliary and pink hue to the back. This adult was responsible for nine of the trips to the nest. We did not observe the more extensive buff crissum of the female reported by Ridgely & Greenfield (2001). Both adults arrived from the front of the nest and clung to the outside of the cup below the entrance, then leaned inside to deliver the food. On only one occasion did we observe an adult actually perch on the rim, this time seeming to do so to better deliver food to the harder to reach nestling.

The adults' average time away from the nest was 5.1 min (± 1 SD 3.95 min), and their average time spent at the nest was 6.5 s, (± 1 SD 3.5 s). The adults averaged 5.9 trips to the nest per nestling/h. In general, due to their small size, we could not identify the food items that were delivered. On two occasions, however, the adults delivered fairly large (c. 4 cm long) stick insects (Phasmida) that appeared to present both consumption and delivery problems. On the first occasion, the nestling struggled with the insect for a few seconds before the adult agitatedly left with it. Fourteen minutes later, the other adult attempted to feed a nestling a similar insect, but had to reposition higher along the rim before the nestling finally succeeded in consuming it. This was by far the longest adult feeding visit (20 s) and, interestingly, was the one occasion where the adult did not wait while the nestling defecated. Four defecations by the nestlings were noted, and aside from the above-mentioned event, the fecal sac was seized in midair by the adult and removed. The rate of removal by the adults was 0.7 fecal sacs per nestling/h.

Nestling appearance and behavior. The nestlings were well-developed, and we predicted that they would fledge within a day or two. Like older nestlings of other Ochthoeca species (Greeney 2007), the superciliary, including the yellow spot, was already prominent. As in the adult, the bill was dark and the wing bars rufous. Head and back were charcoal gray, with only a faint pink flush. The throat and breast were light gray, as in the adult, but the flanks were a more obvious buff color.

The proximity of the camera to the nest allowed us to differentiate between the two nestlings based on their position in the nest. Behaviors were quantified for each nestling for the 1-h period from 11:35–12:35. This period qualitatively resembled the other 1 h of video we filmed. One of the nestlings spent

30% of this hour sitting below the rim of the cup, 59% standing such that its head was above the rim of the cup, 4% with its head extended outside of the nest, 3% preening, 3% receiving food, 2% picking at objects within the nest, 1% exercising its wings while clinging to the outside of the nest, and less than 1% defecating outside the nest. The other nestling spent 50% of this time sitting below the rim of the cup, 30% standing such that its head was above the rim of the cup, 4% with its head extended outside of the nest, 12% preening, 3% receiving food, 1% picking at objects within the nest, 2% exercising its wings while clinging to the outside of the nest, and less than 1% defecating outside the nest. While exercising their wings, the nestlings actually left the cup and clung to the outside of the nest, head-up (hang-up, *sensu* Remsen & Robinson 1990), and walk-fluttered in a loop around the outside of the nest.

OCHTHOECA DIADEMA

Nest site and nest architecture. On 10 November 2002, E. C. Hannely discovered a nest of the Yellow-bellied Chat-Tyrant (Hannely & Greeney 2008) in the private birding reserve of Cabañas San Isidro next to the Yanayacu Biological Station and Center for Creative Studies (00°35.9'S, 77°53.4'W). The station is located in the Napo Province about 5 km west of Cosanga, on the eastern slope of the Ecuadorian Andes, at elevations ranging from 1950 to 2300 m.

The nest was built 1.2 m off the ground in an area of naturally disturbed forest dominated by *Chusquea scandens* bamboo (total dominated patch c. 432 m^2). The nest had a southern exposure (194°) and faced a small, fast-flowing stream 10 m away. For a complete habitat description, see Greeney *et al.* 2006.

The nest was a partially domed cup built into a vertical sheet of moss that hung from a horizontal vine. The thick cup was composed of moss and bryophytes and was sparsely lined with feathers. The dome extended upwards from the back of the nest and covered approximately one third of the cup. Because the nest was built into this hanging moss, it appeared at first to be a neat ball with a side entrance, but upon closer examination we determined that the entire dome had not been constructed by the birds. Externally, the nest was 10.3 cm tall, 6.8 cm wide, and 12.2 cm deep. The entrance was 6.6 cm tall and 3.7 cm wide. The shallow cup was 2.5 cm deep. As in Jelski's Chat-Tyrant, the width of the entrance approximates the inside diameter of the cup, which was 3.8 cm long and 3.5 cm wide.

