# Breeding biology of Long-tailed Cinclodes *Cinclodes pabsti* Sick, 1969 (Passeriformes: Furnariidae)

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**Abstract.** *Cinclodes pabsti* is an endemic passerine restricted to the highland areas in southern Brazil. The aim of this study was to provide information on its breeding biology. The nesting cavities along road cuts were monitored from May 2008 to March 2011. The survey was carried out monthly from May to July 2008, February to July 2009, 2010 (non-breeding season), weekly from August 2008 to January 2009, 2010 (breeding season), and on a 2 to 4-days basis from August 2010 to January 2011. The geographic location, physical characteristics, and soil/substrate type in which the nesting cavities were situated were recorded. The total number of cavities used in the three breeding seasons was 136, resulting in 295 nests. The distance of a nest to its nearest neighbor ranged from 24-2,368 m, with a higher number of nests (n = 34; 59.7%) in the distance interval of 24-500 m. There was a greater usage of cavities located in Inceptisols, and the distances of nesting cavity entrances to the ground and to the top of road cuts were  $1.6 \pm 0.9$  m and  $0.8 \pm 0.62$  m, respectively. The breeding season lasted 148 days from mid-August to early January. Clutch size (n = 256) varied from 2 to 3 eggs, and the eggs (n = 155) had a total length of 27.2 ± 1.3 mm, breadth of  $20.9 \pm 0.8$  mm, and mass of  $6.2 \pm 0.7$  g. The incubation phase lasted  $17.3 \pm 0.8$  days and the nestling phase for  $18.3 \pm 1.5$  days. The body mass of the chicks was  $6.0 \pm 1.0$  g just after hatching and reached a maximum of  $59.6 \pm 2.4$  g at 16 days of age. Our results can contribute to filling the gaps in knowledge of *C. pabsti* ecology, because its habitat is under high anthropic pressures and the information on its life history is yet limited.

Keywords. Breeding phenology; Cavity nesting; Highland grasslands; Parental care; Southern Brazil.

## INTRODUCTION

Cinclodes pabsti Sick, 1969 is one of the 15 species (Remsen et al., 2020) in the monophyletic genus Cinclodes Gray, 1840 (Furnariidae) found in South America (Chesser, 2004; Remsen et al., 2020). It is an isolated lineage, basal to all other species in the genus (Chesser, 2004; Remsen et al., 2020), along with the recently discovered Cinclodes espinhacensis Freitas, Chaves, Costa & Rodrigues, 2012 (hereinafter Cinclodes pabsti espinhacensis, according to Pacheco et al., 2021). Cinclodes pabsti is endemic to the Brazilian highland areas of more than 750 m above sea level in the states of Rio Grande do Sul and Santa Catarina, South Brazil (Sick, 1969, 1973), while C. espinhacensis is endemic to highland areas of more than 1,100 m above sea level in the state of Minas Gerais, Southeast Brazil (Freitas et al., 2012).

**Pap. Avulsos Zool., 2021; v.61: e20216184** http://doi.org/10.11606/1807-0205/2021.61.84 http://www.revistas.usp.br/paz http://www.scielo.br/paz Edited by: Luís Fábio Silveira Received: 03/05/2021 Accepted: 09/08/2021 Published: 27/09/2021 *Cinclodes pabsti* inhabits open grasslands and places with easy access to water, feeds on a wide range of invertebrates, and forages in rocky hills (Sick, 1973, 1997; Belton, 1984). However, it is not as closely associated with water as other *Cinclodes* spp. (Sick, 1997). Nesting is done in an underground nest located at the end of a gallery (Sick, 1997) excavated on natural cliffs and road cuts and in spaces under roofs in farm buildings (Belton, 1984). Sick (1973, 1997) reported reproductive activities in September and November.

Over the past few decades, numerous studies have been conducted on various species of this genus that dealt with a range of topics such as phylogenetics (Chesser, 2004; Sanín *et al.*, 2009; Freitas *et al.*, 2012; Rader *et al.*, 2015), biogeography (Chesser, 2004; Chaves *et al.*, 2015), osmoregulation and/or physiology (Sabat, 2000a, b;

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Sabat & Martínez Del Rio, 2002, 2005; Sabat & Gonzalez, 2003; Sabat et al., 2003; Sabat et al., 2004a, b; Sabat et al., 2006a, b), and general ecology (Atkins, 1980; Hahn, 2006; Vizcarra, 2007, 2010; Martínez Del Rio et al., 2009; Aucca et al., 2015; Newsome et al., 2015; Rader et al., 2017). However, the life history, especially the breeding biology of most Cinclodes spp., remains poorly understood, as most studies till date have been short-term. There are some studies on the nesting of some species of Cinclodes, such as Cinclodes antarcticus antarcticus (Garnot, 1826) (Cawkell & Hamilton, 1961; Robbins et al., 2001), Cinclodes excelsior Sclater, 1860 (Graves & Arango, 1988), Cinclodes taczanowskii Berlepsch & Stolzmann, 1892 (Bertolero & Zavalaga, 2003; Vizcarra et al., 2018), Cinclodes oustaleti baeckstroemii Lönnberg, 1921 (Hahn et al., 2005), Cinclodes comechingonus Zotta & Gavio, 1944, Cinclodes olrogi Nores & Yzurieta, 1979, Cinclodes atacamensis schocolatinus Reichenow, 1920 (Salvador & Salvador, 2012), Cinclodes aricomae (Carriker, 1932) (Avalos & Gómez, 2014), and Cinclodes fuscus Vieillot, 1818 (Ojeda, 2016).

Information about the biology of *C. pabsti* is limited to habitat use, nest site, nesting biology, reproduction (Belton, 1984; Sick, 1997), and nestling predation (Zocche *et al.*, 2017). Apart from the notes made by Sick (1969, 1973, 1997) and Belton (1984), preliminary data on Brazilian species ecology were published by Freitas *et al.* (2012), Zocche *et al.* (2017), Costa *et al.* (2019), and Freitas *et al.* (2019) only in the last decade. The last two cited studies presented information about the breeding biology and population and spatial ecology of *C. espinhacensis*.

The restricted area where *C. pabsti* occurs is under strong anthropic pressure, and the absence of basic biological information has led BirdLife International (2021a) to classify this species as "near threatened". Therefore, it is necessary to determine the basic aspects of the natural history of this species for future conservation action plans, especially to determine the species' resilience to habitat modification and investigate reports that it survives in cities and along roads (BirdLife International, 2021b). The aim of this study was to provide information on the breeding biology of this species in this regard.

