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# TREE-CAVITY NESTING IN BUFF-WINGED CINCLODES (*CINCLODES FUSCUS*) POPULATIONS FROM NORTHWESTERN ARGENTINE PATAGONIA

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**ABSTRACT** *Cinclodes* ovenbirds (Furnariidae) inhabit open habitats of South America, usually near water. The Buff-winged Cinclodes (*C. fuscus*) was recently recognized as a separate species, and data on its natural history are scarce. This species breeds in Patagonia and winters further north in Argentina and adjacent countries, although some populations in Chile breed in the Andes and winter on the Pacific coast. The few nests that have been described were placed in holes on cliffs, bridges, and road cuts in open Patagonian landscapes. Based on these data, the species is considered a typical representative of the genus (i.e., open habitat, ground-nesting ovenbird), and potential associations with forests have not been documented. Here I report on the breeding habits of *C. fuscus* in native forests of northwestern Argentine Patagonia, where these birds are regular summer residents. On the course of a long-term (1998–2016) research on the cavity-nesting birds of north Patagonian forests, I found 51 nests in 26 nesting cavities located in large lenga (*Nothofagus pumilio*) trees. Most nesting cavities were reutilized in different years. No nests were found in other substrates. This is the first time that consistent tree hole-nesting is documented for any species of *Cinclodes*. Future studies should determine whether differences in nesting behavior (ground nesting vs. tree-hole nesting) are explained by behavioral plasticity or represent patterns of genetic differentiation between forest and steppe *C. fuscus* populations.

**RESUMEN · Nidificación en huecos de árboles por la Remolinera Común (*Cinclodes fuscus*) en el noroeste de la Patagonia Argentina**
Las especies del género *Cinclodes* (Furnariidae) son habitantes terrestres de campos abiertos de Sudamérica, generalmente cerca del agua. La Remolinera Común (*C. fuscus*) se reproduce en Patagonia y pasa el invierno más al norte en Argentina y países limítrofes, mientras que algunas poblaciones chilenas se reproducen en los Andes y en invierno descienden a la costa del Pacífico (migradores altitudinales). *Cinclodes fuscus* ha sido definida como especie separada de otras remolineras recientemente, y los datos sobre su historia natural son escasos. Los pocos nidos documentados se encontraban en oquedades a baja altura en acantilados, puentes y barrancos, en ambientes abiertos de Patagonia. En base a estos datos, la especie es considerada como una fiel representante del género (especie que nidifica a baja altura en áreas abiertas) y posibles asociaciones con ambientes de bosque han sido ignoradas. Aquí describo los hábitos de nidificación de *C. fuscus* en bosques del noroeste Patagónico (Argentina), donde la especie es residente estival. Durante un estudio de largo plazo (1998–2016) de las aves que nidifican en huecos de árboles en bosques de Patagonia norte localicé 51 nidos en 26 cavidades de grandes árboles de lenga (*Nothofagus pumilio*). La mayoría de las cavidades fue reutilizada en diferentes años. Ningún nido fue encontrado en sustratos de otro tipo. Esta es la primera documentación de nidificación generalizada en cavidades arbóreas de *Cinclodes*. Futuros estudios deberían determinar si las diferencias en hábitos reproductivos entre poblaciones de esta especie se explican sólo por una plasticidad comportamental, o representan patrones de diferenciación genética entre poblaciones de *C. fuscus* de bosque y de estepa.

**KEY WORDS** Breeding behavior · Cavity-nesting · Forest · Furnariidae · *Nothofagus* · Ovenbird · Patagonia

## INTRODUCTION

In the last decades, the phylogenetic tree of the Furnariidae (ovenbirds, treecreepers, and allies) has been under intense scrutiny, and the high levels of morphological and behavioral variation in this large Neotropical family have been reinterpreted in view of new data (e.g., Fjeldså et al. 2005, Irestedt et al. 2006, Chesser et al. 2007, Moyle et al. 2009, Derryberry et al. 2011). In parallel to the growing knowledge about the family's biology and ecology, new studies have revisited the phylogenetic relationships within the genus *Cinclodes* (Chesser 2004, Sanin et al. 2009, Rader et al. 2015, Freitas et al. 2012). Its members are dull colored terrestrial inhabitants of open grasslands in South America. While *Cinclodes* members are typically found near freshwater sources, some species inhabit coastal habitats and feed on marine resources, which is possible due notable adjustments in osmoregulatory function to excrete salt (Sabat et al. 2006).