On 29 October 2004, we discovered another nest of the same species in the Tapichalaca Biological Reserve (04°30S, 79°10W), Important Bird Area EC088 (Birdlife International 2006), located north of Valladolid in the southeastern Zamora-Chinchipe Province of Ecuador. The nest was built 1.5 m off the ground near the top of a ridge. The surrounding vegetation was copiously moss-covered and grew beneath an open canopy of wind-stunted trees 6–10 m tall. *Chusquea* bamboo dominated the landscape but did not occur near the nest.

This nest was also a partially domed cup of moss with a sparse feather lining built on a vine into hanging moss. Half of the cup of this nest was covered by the partially constructed dome. In form, the dome again appeared to completely cover the nest, but after careful examination we again concluded that the adults had built into hanging moss to create this effect. The exterior of the nest measured 15 cm tall, 9.5 cm wide, and 11.5 cm deep. Inside, the cup was 6 cm long, 4.5 cm wide, and 3.5 cm deep. The entrance hole was not measured, but extrapolating from the past two examples yields a measure of approximately 8 cm tall by 4.5 cm wide. As

FIG. 3. View into the unfinished cup of a Crowned Chat-Tyrant (*Ochthoeca frontalis*) nest. Naturally overhanging moss and ferns obscure the actual nest as built by the adults. Material brought in by the adults is distinguishable upon careful examination; note, for instance, the well-formed moss of the rim of the cup.

the nest contained two mid-aged nestlings at the time, it had begun to sag at the bottom, and the cup was tilted down at a nearly 45° angle. We do not have photos of these nests, but see Figure 2 for an illustration of similar nest placement.

OCHTHOECA FRONTALIS

Nest site and nest architecture. On 19 December 2006, we discovered a pair of Crowned Chat-Tyrants building a nest in the Cordillera de Huacamayos (77°57.00”W, 0°48.00”S) near Yanayacu Biological Station (Important Bird Area EC051, Birdlife International 2006). This series of steep, stream-carved, forested ridges lies on the eastern slope of the Ecuadorian Andes, rising out of the western Amazon Basin at elevations of 1200 to 2600 m. The area provides habitat for a number of resident and migrant species of concern (Birdlife International 2006).

The nest, shown in Figures 1b and 3, was situated a few meters away from and below a

rarely traveled trail. This trail ran close to and parallel with a ridgeline, an area subject to fog drifting up from the basin below, as well as to a large amount of precipitation. Though much of the forests in the Huacamayos are subtropical, temperate cloud forest grows on ridges such as these. A dense understory dominated by *Chusquea scandens* bamboo grows beneath a thick, epiphyte-heavy canopy approximately 20 m tall.

The nest had an eastern exposure and faced downhill. It was built into a clump of moss that dangled below a horizontal trunk extended out from the slope. The nest was 50 cm below this trunk and 1.9 m above the steep slope below. Though the view from the nest was unobstructed in the downhill direction, from upslope it was well concealed by the trunk and dense vegetation.

On the day we found the nest, both adults were present, though we did not confirm if both participated in construction. No further observations were made on this day. On 1 January 2007, we returned to examine the nest more closely. No adults were observed at the nest, and though unlined, it appeared to be structurally complete. The nest was a partially domed cup of mosses and bryophytes built into hanging moss and ferns. Externally, the nest was 14.2 cm long, 10.6 cm wide, and 10.4 cm deep. A 23 cm tail of moss dangled below that appeared to extend naturally from above the nest. The entrance was 3.7 cm tall and 5.0 cm wide. The cup was 6.6 cm outside diameter and 5.7 cm deep inside. As in previous species, the entrance width describes the inside diameter of the cup.