# MATERIAL AND METHODS

## **Study site**

The study site was located in the municipalities of São José dos Ausentes (28°43'05"S and 50°02'59"W) and Bom Jesus (28°39'44"S and 50°26'23"W), northeastern state of Rio Grande do Sul, and Bom Jardim da Serra (21°28'32"S and 56°08'58"W), southeastern state of Santa Catarina (Fig. 1). The area lies within the realm of the Campos de Cima da Serra, a phytophysiognomy typical of the highlands of southern Brazil, characterized by a mosaic of open grasslands and *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae) forests interspersed

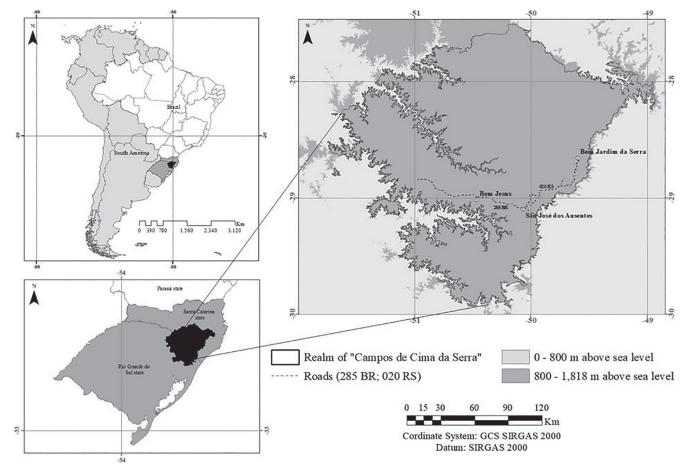


Figure 1. Location of the study area in the region of Campos de Cima da Serra, southern Brazil.

by rocky cliff faces (Behling *et al.*, 2004; Behling & Pillar, 2007; Overbeck *et al.*, 2007). The topography is undulating, with a maximum elevation of 1,800 m above sea level in the Santa Catarina state (Nimer, 1989).

The Köppen climate classification is Cfb (humid subtropical, without a dry season, and temperate summers) with a mean annual temperature of 14.0°C but ranging from -10.0-28°C (Alvares *et al.*, 2014). The mean winter temperature is 5°C, and the mean summer temperature is 14°C. Frost and snow occur during winter. Precipitation ranges from 1,450 to 1,650 mm per annum, and rainfall is well-distributed throughout the year (Nimer, 1989).

Grazing is the main land use activity and is traditionally associated with anthropogenic burning at the end of winter (August) (Quadros & Pillar, 2001). Both grazing and fire are essential for maintaining the physiognomic characteristics of the biome (Quadros & Pillar, 2001; Overbeck & Pfadenhauer, 2007). Extensive areas of grassland have also been transformed by plantations of *Pinus* spp. (Pinaceae), cultivated pastures, and crops of *Malus pumila* Mill. (Rosaceae), and more recently, vegetables including *Solanum tuberosum* L. (Solanaceae), *Brassica oleracea* L. (Brassicaceae), and *Capsicum annuum* L. (Solanaceae).

#### **General protocol**

Two existing roads were used as transects for sampling. The first had a south to north orientation and lay along a 120 km stretch of the RS-020 between the cities of São José dos Ausentes, Rio Grande do Sul, and Bom Jardim da Serra, Santa Catarina. The second was oriented from east to west and stretched along 50 km of the BR-285 from the border between Rio Grande do Sul and Santa Catarina states to the city of Bom Jesus, Rio Grande do Sul (Fig. 1). The differences in length and orientation of the two transects were because the area occupied by *C. pabsti* is longer on the north-south axis than on the east-west axis, as shown by Cordeiro (2001).

The existing nest cavities in road cuts along both transects were found in May 2008. The GPS coordinates for each cavity were recorded with an accuracy of 10 m, and the height and width of the entrance hole and its distance from the ground and the cliff edge were measured using a measuring tape. This procedure was repeated between May 2009 and May 2010. The survey was carried out monthly from May to July 2008, February to July 2009, and February to July 2010 and weekly from August 2008 to January 2009 and August 2009 to January 2010. The length of the transects surveyed was reduced to 70 km (40 km south-north and 30 km east-west) from August 2010 to January 2011 for feasibility, as monitoring was carried out at intervals of 2-4 days. It was possible to define the exact duration of the breeding season and the mean duration of each phenological phase by monitoring the nests every 2-4 days. The usage of the complete (170 km) or reduced (70 km) transect datasets was clearly stated in the analyses. Two researchers would then drive along both transects at a constant speed of 15 km/h looking for the presence of C. pabsti in or near

marked cavities, or in or near new nesting sites, without the use of playback. Sampling was only performed when the meteorological conditions were favorable for the detection of birds. Thus, sampling was avoided on days with rain, strong to moderate winds, and fog (Best, 1981; Bibby *et al.*, 1992). Surveys began an hour after sunrise and ended at sunset, with a break during the hottest period of the day (usually between 12:00 and 14:00 h). The starting point was altered for each sampling event to minimize the time-related biases (Robbins, 1981).

#### **Reproductive biology**

The cavities in which adult birds were observed to be engaging in behaviors clearly related to reproduction, such as taking material into the cavity, extended length of time spent inside the nest, and feeding of the nestlings, were classified as nesting sites. Each occurrence of a nesting site was checked to see if it was a new record or had already been georeferenced, and all the required physical and biological data were recorded (see below). In addition to the data recorded in May 2008, May 2009, and May 2010, the total length of the cavity (tunnel plus nesting chamber) was recorded for each nesting site, and the soil/substrate type in which it was situated was identified using the United States Department of Agriculture Soil Taxonomy (USDA) (USDA, 2014).

The following variables were recorded for each nesting cavity in the 2010-2011 breeding season: digging, taking material into the cavity, number of eggs laid, number of eggs hatched, and number of nestlings produced. It was possible to exactly define the following by monitoring the nests every 2-4 days from August 2010 to January 2011: the laying phase duration (time between the first and last eggs being laid), incubation phase duration (time between the last egg laid and hatching of the first chick), nestling phase duration (time between the first chick hatching and the last one leaving the nest), reproductive event duration (time between the first egg being laid and the last nestling leaving the nest, in the same reproductive event), inter-reproductive event duration (time between subsequent reproductive events in the same cavity, in the same breeding season), number of reproductive events per cavity per breeding season, and the breeding season duration (time between the first egg being laid and the last nestling leaving the nest). The phenophases of nests that were inaccessible were determined from direct observation of the behavior exhibited by the occupants (e.g., digging, taking material into the cavity, length of time spent inside the nest, and feeding of the nestlings) after the monitoring of nests began to be conducted every 2-4 days.