Among the recent taxonomic changes within the genus, the nominate race of the Bar-winged Cinclodes (*C. fuscus fuscus*) was proposed as a distinct biological species: the Buff-winged Cinclodes (*C. fuscus*), since the different subspecies hitherto included in *C. fuscus* do not constitute a monophyletic clade (Sanín et al. 2009). *Cinclodes fuscus* has a South American Cool Temperate Migration System (Joseph 1997), breeding in Patagonia (southern Argentina and Chile) and wintering in central and northeastern Argentina, reaching southeastern Brazil and Paraguay (Figure 1, Ridgely & Tudor 1994). However, this species is also a year-round resident in wetlands of Central Chile (e.g., Simeone et al. 2008), and an altitudinal (west-east) migrant in and around central Chile (Housse 1945, Johnson 1967, Sabat et al. 2006, Newsome et al. 2015). In the Cape Horn Biosphere Reserve (southernmost South America), this species overwinters by performing local migrations, moving to more protected environments (low altitude evergreen forests), where it has been observed in search of invertebrates in pools and wet areas under the canopy, even in the midst of the winter snow (Rozzi & Jiménez 2013). In the southern part of its distribution (i.e., Magellanic and Tierra del Fuego regions), *C. fuscus* breeds both inland and on the coast (Humphrey et al. 1970, see reference 1 in Figure 1). It also breeds on several locations near rivers along the Atlantic coast (Zapata 1967, Albrieu et al. 2004), as far north as the mouth of the Negro river, where some individuals may be year-round residents (Llanos et al. 2011). Breeding inland in the arid Patagonian steppe has not been documented, and its residence there is questionable (see Bettinelli & Chébez 1986, Lambertucci et al. 2009, Llanos *et al.* 2011, and especially Pruscini et al. 2014).

Patterns of habitat use and reproduction of *C. fuscus* are not well known. Because of its previous sub-specific status, much of the nesting data in the literature belong to other subspecies distributed farther north along the Andes. Few nests have been described for Patagonia or central Chile that can be assigned to *C. fuscus* (e.g., four nests in Narosky et al. 1983, with only one described in detail; a few nests compiled by Humphrey et al. 1970 for Tierra del Fuego; a few others mentioned by Johnson 1967 for Chile). Most described nests were in open Patagonian landscapes (sometimes close to human settlements), and consisted of holes or crevices in bridges, roofs, cliffs, road cuts, and ground burrows (Johnson 1967, Humphrey et al. 1970, Narosky et al. 1983, Christie et al. 2004), with a single mention to "hollows in logs" (without further details, Housse 1945). Adding to the low number of reported nests, most first-hand descriptions only contained general information (substrate and habitat type), with no reference to nest dimensions or other attributes.

Although *C. fuscus* has been recorded (always at low densities) in association with open woodlands in Argentina (e.g., Humphrey et al. 1970, Vuilleumier 1985, Christie et al. 2004, Becerra Serial & Grigera 2005, Imberti 2006) and, to a lesser extent, in Chile (e.g., Estades 1997), most bibliographic sources (e.g., Canevari et al. 1991, Couvé & Vidal 2003, Martínez & Gonzalez 2004) describe this species as an inhabitant of open environments such as rocky terrain, grassland, hillsides, shrubbery, and steppe, usually close to water. Based on these data, *C. fuscus* is considered a typical representative of the genus, i.e., an open habitat, ground-nesting furnarid (Collias 1997, Zyskowski & Prum 1999).

At the onset of a long-term (1998–2016) research on the cavity-nesting birds of north Patagonian forests, *C. fuscus* emerged as an unexpected member of such breeding bird community. Here I provide information on the breeding habits of *C. fuscus* in forests of NW Argentine Patagonia, mostly based on the study on cavity-nesting birds at the Challhuaco Valley, near the city of Bariloche. I describe the trees and tree-cavities that were used as exclusive nesting substrates by the Challhuaco population, providing the first evidence of consistent (i.e., widespread and stable in time) tree-cavity nesting in any species of *Cinclodes*.