DISCUSSION

The three species discussed here, the Jelski's, Yellow-bellied, and Crowned chat-tyrants, belong to the *Silvicultrix* clade, a poorly studied group of flycatchers whose breeding habits are virtually unknown. The described nests of *Ochthoeca* flycatchers are open cups, either fur-lined and placed near the ground, as in the basal Brown-backed Chat-Tyrant (*O. fumicolor*, Fig. 1d), or else mossy cups placed on ledges, such as those built by the montane forest border and ravine species Rufous-breasted (*O. rufipectoralis*) and Slaty-backed chat-tyrants (*O. cinnamommeiventris*, Fig. 1c) (Hilty & Brown 1986, Greeney 2007). The nests of the final radiation of *Ochthoeca*, the *Silvicultrix* clade, were the least known. Both the Yellow-bellied and Crowned chat-tyrants have been described as open cups (Sclater & Salvin 1879, Farnsworth & Langham 2004) but, for the former at least, this description is considered suspect (Hilty & Brown 1986, Hilty 2003, Farnsworth & Langham 2004).

Here we show that members of this clade have departed from the ancestral nest form and build partially domed cups into hanging moss (Fig. 2). This lends behavioral support to the morphological and genetic distinctness of the *Silvicultrix* clade noted by Lanyon (1986) and García-Moreno *et al.* (1998), respectively. Despite seemingly conflicting nest descriptions published alongside each other (Sclater & Salvin 1879, Taczanowski 1879), it has taken almost 130 years for clarification. Phylogenetic studies, however, have been produced at regular intervals (Fitzpatrick 1973, Traylor 1985, Lanyon 1986), culminating in the molecular phylogeny published by García-Moreno *et al.* (1998). In addition, the recent results of Ohlson et al. (2008) suggest that this phylogeny may need to be further refined with wider taxon sampling.

By mapping nest architecture onto this most recent phylogeny (García-Moreno *et al.* 1998), as in Figure 1, we can make some generalizations about the nests of *Ochthoeca* flycatchers. Nests of all described species are constructed primarily of moss and bryophytes

(Hilty & Brown 1986). This outer structure generally seems to be packed hastily together, and often, as a result of the humid climates in which these Andean tyrannids are found, are water-logged and messy-looking (pers. observ.). The cup, in contrast, is lined with soft and presumably quick-drying and non-absorbent materials like lichen, as in Jelski's Chat-Tyrant, feathers, as in the Brown-backed (Hilty & Brown 1986) and the Yellow-bellied chat-tyrants, and tree fern scales, as in the Slaty-backed Chat-Tyrant (Greeney 2007). The *Silvicultrix* radiation, however, diverges with respect to nest form, building a partially domed nest. It is interesting to note that this shift in form parallels the shift in habitat undergone by the *Silvicultrix* radiation. Perhaps the nests built by the *Silvicultrix* species represent an adaptation that helped them to colonize the more vegetated forest-interior habitats. The partial dome may represent the modern outcome of selection imposed by the dense montane and submontane forest environments on what was once a phenotypically plastic trait. Indeed, nests of the páramo-dwelling Brown-backed Chat-Tyrant are seemingly variable in the extent of development of the rear portion of the cup (pers. observ.).

As mentioned above, three species of the now-known-to-be polyphyletic genus *Myiophobus* were recently discovered to be members of the *Ochthoeca* clade (Ohlson *et al.* 2008). These three species, *M. flavicans*, *M. phoenicomitra*, and *M. roraimae*, were tentatively placed as a monophyletic clade of recent divergence from the *Silvicultrix* clade (Ohlson *et al.* 2008). However, the low posterior probability for this assignment indicates that the clade's exact position within the *Ochthoeca* radiation is still undetermined (J. Fjeldså pers. comm.). Breeding data on these species is scanty, though Hilty and Brown (1986) describe the nest as a cup of twigs and small vines, lined with feathers. It would be interesting to know whether these nests are indeed open cups, especially if these three *Myiophobus* did diverge from the *Silvicultrix* clade, as that would represent a switch in nest form back to the ancestral state.

Natural history studies like this can offer an important complement to genetic work. For example, using mtDNA, García-Moreno *et al.* (1998) were able to offer a coherent explanation for the adaptive radiation by the *Ochthoeca* flycatchers to the newly formed environments created by the uplift of the Andes. Such speciation in the Andes is an often discussed but rarely tested idea (though see Patton & Smith 1992, Arctander & Fjeldså 1994, Willmott *et al.* 2001). The speciation pattern offered by García-Moreno *et al.* (1998) seems to us more complete than those based solely on morphological data (Fitzpatrick 1973, Traylor 1985, Lanyon 1986), but would be well-complemented by a comparative analysis of nest construction within the group. Such a study might help to explain the evolution of new behaviors in a rapidly speciating clade of birds.

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