# **Biometry and sexing**

Adult birds in their nests were captured for biometric measurements using a hand-held net (Fig. 2) in the 2009-2010 and 2010-2011 breeding seasons, and the eggs and nestlings were picked up directly. The *Instituto*  Chico Mendes de Conservação da Biodiversidade – ICMBio (SISBIO no. 17985) and Centro Nacional de Pesquisa para a Conservação das Aves Silvestres – CEMAVE (CEMAVE no. 3163) granted the necessary ethical permission for the methods employed. According to the procedures recommended by MMA/IBAMA (1994), all adult birds

and nestlings older than 14 days were marked with a numbered metallic leg band. Additionally, adults (n = 22, from 18 nests) with a specific combination of colored bands were marked in the 2009-2010 and 2010-2011 breeding seasons to identify the nesting cavity of origin, while nestlings (n = 28, from 11 nests) received a combi-



Figure 2A-2B. Hand-held net used to capture adult birds of *Cinclodes pabsti* in their nests in the breeding seasons of 2008-2011 in Campos de Cima da Serra, southern Brazil.



**Figure 3A-3D.** Road cuts with the presence of holes used by *Cinclodes pabsti* as nesting cavities in the breeding seasons of 2008-2011 in Campos de Cima da Serra, southern Brazil. (3A) road cut with the presence of one nesting cavity in the B horizon of Inceptisol; (3B) researcher taking the measurements of the hole; (3C) road cut with the presence of several cavities side by side in the thin organic soil layer; (3D) detail of cavity proximity from the top of the road cut.

nation of colored bands corresponding to their parents' territory. This information was used to identify the reuse of cavities by the same adult individuals and the permanence of juveniles in their parents' territory.

The wing length (the flattened wing-chord), tail length (from the base of the tail to the tip of the longest rectrix), tarsus length (from the "knee" or depression in the angle of the inter-tarsal joint to the base of the last complete scale before the toes diverge), exposed culmen, and body mass were measured for adult birds (n = 23, from 23 nests). The body mass of nestlings was measured every 2 days from the day they hatched (n = 18, from eight nests) only in the 2010-2011 breading season. Biometric data were recorded using digital calipers (0.1 mm precision), a metallic roller (0.1 mm precision), and mass balance (0.1 g precision). The linear length and breadth of the eggs (n = 155, from 57 nests) were recorded using digital calipers (0.1 mm precision), while their mass (n = 122, from 57 nests) was recorded using a mass balance (precision of 0.1 g). Blood samples for identifying the sex of the adult birds (n = 23, from 19 nests) were collected on Whatman® FTA® cards throughout the 2009-2010 and 2010-2011 breeding seasons, and the polymerase chain reaction (PCR) technique was used, as described by Griffiths et al. (1998).

#### **Data analysis**

The physical data on nesting cavities was presented as histograms, and the class width was calculated for each variable according to Sturges (1926). The Chi-square test for equal expected proportions was used to determine whether there was selection for soil/substrate type associated with the occupation of the cavities for equal expected portions. Data are presented as mean ± SD standard deviation (SD). The variables were checked for normality using the Kolmogorov-Smirnov test and tested for adult sexual dimorphism in mass (g) and wing, tail, and tarsus lengths (mm) using the Student's t-test. The PAST 3.25 software (Hammer et al., 2001) was used for all the statistical tests, and the statistical significance was set at a P value of 5%. We calculated the proximity between the nesting cavities in the Spatial Analysis Module of ArcGIS® v. 10.2.1, using as algorithm the Distance to the Nearest Neighbor.

#### RESULTS

The presence of 450 *C. pabsti* nesting cavities (Figs. 3A-3D) was recorded for use along the complete set of transects in May 2008, while 290 nesting cavities were recorded along the reduced set of transects in August 2010 (Table 1). Birds used 119 cavities (22%) for nesting in the breeding seasons of 2008-2009 and 2009-2010 (complete set of transects: 170 km) and 52 cavities (17.9%) for nesting in the 2010-2011 breeding season (reduced set of transects: 70 km). The proportion of cavities used in the complete set of transects in each season was 17.3% in 2008-2009 (n = 78) and 16.5%

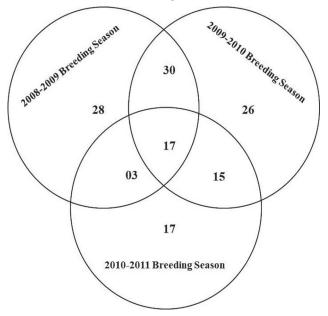
**Table 1.** Existing cavities and cavities occupied for nesting by *Cinclodes pabsti* recorded in the road cuts in Campos de Cima da Serra, southern Brazil, between May 2008 and January 2011.

	Nu	mber of Cav	ities Re	corded in ea	ch Transec	t
Breeding Seasons		e Set of Tra (170 km)	nsects	Reduced	l Set of Traı (70 km)	isects
	Existing	Occupied	%	Existing	Occupied	%
2008-2009	450	78	17.3			
2009-2010	495	88	16.5			
2008-2009 and 2009-2010	540	119	22.0			
2010-2011				290	52	17.9

in 2009-2010 (n = 88). The total number of cavities used across the three breeding seasons was 136, and the Venn diagram in Fig. 4 shows the use and reuse of nesting cavities across breeding seasons.

The shortest distance between two nesting cavities that were used simultaneously ranged from 31 to 5,390 m (in the 2008-2009 breeding season), 61 to 1,371 m (in the 2009-2010 breeding season), and 24 to 5,368 m (in the 2010-2011 breeding season) (Table 2). Considering the three breeding seasons together, there was a higher number of nesting cavities in the distance interval of 24-500 m (n = 34 cavities, 59.7%).

There was a greater usage of nesting cavities located in Inceptisols (n = 77), followed by cavities dug in the thin organic soil layer (n = 33), while the number of cavities located in other types of soil/substrate was much lower (Fig. 5A). *Cinclodes pabsti* had a greater affinity ( $\chi^2$  = 14.23;  $\chi^2_{0.001}$ ; 1 = 10.827) towards cavities located in clay-type soils (Inceptisols and Psammentic Entisols), with almost 66.2% of the total number of nesting cavities in these substrate types. Out of the number of nests located in non-clay substrates, ten (7.3%) were in saprolite banks (Regolith) and three (2.2%) in other substrates (one in a rock wall at the base of a bridge and two in house roofs).