## METHODS

**Study area.** The study area corresponds to the Andean portion of northern Patagonia, in Argentina. Because of the rain shadow effect of the Andes (> 2000 m a.s.l.) on the westerly winds, mean annual precipitation declines from ca. 3000 mm at the continental divide to less than 500 mm only 70–80 km to the east in the steppe. The climate of northwestern Argentine Patagonia is characterized by a long winter period of precipitation (rain and snow) and dry summers (December–March), with mean annual temperature around 8°C (Paruelo et al. 1998). The strong west-to-east decline in precipitation is paralleled by a vegetation gradient, from humid to dry forests to steppe. Region wide, *Nothofagus* (Nothofagaceae)
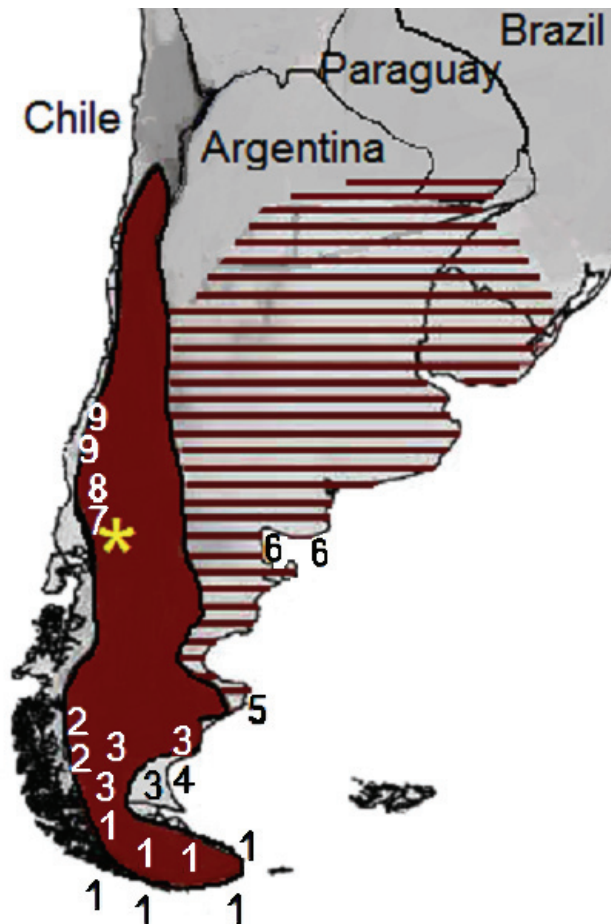
**Figure 1.** Distribution and known breeding locations of *C. fuscus*, modified from Sanin et al. 2009. The lined area represents the winter range of the south-north migratory populations; dark area represents presumed breeding range. The asterisk shows the location of the present study, and numbers correspond to the approximate location of breeding sites from bibliographical sources or personal communications, from south to north: 1) Reynolds (1935)/Crawshay (1907)/Humphrey et al. (1970) (these sources name several localities in Tierra del Fuego, Chile and Argentina, sometimes mutually citing each other); 2) Imberti (2006) (Los Glaciares National Park, W Santa Cruz province, Argentina); 3) S Imberti pers. comm. (much of continental southern Santa Cruz province, close to rivers); 4) Albrieu et al. (2004) (Rio Gallegos Estuary, coastal Santa Cruz, Argentina), 5) Zapata (1967) (Puerto Deseado, coastal Santa Cruz, Argentina); 6) Llanos et al. (2011) (two localities at the coast in Río Negro province, Argentina); 7) Christie et al. (2004) (Lanín and Nahuel Huapi National Parks, Andean Río Negro and Neuquén provinces, Argentina); 8) JM Girini pers. comm. (Lanín National Park, Andean Neuquén province, Argentina); and 9) Goodall et al. (1957) (various localities in and around central Chile). Numbers that were placed over the sea indicate coastal nesting sites (river mouths). When more than two sources were available for the same locality, only one was depicted, to avoid overplotting. Nests described by Housse (1945) and Johnson (1967), both in Chile, lack specific geographic references and are not depicted in the map.

trees dominate the forests, with lowland stands of the evergreen coihue (*N. dombeyi*), and pure stands of the deciduous lenga (*N. pumilio*) on slopes above 900 m a.s.l.

Breeding *C. fuscus* were mainly studied at the Challhuaco Valley (41°15′30′′S, 71°17′50′′W), 15 km south of Bariloche city (Figure 2) during the course of a long-term (1998–2016) study on cavity-nesting birds. Challhuaco is a rugged mountainous area with slopes covered by pure old-growth lenga forest that occupies approximately 2400 ha (tree line at ca. 1650 m a.s.l.), and is contiguous with native forests from adjacent valleys. These forests are located near the xeric limit of the lenga distribution (confined by the Patagonian steppe in the east), so the understory is open, dominated by a few shrubs and herbaceous species. Snow covers the valley from late autumn (June) through mid-spring (October).

Other lenga forests where I opportunistically studied nests of *C. fuscus* were: Cerro Volcánico (41°15'27.14"S, 71°49'16.10"W, 1491 m a.s.l.), Paso Puyehue (40°43'33.54"S, 71°55'40.80"O, 1175 m a.s.l.), trail to Laguna Negra (41° 8'32.76"S, 71°33'43.02"W, 1158 m a.s.l.), and Cerro Goye (41°7'43.23"S, 71°30'36.02"W, 1445 m a.s.l.) (Figure 2). These sites are included within a square of about 60 x 60 km (40°43′–41°16′S and 71°16′–71°56′W), and are located inside Nahuel Huapi National Park.

**Figure 2.** Map showing locations of forest breeding sites for *C. fuscus* (red baloons) that were found in this study. As shown by the change in background coloration (from green to sand), the main study site (Challhuaco) lays at the transition between forests and the Patagonian arid steppe. Google Earth™ desktop 7.1.5.1557 free version was used.

**Data collection.** Every reproductive season during the years 1998–2016, I surveyed the valley core area (ca. 1200 ha) for active nests of several cavity-nesting species. Challhuaco Valley was visited for nest searches between early September and late January each year, 2 days/week, on average. A network of trekking trails was used to access the different parts of the valley, and off-trail searches were conducted *ad-libitum* in appropriate areas. Sampling effort for sites outside Challhuaco cannot be quantified because nests were located while conducting other unrelated activities.

The nests of *C. fuscus* were located by monitoring the movements of birds around waterlogged soils, marshes, streams and lagoons within the forest, where these birds frequently (although not exclusively) search for food. Location and elevation of the nests were recorded using a handheld GPS (Garmin eTtrex Legend, and GPSMAP 60CSx), which were used to re-locate nests later on. When an active nest was discovered, I estimated nest development stage from the behavior of the adults. I observed the nest entrance until witnessing the pair carrying nest material, food or fecal sacs, or taking turns at incubation (as in Supplementary Material). In addition, about one quarter of the active nests in Challhuaco were

also checked for contents with the aid of a mirror and flashlight. These were (1) nests below 2 m that could be accessed without the need for tree climbing or (2) nests below 5 m and close enough to vehicle roads as to carry a ladder. Sometimes, the nature of the cavity entrance prevented direct observation of nest contents although it was possible to hear the nestlings. In order to assess nest contents as quick as possible (max. 5 min) to avoid disturbing the adults, climbing appareil and operations were not used, so active nests placed 2–5 m high that were located far from vehicle roads, and all active nests placed over 5 m high, were not inspected.