**Figure 4.** Venn diagram showing the reuse of cavities by *Cinclodes pabsti* between the breeding seasons of 2008-2009, 2009-2010, and 2010-2011 in Campos de Cima da Serra, southern Brazil.

**Table 2.** Number of nesting cavities used simultaneously by *Cinclodes pabsti* in the 2008-2009, 2009-2010, and 2010-2011 breeding seasons in Campos de Cima da Serra, southern Brazil, arranged according to the interval of distance from the nearest neighbor.

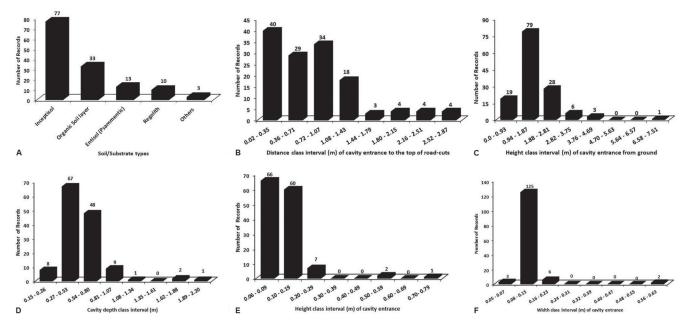
Distance	Number of Nestin	ng Cavities in each	Breeding Season	Totals	%
Interval (m)	2008-2009	2009-2010	2010-2011	TOLAIS	70
24 – 150	2	4	3	9	15.8
151 — 500	10	10	5	25	43.9
501 – 1,000	5	3	4	12	21.1
1,001 - 2,000	0	3	4	7	12.3
2,001 - 5,500	2	0	2	4	7.0
Totals	19	20	18	57	100

The distance between the cavity entrances and the top of road cliffs (or roofs) ranged from 0.02 (in the roofs) to 2.87 m (0.8  $\pm$  0.62 m), with a higher number in the first three distance classes from the top of road cliffs (0.02-1.07 m; Fig. 5B). The greatest number were in the 0.02-0.35 m class (n = 40), followed by the class 0.70-1.07 m (n = 34) and 0.36-0.71 m (n = 29). The height of the cavity entrances above the ground (Fig. 5C) ranged from 0 to 7.51 m (1.6  $\pm$  0.9 m), with the majority (58.1% of records) in the second height class above the ground (0.94-1.87 m).

The records of the depth, height, and width of the cavity entrances used by *C. pabsti* were plotted (Figs. 5D-5F). Cavity depth (tunnel plus the nest chamber) ranged from 0.15 to 2.20 m ( $0.6 \pm 0.3$  m) and was often (in about 84.6% of the depth classes) in either the 0.27-0.53 m (n = 67) or the 0.54-0.80 m (n = 48) classes. Abandoned *Colaptes campestris* (Vieillot, 1818) nesting cavities were also seen to be occupied by this species (n = 11). Entrance height ranged from 0.06 to 0.79 m ( $0.1 \pm 0.1$  m) with most cases (92.6%) in the 0.06-0.09 m (n = 66) and 0.10-0.19 m classes (n = 60). Cavity entrance width ranged from 0.05 to 0.63 m (0.1  $\pm$  0.1 m) with most cases (91.9%) in the 0.08-0.15 m class (n = 125).

Cinclodes pabsti exhibited biparental care during all phases of the breeding cycle. Both sexes actively participated in the construction of both the cavity and the nest, using their beaks for excavation. As the depth of the cavity into the cliff increased, it formed a straight tunnel that varied from horizontal to a slight upward inclination at an angle between 5° and 15° from the horizontal. The end of the tunnel widened to form an oval-shaped chamber (bowl) with a diameter of approximately 0.20 m. The underside of the chamber was located slightly lower than the floor of the tunnel to form a slight depression to accommodate the nest. During excavation, the material was disposed of through the tunnel entrance in the form of small lumps with the aid of the feet, wings and tail. Cavity excavation occurred over the entire non-breeding season but intensified in the months prior to the start of the breeding season. During the breeding season, excavation mainly occurred between reproductive events. However, excavation was also recorded in cavities that were used for nesting, mainly at the beginning of incubation, with material deposited at the entrance of the nesting chamber probably for purpose of thermoregulation and to prevent predator access.

Nest construction generally began 2-3 days prior to laying the first egg. Nevertheless, eggs were sometimes laid before the nest construction had begun or before its completion. The nest was constructed quickly (between 4 and 6 h) around the egg in the latter cases. The bowl (Figs. 6A and 6B) was made with materials like roots, chaff, grass stems, and wing and tail feathers of other bird species (Table 3) that were deposited circularly and evenly intertwined to ensure that they remained intact even if removed from the cavity. Hair from cattle tails, wool, wads of mammal fur, and down feathers were also recorded



**Figure 5A-5F.** Physical characteristics of cavities used by *Cinclodes pabsti* as nesting cavities between 2008 and 2011 in Campos de Cima da Serra, southern Brazil. (5A) number of nesting cavities by soil/substrate types; (5B) number of cavities by distance class interval of cavity entrance from the top of road cuts; (5C) number of cavities by height class interval of cavities by height class interval of cavities by height class interval of cavities by width class interval of cavity entrance.



Figure 6A-6B. Nest of *Cinclodes pabsti* from Campos de Cima da Serra, southern Brazil, collected in the breeding season of 2009-2010. (6A) top view; and (6B) side view of *Cinclodes pabsti* nest showing the shape and materials used in the construction.

(Table 3), which were used to form a moderately deep cup. In addition to these materials, the pair would deposit chaff and wing and tail feathers of non-Passerine species along the entrance tunnel over the excreta of the nestlings during the nestling phase, possibly to avoid contact with it as they entered and exited the nest to attend the nestlings. Owl pellets, fresh sheep droppings, pieces of mammal skin with fur, and pellets of wool from sheep and wild mammals around the nest were often recorded in the nesting chamber of *C. pabsti* (Table 3). Oviposition occurred at 24 h intervals, and incubation began only after laying was complete (maximum clutch size of three). The nests remained vacant until laying was complete.

A total of 748 eggs produced in 295 nesting events in 136 monitored nesting cavities were recorded during the three reproduction seasons (Table 4). Most nesting cavities were home to only a single breeding event (n = 113 nests), while 55 were home to two (n = 110 nests), and 11 were home to three complete and consecutive reproductive events (n = 33 nests), highlighting the reutilization of cavities within and across breeding seasons. It was seen that certain cavities were used throughout the year, whereas others were used only during the reproductive season. As a rule, cavities that were used repeatedly during the breeding season were also used in the non-breeding season. The clutch size ranged from 1 to 3 eggs. Three eggs were recorded in most of the nests (81%) (Table 5), two eggs in 4.8% of the nests (n = 14 nests), and only one egg in 1% of the nests (n = 3 nests). No egg-laying was observed in 15 finished nests, while 24 nest cavities were inaccessible (Table 5). The eggs of C. pabsti (n = 155) obtained from 57 nests during the three breeding seasons were elliptical in shape, with a pure, translucent white coloration (Table 6). The length ranged from 22.2 to 29.6 mm ( $27.2 \pm 1.3$  mm), the breadth from 17.4 to 22.4 mm (20.9  $\pm$  0.8 mm), and the mass from 3.0 to 8.0 g (6.1  $\pm$  0.7 g) (Table 6).

The nestlings hatched with their ears open and eyes sealed. Hatching was highly synchronous within each

clutch, with the nestlings hatching not more than 4 h apart. The nestling bodies were half-covered with brown, natal down feathers (neossoptiles) distributed over the head, wings, back, sides, thighs, and belly (Figs. 7A and 7B). The body mass of the nestlings at hatching (n = 18) ranged from 4.0 to 7.0 g ( $6.0 \pm 1.0$  g). The eyes opened partially at 4 days of age, and pin feather sheaths developed on the wings, tail, and some regions of the back, chest, and belly at 6 days of age. The nestlings were covered by feathers at 11 days of age, except for the neossoptiles beside the feather sheath in the wings and tail (Figs. 7C and 7D). The nestlings reached their maximum body mass at 16 days of age, ranging from 56 to 63 g (59.6  $\pm$  2.4 g). Nestlings weighed on average  $58.0 \pm 4.6$  g at the final weigh-in a day before leaving the nest, exceeding the average body mass of adults in the breeding season, where the body mass of males was 52.0  $\pm$  2.4 g (n = 6) and that of females was  $54.4 \pm 3.4$  g (n = 17) (Table 7). The parental pair removed fecal sacs from the nest in the days following the hatching of chicks and covered feces along the tunnel floor with several materials as the nestlings grew and the defecation rate increased. The time spent in the cavity by the parents decreased as the days passed. The parents remained near the nesting cavity on the day that the nestlings left the nest but were not seen feeding the nestlings. No differences were found in the average morphometric measurements between the sexes in adults of C. pabsti (Table 7).

Figure 8 shows the 148-day breeding chronology of *C. pabsti* in the 2010-2011 breeding season. It began with the first egg laid on August 15, 2010, and ended with fledgling by the last nestling on January 9, 2011. The duration of the reproductive phases of *C. pabsti* (incubation, nestling, and interval between two reproductive events) did not seem to vary a lot between pairs and breeding events. The incubation phase in the first reproductive event (n = 25 nests) ranged from 17 to 19 days (17.2  $\pm$  0.5 days) and the nestling phase (n = 23 nests) from 17 to 22 days (18.4  $\pm$  1.8 days), while the interval between the first and second reproductive Table 3. Nest site data and nesting materials used by *Cinclodes* spp. according to the respective references, along with data collected between 2008 and 2011 in Campos de Cima da Serra, southern Brazil. References and number of obser-(7) Graves & Arango (1988) (n = 1 nest and 285 nesting cavities); (8) Hahn et al. (2005) (n = 6 nests); (9) Avalos & Gómez (2014) (n = 1 nest); (10) Salvador & Salvador & 2012) (C. comechingonus (n = 16 nests); C. olrogi (n = 19 nests); and vations: (1) Cawkell & Hamilton (1961) (n = 2 nests); (2) De La Peña (2016); (3) Vaurie (1980); (4) Viskarra *et al.* (2018) (n = 1 nest); (5) Bertolero & Zavalaga (2003) (n = 3 nests); (6) Ojeda (2016) (n = 51 nests from 26 nesting cavities);

uncroaes spp. C. antarcticus C. albiventris (R.A. Philippi y Landbeck, 1861)	Marsh Carbon and De 161 and	Nest Distance Entrance	e Cavity Depth		<b>Cavity Entrance</b>	Name and American	
C. antarcticus C. antarcticus C. albiventris (R.A. Philippi y Landbeck, 1861)	Nest Substrates and Positions	from the Ground (m) from the Top (m)	_	Height (m)	Width (m)	- Nesting Material	kererences
<i>C. albiventris</i> (R.A. Philippi y Landbeck, 1861)	Crevices between stones, ground cavities, vertical banks, artificial cover ( <i>e.g.</i> , inverted bucket)					Dry grass, feathers, and wool	1
C. albiventris (R.A. Philippi y Landbeck, 1861)	Crevices and tunnels					Dry grass, and feathers	2
	<i>C. albiventris</i> (R.A. Philippi y Landbeck, 1861) Hollows, Crevices between stones, tunnels, cavities and, pipes	0.80 – 2.50	0.35	0.08	0.08	Soft vegetables, straws, hairs, bristles, wool, and feathers	2
C. patagonicus	Hollow in ravines and tree trunks, stone walls and constructions	4.0	0.35	0.16	0.16	Grass, and feathers	2
C. oustaleti Scott, 1900	Crevices or borrows in earth ravines					Fine vegetable fibers, cow hair, and hare hair	2
C. atacamensis (R.A. Philippi, 1857)	Holes or crevices in earth ravines or stones	2.6	0.4 - 1.0	.0 0.06-0.1	0.06 – 0.1	Grass, hair, wool, feathers, and threads	2
. nigrofumosus	Crevices of rocks or slopes, burrows in the earth, under the roofs, within the walls of edifices						m
C. taczanowskii	Dodi and a star marked of the sheet of the start of the s					Vegetable remains, algae and feathers	4
	אטנג נופעוכפי, עפונוכם שמווגי מוום פיכמוטווופווני מוטווץ נווב נטמאנ	2.0 - 3.0	0.5	0.2	0.1	Pieces of vegetation, thin branches, and feathers	5
C. fuscus	Crevices, borrows, and pipes					Bristles, wool, and fur	2
	Holes in dams, under rock edges along streams, walls of manmade structures, under the roofs, under bridges, interior of occupied dwellings						2
	Tree cavities	0.9.0	$0.3 \pm 0.2$	1.2 0.05 – 0.4	< 0.1		9
C. excelsior	Vertical embankments, in pumice strata of diff faces formed by road cuts located in strata composed of pumice	0.8 - 10.0 0.05	- 2.3 0.6 - 1.1	.1 0.7 – 0.9	0.7 – 0.9	Dry grass	7
C. o. baeckstroemii	Natural holes in steep rock faces and on rocky slopes/ridges	0-5.0 1.0-	1.0 – 7.0 0.2	0.05-0.2	0.05 - 0.2		8
C. aricomae	Among large rocks on hillsides and on cavities and cracks in cliff faces	6.0	0.30	0.1	0.3	Dry grass	6
C. comechingonus	Hollows, crevices between stones, tunnels, cavities and, pipes					Soft vegetables, straws, hairs, bristles, wool, and feathers	2
	Earth ravines, rock crevices and old rock walls	0.8 – 3.8				Grass, thin branches, feathers, and bristles	10
C. olrogi	Crevices or burrows in earth ravines					Fine vegetable fibers, cow hair, hare hair	2
	Earth ravines, rock crevices and old rock walls	0.7 - 4.5				Grass, straw, fur, bristles, and feathers	10
C. a. schocolatinus	Earth ravines (usually wet), stream banks and rock crevices	1.8 - 8.0				Grass, straw, fur, bristles, and feathers	10
C. espinhacensis	Cavities in rocky outcrops	0.9 – 2.9 0.3 -	- 0.4 0.4 - 1.1	.1 0.05 – 0.4	0.7 – 0.6	Dry grass like narrow leaves, inflorescences of small Eriocaulaceae, green moss, mammal hair, and feathers	11
C. pabsti	Cliff faces						12, 13
	Road cuts, and in spaces found under roofs in farm buildings						14
	Road cuts, rock wall, base of bridges, and in house roof	0-7.51 0.02 -	- 2.87 0.15 - 2.20	.20 0.06 - 0.79		0.05 – 0.63 Roots, chaff, grass stems, wing and tail down feathers of other bird species, hair from cattle tails, wool, wads of mammal fur, and feathers	Present study