I recorded for all cavities: entrance orientation (assigned to the main cardinal points) and shape (round, etc.), origin (woodpecker or decay), height above ground, and location on tree (fork, trunk, branch). For the shape of the entrances, three categories were defined: round to oval (corresponding to cavities left by fallen branches), oval to droplet-like as typical for holes excavated by Magellanic Woodpeckers (*Campephilus magellanicus*), and fissure (vertical cracks of bark and wood). For all nest trees, I recorded: condition (% of live crown), height, and diameter at breast height (DBH). While the above characterization was conducted for all cavities and

nest trees, more detailed descriptions of the cavities (i.e., entrance and chamber dimensions) were performed in Challhuaco for nests that were safely accessible. I accessed these cavities when they were no longer active using ladders or by climbing the trees by secured free climb (static rope and climbing equipment).

An electronic clinometer was used to measure heights, a global compass for orientation, and metric tape for all other dimensions. I report the range and means ± SE for quantitative variables.

## RESULTS

**Breeding season**. *Cinclodes fuscus* was recorded at the Challhuaco forest during all breeding seasons (1998–2016), arriving between late September and early October (Figures 3A and 3B), and leaving the area between late March and early April. Patterns of presence-absence opportunistically recorded at other forests in Nahuel Huapi National Park, were in agreement with those of Challhuaco.

**Territorial behavior.** Soon after arrival, individuals of *C. fuscus* engaged in territorial displays (long trill while fluttering wings, as described by Crawshay 1907) performed at exposed locations like ledges on standing trees, the top of snow drifts, or in the middle of frozen ponds. Pair formation occurred soon after courtship (November), usually with both pair members seen arriving at nest sites carrying nest materials.

**Nest sites.** Altogether 26 *C. fuscus* nest-sites were located, all in cavities in very large trees (Table 1). Most (24) trees containing cavities were alive, and two were dead (one of them was a fallen log). Twenty-one nest-sites were located in Challhuaco Valley while five others were opportunistically found elsewhere in Nahuel Huapi National Park. Two of the latter were located during the 2012–2013 season at Cerro Goye, one nest was found at Cerro Volcánico, one at Paso Puyehue, and the last one on the trail to Laguna Negra, during the 2015–2016 breeding season. These other nest sites were located in woodlands similar in structure and composition to those in Challhuaco (i.e., middle-age to mature continuous lenga forests), except for Cerro Volcánico, where the forest was discontinuous and the nest was located in one of several low (< 15 m in height) forest patches at the treeline surrounded by a matrix of high-Andean steppes and wetland meadows (locally named "mallin"). The lenga forest in Laguna Negra was peculiar for containing some bamboo thickets (*Chusquea* sp., Poaceae) along with the same shrubs and herbaceous species found at the other nest-sites.

The nest-sites in Challhuaco (n = 21) were inside the forest (always > 100 m from forest edges) and dispersed across the valley (see Figures 3C and 3D for typical forest at the Challhuaco breeding site). The closest breeding neighbors recorded were 45 m apart

in the surroundings of a permanent lagoon, but most other nests were located > 300 m apart. The average distance to the closest wetland (snowmelt stream, pond, lagoon, etc.) was 28.8 ± 5.2 m (range: 2–78, n = 25), with the exception of one nest located > 100 m away (excluded from the average). The altitude of nesting sites ranged between 1158–1543 m a.s.l. (1389.6 ± 22.3).

**Nest attributes.** All nests (n = 26) were found in cavities due to natural decay, with one exception, located inside a cavity excavated by the Magellanic Woodpecker. This single case of a woodpecker hole use was a very old and incomplete excavation (no vertical chamber) that had been widened by decay. This cavity was only used by a pair of *C. fuscus* for one season (2001, successfully).

Six of the Challhuaco cavities, and all nests outside Challhuaco, were not accessed (i.e., could not be examined closely) for safety or logistic reasons. For the rest (n = 15), entrances varied in shape (round, oval or fissure) and size (5–40 cm high), but all contained a narrow (< 7 cm wide) tunnel leading to the breeding chamber, formed by the entrance itself or by additional woody structures located inside (Figure 4A). Thus, irrespective of entrance shape and size, all nests chambers (which were horizontal inner expansions, Figures 4A–F), could only be accessed through narrow, sometimes (n = 5) tortuous, passages. The average horizontal depth of nest cavities (the distance from the entrance to the rear wall of the chamber) was 29.5 ± 1.7 cm (21–42 cm, n = 11; four cavities could not be measured). The nest cups observed (n = 10) were rudimentary, and made of loose grass or roots. Additional attributes of nesting holes and trees are shown in Table 1.

**Nest reutilization.** Of the 18 nesting cavities in Challhuaco that were visited repeatedly after being found, 72.2% were reutilized (some across multiple seasons), totalizing 46 breeding events. The five active nests detected elsewhere (not yet visited for a second time) complete the total 51 breeding events recorded for the species.