Denne du stive Frants in each -		· · · · · ·	Numbers of Occ	pied Cavities and Cons	tructed Nests in each	Breeding Season		
Reproductive Even Breeding Se		2008-	2009	2009-	2010	2010-	2011	Totals of Nests
breeding se		Cavities	Nests	Cavities	Nests	Cavities	Nests	- · · · · · · · · · · · · · · · · · · ·
One Event		50	50	44	44	19	19	113
Two Events		17	34	19	38	19	38	110
Three Events		4	12	5	15	2	6	33
Without Egg Laying		6	6	6	6	3	3	15
Nest not Accessible		1	1	14	14	9	9	24
Total	Cavities	78		88		52		
	Nests		103		117		75	295

**Table 4.** Numbers of occupied cavities, constructed nests, and reproductive events of *Cinclodes pabsti* in each breeding season between 2008 and 2011 in Campos de Cima da Serra, southern Brazil.

**Table 5.** Clutch size of *Cinclodes pabsti* recorded between 2008 and 2011 in

 Campos de Cima da Serra, southern Brazil.

Clutch Size	Number of N	ests in each Bre	eding Season	Totals	%
Clutch Size	2008-2009	2009-2010	2010-2011	TOLAIS	%0
Three Eggs	92	89	58	239	81
Two Eggs	3	6	5	14	4.8
One Egg	1	2	0	3	1
Without Egg Laying	6	6	3	15	5.1
Nest Not Accessible	1	14	9	24	8.1
Total	103	117	75	295	100

events (n = 18 nests) ranged from 9 to 31 days ( $21.8 \pm 6.4$ days). The incubation phase in the second reproductive event (n = 23 nests, with 17 reused cavities and six new nests) ranged from 17 to 21 days (17.4 ± 1.0 days) and the nestling phase (n = 19 nests) from 17 to 21 days  $(18.2 \pm 1.3 \text{ days})$ . However, the interval between the second and third reproductive events (n = 3 nests) ranged from 15 to 23 days (18.7  $\pm$  4.0 days). Both the incubation (n = 4 nests) and nestling phases (n = 2 nests) occurred in exactly 17 days in the third reproductive event. The mean duration of the incubation phase during the 2010-2011 breeding season (n = 52 nests) was  $17.2 \pm 0.8$  days. The nestling phase (n = 45 nests) lasted on average  $18.2 \pm 1.5$ days, with practically the same number of days in the first two reproductive events but shorter in the third reproductive event. The mean interval between reproductive events was  $21.4 \pm 6.1$  days (n = 21 nests).

The progression of reproductive phenophases in the 2010-2011 reproductive season (Fig. 9) indicated that peak laying (n = 28) and incubation (n = 33) occurred in September, and the greatest number of nestlings (n = 30) was found in October. The greatest number of active nests (n = 45) were recorded in October (approximately the middle of the breeding season), resulting from a combination of nests with nestlings from the first reproductive event and others with eggs from the second reproductive event.

#### DISCUSSION

*Colaptes campestris* plays an important role in the southern Brazil highland grasslands, providing a key structural feature (in the form of shallow cavities) which is

a critical resource for C. pabsti. Colaptes campestris feeds almost exclusively on ant eggs, larvae, and pupae and forage by excavating several consecutive shallow cavities in cliff faces and road-cuts (Short, 1972). These shallow cavities were seen to be deepened later by C. pabsti and used as nesting cavities. Although C. pabsti is commonly reported to excavate its own burrows in the literature (Sick, 1973; Belton, 1984), there were no records of cavities excavated entirely by this species even after three years of fieldwork. Active cavity excavations were also not observed in C. espinhacensis (Costa et al., 2019). Cinclodes pabsti was observed using abandoned C. campestris nesting cavities and increasing the depth of shallow cavities, in some cases, just after they had been excavated. Cinclodes pabsti individuals were found using the same cavity for both breeding and roosting during the breeding season. This has been recorded for other species in the genus, such as C. fuscus (Vaurie, 1980; Ojeda, 2016).

Studies on cavity-nesting birds have often supported the hypothesis of nest site limitations (Wiebe et al., 2006; Wiebe, 2011). However, the conclusions of these studies are weakened by the fact that they are multivariate and do not involve the treatment of each factor independently, masking their true importance as limiting resources in the habitat (Brush, 1983). Considering that potential nesting cavities vary in quality, the availability of high-quality nesting cavities may be subject to a high degree of competition (Nilsson, 1984). However, no direct competition or heterospecific antagonistic behavior over C. campestris cavities by individuals of C. pabsti was observed. Several unoccupied nesting cavities were found next to each other, and several cavities that remained unused for several years were observed, leading to the conclusion that there was a surplus of cavities available for the use of C. pabsti in the study area. Nests were rarely located close together when the nesting was synchronous. The closest synchronous nests recorded were 24, 31, and 61 m away from each other, and this pattern could be related to the territory size of the pairs of Long-tailed Cinclodes. In addition, our data showed that between a fifth and a sixth of the total existing cavities on both sets of transects (complete and reduced) were occupied, providing evidence against the hypothesis of competition for high-quality cavities.

Burrowing birds discriminate the nesting substrates not only according to their quality but also by the position of the soil horizon in the bank in which the holes will be **Table 6.** Characteristics of eggs and reproductive biology of *Cindodes* spp. according to the respective references, along with data collected between 2008 and 2011 in Campos de Cima da Serra, southern Brazil. References and number (15 eggs were measured, and 8 were weighed)); and *C. a. schocolatinus* (n = 8 nests and 6 eggs)); (3) De La Peña (2016); (4) Costa *et al.* (2019) (n = 6 nests and 8 eggs); (5) Graves & Arango (1988) (n = 1 egg); (6) Bertolero & Zavalaga (2003) (n = 3 nests) and 3 eggs); (7) Hahn *et al.* (2005) (n = 6 nests): (8) Oieda (2016); (9) (9) Avalos & Gómez (2014) (n = 1 nest); (10) Viskarra *et al.* (2018) (n = 1 nest); Present study (n = 155 eggs from 57 nests). of observations: (1) Cawkell & Hamilton (1961) (n = 2 nests and 5 eggs); (2) Salvador & Salvador (2012) (C. comechingonus (n = 16 nests and 22 eggs (22 eggs were measured, and 18 were weighed)); C. olrogi (n = 19 nests and 15 eggs