**Timing of reproduction.** Based on the 46 events recorded at Challhuaco, incubation occurred during November (exceptionally, in early December), and chick-rearing and fledging took place in late November or during December (exceptionally, as late as early January). A pair was once recorded carrying nest material in January, but their nest was deserted shortly after. The dates recorded for the last breeding season (2015–2016) were later than those shown above, due to a notorious delay in the arrival dates of migratory species (including *C. fuscus)* in northwestern Patagonia, possibly due to climatic alterations caused by El Niño Southern Oscillation (ENSO). During this last breeding season, incubation mostly took place during December (observed in 16 nests), and chick rearing extended to early and mid January
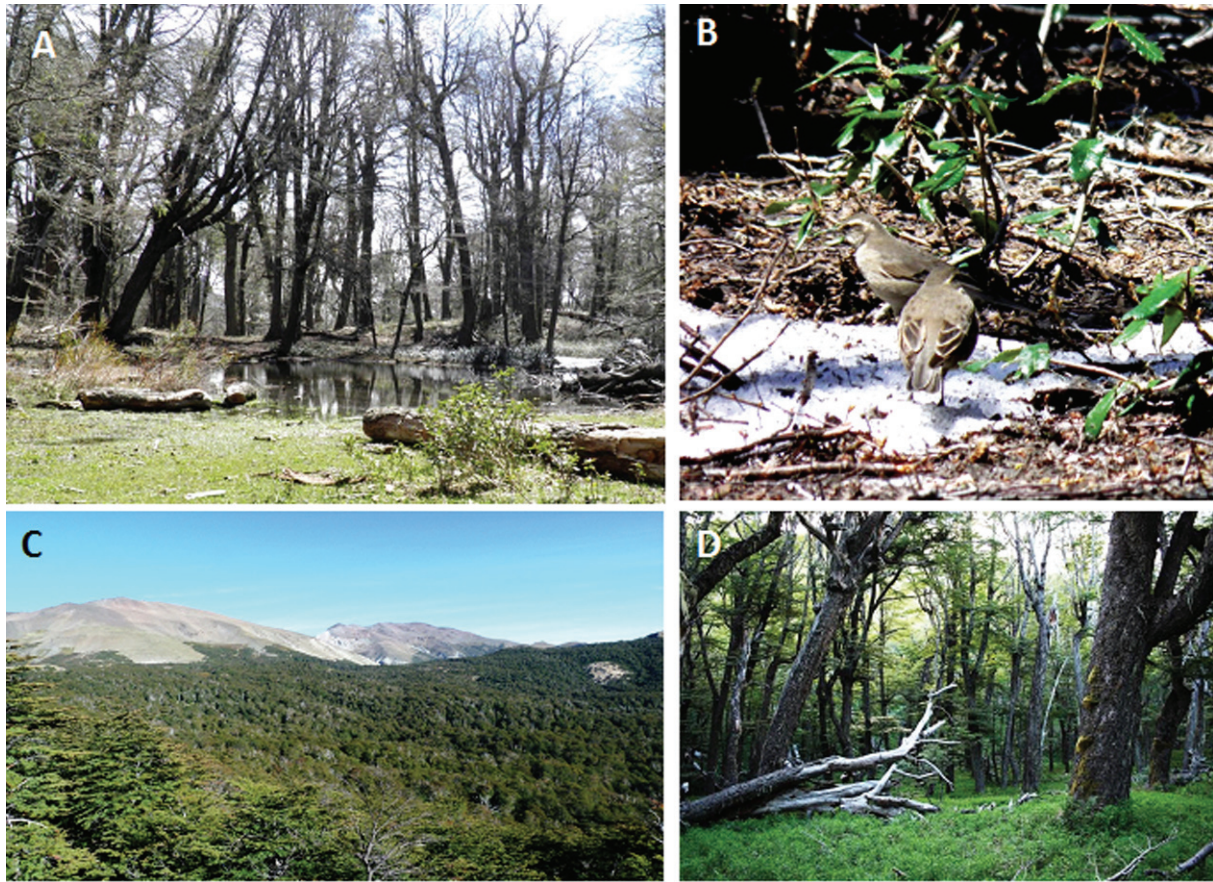
**Figure 3.** Breeding habitat of *C. fuscus* in the old-growth lenga (*Nothofagus pumilio*) forests of Challhuaco Valley, northwestern Argentine Patagonia. A) Appearance of the Challhuaco forest (around a temporary pond) in early October (spring), when *C. fuscus* arrive from migration (no leaves on the trees, no herbaceous understory, some snow still covering ground). B) A *C. fuscus* pair foraging on the forest floor among snow patches in mid spring. C) Challhuaco landscape (valley core area, ca. 1200 ha) in January (summer). D) Summer appearance of the forest; note the old-growth tree structure and very open understory. Photos: A, B, and C, by the author; D by M Lammertink.

(observed in 19 nests, including three nest-sites located for the first time).

**Breeding parameters.** Clutch size was observed for 13 nesting events (at 8 different cavities), with 2 eggs (n = 4), 3 eggs (n = 8), and 4 eggs (n = 1), respectively. However, given that these nests were not monitored in detail, some of these clutches may not have been complete, so this information should be treated with caution.

Nestlings (2, at 7 nests; 3, at 5 nests) in different developmental stages were observed (12 times) or heard (23 times) in different seasons at the most accessible nests. Nestling calls were detectable once a nest was already known, but were of little aid at locating the nests since their calls (whistles) were very soft.

**Parental behavior.** When the adults detected the presence of an observer, they became alarmed and uttered a long series of alarm calls away from the nest (without revealing nest location). Alarm calling could last for long (up to 10 minutes), with the par-

ents remaining in the surroundings of the nest, but not entering the nest to incubate or feed (even though in some cases they carried food in their beaks). In those cases I often abandoned the site soon to reduce disturbance.

**Fledging and pre-migratory behavior.** Fledging was not observed at any nest, but small groups of presumably related *C. fuscus* were observed from January onwards within some of the territories. These groups became larger later, at the onset of migration time (4–10 individuals by April).

**Confirmed nest failures.** Although I did not monitor nests success in a systematic manner, I confirmed the failure of four of the five nests that were located closest to the ground (0, 0.2, 0.8, and 1.4 m high, respectively) in Challhuaco. Moreover, three of the unsuccessful cavities were not reutilized by the birds in subsequent years, as most nests reutilized in several seasons were placed > 2 m high. The fourth unsuccessful cavity was located last season, so reutilization could not yet be checked.

**Table 1.** Attributes of Buff-winged Cinclodes *(Cinclodes fuscus)* nesting cavities and trees in forests of Nahuel Huapi National Park, in northwestern Patagonia (Rio Negro and Neuquén provinces, Argentina). [1] Tree height and crown condition could not be recorded for a broken trunk (snag), and for a fallen log. [2] Impossibility to measure a nest on a fallen log whose entrance looked upwards (see text for details). [3] Old, incomplete cavity of Magellanic Woodpecker (*Campephilus magellanicus*).

| | NESTS (all breeding sites) | |
|---|---|---|
| | Mean ± SE or number of cases | Range (*N*) |
| Tree height (m) | 16.2 ± 0.5 | 11–20 (24[1]) |
| Tree DBH (cm) | 89.4 ± 5.6 | 48–158 (26) |
| Tree condition (% of live crown) | 62.2 ± 2.7 | 40–80 (24[1]) |
| Height of nest above ground (m) | 4.7 ± 0.6 | 0–9 (26) |
| Entrance orientation | E = 5 | |
| | S = 3 | (25[2]) |
| | W = 7 | |
| | N = 10 | |
| Nest location on tree | Trunk = 16 | |
| | Branch stub or scar = 4 | (26) |
| | Roots = 2 | |
| | Fork = 4 | |
| Entrance shape and cavity origin | Round-fallen or broken branch = 18 | |
| | Fissure-broken tree = 7 | (26) |
| | Oval-woodpecker = 1[3] | |

In one case, the failure was due to flooding of the cavity after strong rain. This nest had been built among the roots of a large hollow lenga tree, and the entrance was not completely vertical (somewhat exposed to weather, Figure 4 E). I found three drowned nestlings about a week old, and the parents were not seen. The other two low nests were deserted for unknown reasons; one of them was also among roots (at ground level). I observed the pair carrying food and heard small nestlings in late November 2006; four days later, the nest was empty, probably depredated. The third failed nest was at breast height, in a large hollow knot of a standing tree beside a tourist trail with much trekking activity. I witnessed nest conditioning behavior during three days in early November 2009, but the nest was deserted afterwards. The fourth failed nest was located in early December 2015, when two birds were seen carrying material to a cavity on the top side of a large fallen tree (Figures 4D and 5B). The cavity itself was horizontal, but the entrance was pointing upwards. This was the only *C. fuscus* nest in such conditions (both substrate and exposition). The pair was found incubating a few days later (mid-December), and 3 eggs were seen at the end of a tunnel-like cavity. The nest was deserted a week after incubation was noticed and the nest cup was empty. A pair (most likely the same individuals) was seen in the vicinity. The fifth nest located low at the base of a tree (Figures 4F and 5A) was presumably successful, as it was re-used later.

## DISCUSSION

*Cinclodes fuscus* is a regular summer resident in the forests surveyed, breeding repeatedly in tree cavities, not necessarily close to water. The consistent tree hole-nesting observed is novel for the species and the genus. Moreover, the data from Challhuaco (72% cavity reutilization) suggest a high nest-site fidelity in this migratory species; although birds in this study were not marked, it seems unlikely that unrelated individuals will use a particular cavity year after year, just by chance. While not previously reported for any species of *Cinclodes*, the use of tree cavities has been suggested as the ancestral nesting condition in the family Furnariidae (Irestedt et al. 2006), and close relatives like the woodcreepers often use cavities low in the trees (Marantz et al. 2003). Nevertheless more information about nest architecture in poorly known genera is needed to get a full understanding of the evolution of nesting strategies in ovenbirds (Irestedt et al. 2006) as well as on the adaptive significance within *Cinclodes*. Among the Furnariidae, *Cinclodes* is one of the least known groups in terms of breeding biology (see Collias 1997, Zyskowski & Prum 1999, Irestedt et al. 2006).

*Cinclodes fuscus* has not been considered in general a tree-cavity breeding species nor a part of forest bird communities (see Altamirano et al. 2012 for recent review), with few exceptions (e.g., Becerra Serial & Grigera 2005, Imberti 2006). I found these birds breeding at low densities in the Challhuaco forest and other forest areas surveyed in Nahuel Huapi
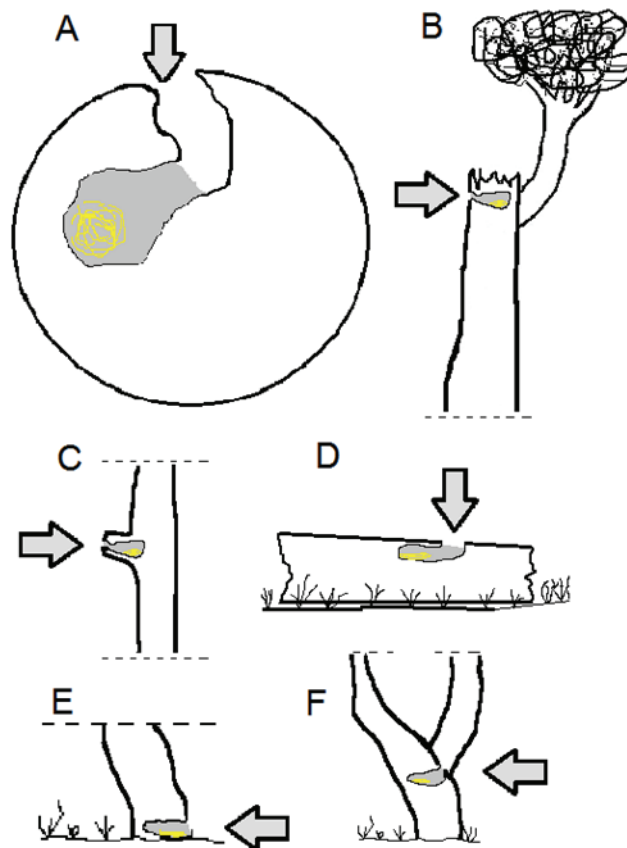
**Figure 4**. Schematic outlines of different *C. fuscus* nests recorded in lenga (*Nothofagus pumilio*) trees in northwestern Patagonia, Argentina. The main direction used by the adults to enter and leave the nest is represented by an arrow. Nest cup position is shown in yellow. A) Transversal cut of a tree at the height of a nest, showing the typical tunnel-like entrance leading to a lateral breeding chamber containing the nest cup. B) Nest with lateral entrance placed > 2 m high in a hollowed portion of the main trunk. C) Nest with lateral entrance placed > 2 m high in a rotten branch stub. D) Nest close to ground, with upper entrance, in a fallen log. E) Nest placed very close to ground, with lateral (or almost lateral) entrance, among roots. F) Nest placed in the trunk between 1–2 m high from ground, with lateral entrance. Locations B and C were the most commonly recorded in this study (about two thirds of all nests).

National Park. The nests that I located were rarely close together, possibly enforced through territorial behavior, since displays and aggressive chases between individuals are often witnessed shortly after the arrival from migration (pers. obs.). Although represented in small numbers, *C. fuscus* has been also recorded in the structurally reduced Magellanic subpolar forests (47°S southwards) (e.g., Humphrey et al. 1970, Clark 1986, Imberti 2006, Rozzi & Jiménez 2013), and in areas of open forests and scrub in northern Patagonia (e.g., Vuilleumier 1985, Estades 1997, Becerra Serial & Grigera 2005). However, it has not been recorded in the structurally diverse lowland forests of Chile (e.g., Willson et al. 1994, Sieving et al. 1996, Díaz et al. 2005) nor in humid lowland forests on the eastern slope of the Andes in Argentina (Ralph 1985, Vuilleumier 1985, Paritsis & Aizen 2008). Based on data collected during my study, the forest habitat used by this species can be described as open deciduous *Nothofagus* forest and scrub. Such habitat is found along the ecotone between forest and steppe (typical "transition forests" on the Andean slope of

Argentina), in the alpine (high altitude) forests shared between Chile and Argentina, and in the subpolar (high latitude) forests typical of southernmost Patagonia (both countries). Although this species was also recorded in the mixed-species matorral of north-central Chile, its breeding status there is uncertain (e.g., Díaz et al. 2002 only mention the species without referring to abundance or habitat, and Reid et al. 2002 did not record the species). The association of *C. fuscus* with open forests reminds of the exclusive use of *Polylepis* woodland and montane scrub by the endangered Royal Cinclodes (*C. aricomae*) (Remsen 2003). However, the latter species is not known to nest in tree holes, instead it nests in cliff cavities or between large rocks near the ground (Ávalos & Gómez 2014).

Among the Austral (i.e., Patagonian) *Cinclodes* species, *C. fuscus* is apparently least dependent from wetlands (Humphrey et al. 1970, Clark 1986, Kovacs et al. 2005, this study). The use of forests as breeding habitat recorded for the studied populations (Challhuaco and other sites) is seemingly also unique

**Figure 5.** Photographs of *C. fuscus* nests in natural cavities of lenga (*Nothofagus pumilio*) trees in northwestern Patagonia, Argentina. A) A successful nest with entrance located in a stem < 2 m high (white arrow), reutilized across multiple seasons. B) A nest in a fallen log (*cf.* Figure 4D), with a Swiss Army knife as reference. C) A pair at the entrance of a nest in a very large standing tree during an incubation switch. Photos by the author.

among the Austral congeners (this study). The three species of *Cinclodes* that are sympatric in my study area do not share the same habitats. Dark-bellied (*C. patagonicus*) and Gray-flanked Cinclodes (*C. oustaleti*) were never recorded in the Challhuaco forest (pers. obs.). *Cinclodes patagonicus* was observed sporadically along the main (permanent) stream in the Challhuaco mid valley (3 km downstream from the forest edge), and *C. oustaleti* was rarely recorded in the broader study area (nearest observations > 20 km away from the Challhuaco site). I recorded *C. patago-*

*nicus* and *C. fuscus* much closer together (i.e., at the same sites, although in different habitats) at Puyehue and Laguna Negra forests. At both sites, permanent streams flow across the lenga forests, which may allow *C. patagonicus* to inhabit forested stream sides. These two species were also recorded together in other forested portions of north Andean Patagonia, for example in Lanín National Park, wherever their respective habitats overlap (JM Girini pers. comm.). In summary, while in my study area *C. fuscus* occupies forested mountain slopes between 900 m a.s.l.

and the treeline with relative independence of water, *C. oustaleti* occurs around streams in open grassy and rocky foothills (usually above the treeline), and *C. patagonicus* is mainly observed along the shores of permanent water bodies at lower altitudes (Gelain et al. 2003, Christie et al. 2004, this study). Thus, these three species are "sympatric but not syntopic" (Rader et al. 2015), as observed for *Cinclodes* species in coastal Chile. These seemingly subtle differences in habitat use between sympatric species of *Cinclodes* may hint at the possible role of ecological specialization in the rapid adaptive divergence that has characterized the southern members of the genus. According to Sabat et al. (2006) the genus *Cinclodes* may constitute an example of a rapid adaptive radiation with low levels of genetic diversification (see Chesser 2004). Further research on other *Cinclodes* species focusing on a wider array of traits (migration and breeding ecology) may shed light on this process.

Identifying conditions that favor forest breeding in *C. fuscus* is important for both habitat management and to better understand the life history of this little-known species. Almost all nests were in cavities caused by natural decay in live trees that were much larger than average, presumably among the oldest in the Challhuaco forest. The nests that I located at other forest sites were also in very large live lenga trees. The fact that *C. fuscus* hardly ever used woodpecker cavities for nesting is probably due to their need for horizontal cavities, different from the largely vertical woodpecker cavities. This implies a dependence on natural decay processes for the generation of suitable nesting cavities. It seems that horizontal cavities are required as breeding sites in this species (as well as in other congeners) with independence of substrate type, since most described nests were in horizontal burrows of variable length (e.g., Zapata 1967, Narosky et al. 1983). Based on the nests that I located in forests of north Andean Patagonia, old-growth forests with little understory are likely the best woodlands in Patagonia to sustain breeding populations of *C. fuscus*, since these forests may provide large horizontal natural tree cavities for breeding, along with the openness required to forage on the ground, a habit common to most *Cinclodes* species. Given that old trees and their cavities are a keystone resource undergoing major declines worldwide (Lindenmayer et al. 2013), the association between *C. fuscus* and these substrates should be investigated in more depth throughout its breeding range.

My data together with published information reveal high levels of intra-specific variation in several life history traits in *C. fuscus*. Breeding habitats are strikingly diverse: from most non-forested, open landscapes in Patagonia to the forests reported here. Similarly, the migratory system is variable. Patagonian populations seemingly exhibit a normal latitudinal migration system ('Austral migrant'), while in the central valley of Chile *C. fuscus* also behaves as an altitudinal seasonal migrant between lowlands and hillsides (Johnson 1967, Sabat et al. 2006). Such levels

of intra-specific variability in major aspects of life history suggest a potentially polytypic species. In this regard, the widespread (and exclusive) hole-nesting in large trees for the Challhuaco population is difficult to explain solely based on behavioral plasticity. Instead, genetically isolated, forest-dwelling populations of *C. fuscus* would be plausible and in line with recent findings for earthcreepers of the *Upucerthia dumetatia-saturatior* complex, both pertaining to the sister group of *Cinclodes* (Chesser et al. 2007). Here, forest-dwelling populations of the Scale-throated Earthcreeper (*U. dumetaria*) were recently split as a separate species, the Patagonian Forest Earthcreeper (*U. saturatior*) (Areta & Pearman 2009).

Both possibilities, a high degree of intra-specific adaptability to live in and breed under variable habitat conditions, and the potential for more than one taxon existing within *C. fuscus*, constitute promising research lines in the light of the data presented here. While the diversification of the genus *Cinclodes* continues to attract attention, the natural history for many species in this group remains little explored. I hope that the present documentation of the singular forest-nesting habits of some *C. fuscus* populations will prompt more studies on basic life history aspects in these furnarids, especially on those that may lead to incompatibilities in social signals and ecology as primary ingredients of reproductive isolation in birds (Gill 2014).

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