Action					Eggs Chara	Eggs Characteristics				-		:	
	Cinclodes spp.		Lengt	(աա) կ	Breadt	(աա) կ	Mas	(b) ss	Clutch Size (eggs)	Period	Fledgling (days)	Breeding Season (1) Moeting (2)	References
of         length         length <thl>length         <thl>length<!--</th--><th></th><th>000</th><th>Range</th><th>Mean ± SD</th><th>Range</th><th>Mean ± SD</th><th>Range</th><th>Mean ± SD</th><th></th><th>(cápn)</th><th></th><th>(z) fillneau</th><th></th></thl></thl>		000	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD		(cápn)		(z) fillneau	
interface         <	C. antarcticus	Pure white, somewhat translucent	27 – 29.4	$27.3 \pm 0.9$	20.5 - 22.7	$21.6 \pm 0.9$			2-3	16	25	Oct. – Nov. (1)	-
\$\$ We here         23           \$\$ Me		White							1 – 3			Sept. – Dec. (2)	°
site         2           Patenic         2           Patenic         2           Mile         2 <td>C. albiventris</td> <td>White</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>2-3</td> <td></td> <td></td> <td>Nov. – Dec. (2)</td> <td>°</td>	C. albiventris	White							2-3			Nov. – Dec. (2)	°
Petenk         2           wite         3           wite         2-4           Mete         2-4	C. taczanowskii											0ct. (2)	10
xx         Mile         3           Mile         2-4           Mile         2-4           Mile         2-4           Mile         2-4           Mile         2-4           Intercanding sightyolosy         355           Mile         2-4           Intercanding sightyolosy         355           Mile         2-4           Intercanding sightyolosy         355           Mile         2-4           Mile         2		Pale pink							2				9
Mite         2-4           Mite         24           Mite         24           Precent oliced, sightyglosy         285         20         24           Precent oliced, sightyglosy         285         20         24           Mite         285         210         21         24           Mite         285         210         20         24           Mite         285         21         23         24           Mite         285         21         23         23           Mite         237-361         23+36         24         24         24           Mite         237-361         23+36         24-36         24         24         24           Mite         237-361         23+36         24-36         24-36         24         24         24         24           Mite         244-35         24-36         24-36         24-36         24	C. patagonicus	White							ĸ			Nov. – Jan. (2)	Υ
Wite         24           Increanceduced slightlyglosy         28.5         20.0         2           Increanced unded slightlyglosy         28.5         20.0         2           Wite         Wite         2         2         2           Increanced unded slightlyglosy         28.5         20.0         2         2           Wite         Mile         2         2         2         2           Increance         237-2.6.1         28.1-19.1         193-6.1         2         2           Increance         237-2.6.1         24.5.2         2         2         2         2           Increance         237-2.6.1         24.5.2         18.1-19.1         193-6.1         2	C. fuscus								2 – 4			Nov. — Mid-Jan.	8
Pure crean colored, signity glosy         28.5         2.0         2           White         Mile         2         2         2         2         2         2         2         2         2         3         2         3         2         3         2         3 </td <td></td> <td>White</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>2-4</td> <td></td> <td></td> <td>Sept. – Dec. (2)</td> <td>m</td>		White							2-4			Sept. – Dec. (2)	m
	C. excelsior	Pure cream colored, slightly glossy	28.5		22.0				2				5
International conditional condi	C. oustaleti	White										Nov. – Dec. (2)	~
ingoins           ingoins         Univenity, comewhattansluent         237-26.1         248±0.8         18.1-19.1         19.3±0.3         46-5.4         51±0.3         2-3           ingoins         Une white, somewhattansluent         237-26.1         248±0.8         18.1-19.1         19.3±0.3         46-5.4         51±0.3         2-3           White         Verwhite, somewhattansluent         244-25.9         25.2±0.5         18.4-19.2         18.9±0.3         44-5.3         2-3         2-3           White         Verwhite, somewhattansluent         244-25.9         25.2±0.5         18.4-19.2         18.9±0.3         44-5.3         2-3         2-3           More whattansluent         244-25.9         25.2±0.5         18.4-19.2         18.9±0.3         44-5.3         2-3         2-3           Inter white, somewhattansluent         244-25.9         25.2±0.5         18.9±0.3         24-5.3         2-3         2-3           Inter white, somewhattansluent         258-273         264±0.5         19.9±0.12         204±0.5         2-3         2-3         2-3           Inter white, somewhattansluent         264-2.84         714-2.14         209±0.6         51-6.1         2-3         16         2-3         16           Interw	C. o. baeckstroemii								2 – 3			Nov. – Feb.	7
ingonus         White         2–3         2	C. aricomae											Sept. – Mar.	6
Inervhite, somewhattanslucent         23.7 - 26.1         24.8 \pm 0.6         18.1 - 19.1         19.3 \pm 0.3         46 - 5.4         5.1 \pm 0.3         2 - 3           White         White         X         X         X         X         X         X           Pure white, somewhat translucent         24.4 - 25.9         25.2 \pm 0.5         18.4 - 19.2         18.9 \pm 0.3         4.4 - 5.3         4.9 \pm 0.3         2 - 3         X           Pure white, somewhat translucent         24.4 - 25.9         25.2 \pm 0.5         18.4 - 19.2         18.9 \pm 0.3         4.4 - 5.3         4.9 \pm 0.3         2 - 3         X <td>C. comechingonus</td> <td>White</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>2 – 3</td> <td></td> <td></td> <td>0ct. – Jan. (2)</td> <td>~</td>	C. comechingonus	White							2 – 3			0ct. – Jan. (2)	~
White         2           Pure white, somewhattanslucent $244-559$ $552\pm05$ $184-192$ $189\pm03$ $44-53$ $49\pm0.3$ $2-3$ ensist         White $244-259$ $252\pm0.5$ $184-192$ $189\pm0.3$ $44-5.3$ $49\pm0.3$ $2-3$ ensist         White $24+2.59$ $25\pm0.5$ $18-21.2$ $20\pm4.65$ $199-21.2$ $20\pm4.65$ $10\pm4.65$ $10\pm4.65$		Pure white, somewhat translucent	23.7 – 26.1	$24.8 \pm 0.8$	18.1 – 19.1	$19.3 \pm 0.3$	4.6 - 5.4	$5.1 \pm 0.3$	2 – 3			0ct. – Jan. (2)	2
Pure white, somewhattans/ucent         24,4-25,9         25,2±0,5         18,4-19,2         18,9±0,3         4,4-5,3         4,9±0,3         2-3           ensist         White         Mile         2	C. olrogi	White							2			Nov. – Dec. (2)	3
ensity       White       2         old thus       Pure white, somewhat tanslucent       25.8 - 27.3       26.4 \pm 0.5       19.9 - 21.2       20.4 \pm 0.5       2 - 3       2 - 3       3 - 3       3 - 3       3 - 3       3 - 3       3 - 3       16       16.2 \pm 1.5       17.4 - 21.6       20.9 \pm 0.8       5.1 - 6.1       5.7 \pm 0.4       2 - 3       16       16       2 - 3       16       16       16       16       16       16       16       16       16       17       17       16       17       17       17       17       1		Pure white, somewhat translucent	24.4 - 25.9	$25.2 \pm 0.5$	18.4 - 19.2	$18.9 \pm 0.3$	4.4 - 5.3	$4.9 \pm 0.3$	2 – 3			0ct. – Jan. (2)	2
colatinus         Pure white, somewhat translucent         25.8 - 27.3         26.4 \pm 0.5         19.9 - 21.2         20.4 \pm 0.5         2 - 3         2 - 3         3 - 3         3 - 3         3 - 3         16         17.2 \pm 0.8         18.2 \pm 1.5	C. atacamensis	White							2			0ct. – Dec. (2)	3
stensis         white         26.4 - 28.4         27 ± 0.7         19.4 - 21.6         20.9 ± 0.8         5.1 - 6.1         5.7 ± 0.4         2 - 3         16           Pure white, somewhat translucent         22.2 - 29.6         27.2 ± 1.3         17.4 - 22.4         20.9 ± 0.8         3 - 8         6.1 ± 0.7         2 - 3         17.2 ± 0.8         18.2 ± 1.5	C. a. schocolatinus	Pure white, somewhat translucent	25.8 - 27.3	$26.4 \pm 0.5$	19.9 – 21.2	$20.4 \pm 0.5$			2 – 3			0ct. – Dec. (2)	2
Pure white, somewhat translucent $22.2-29.6$ $27.2\pm1.3$ $17.4-22.4$ $20.9\pm0.8$ $3-8$ $6.1\pm0.7$ $2-3$ $17.2\pm0.8$ $18.2\pm1.5$	C. espinhacensis	white	26.4 - 28.4	$27 \pm 0.7$	19.4 – 21.6	$20.9\pm0.8$	5.1 - 6.1	$5.7 \pm 0.4$	2 – 3	16		Sept. – Jan.	4
	C. pabsti	Pure white, somewhat translucent	22.2-29.6	27.2 ± 1.3	17.4 – 22.4	$20.9 \pm 0.8$	3 – 8	$6.1 \pm 0.7$	2 – 3	$17.2 \pm 0.8$	18.2±1.5	Mid-Aug. – Early Jan. Present study	Present study

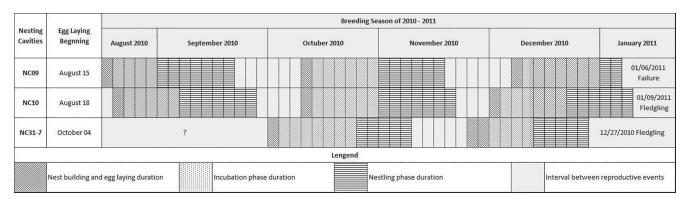
<b>Biometric Data</b>	Males	(n = 6)	Females	(n = 17)
Biometric Data	Range	Mean ± SD	Range	Mean ± SD
Wing (mm)	112.0 - 117.0	113.17 ± 2.71	96.0 - 115.0	$108.59\pm5.43$
Tail (mm)	91.0 - 95.0	93.58 ± 1.69	89.0 - 94.0	91.19 ± 1.97
Tarsus (mm)	31.03 - 33.41	$31.85 \pm 0.85$	29.95 - 33.67	31.80 ± 1.11
Exposed Culmen (mm)	21.93 - 24.44	$22.78\pm0.96$	21.27 - 24.36	$23.07\pm0.88$
Body Mass (g)	49.0 - 55.0	52.01 ± 2.44	48.15 - 60.3	$54.37\pm3.39$

**Table 7.** Biometric data of adult individuals of *Cinclodes pabsti* obtained from six males and 17 females belonging to 23 nesting cavities in Campos de Cima da Serra, southern Brazil, monitored during the 2009-2010 and 2010-2011 breeding seasons.

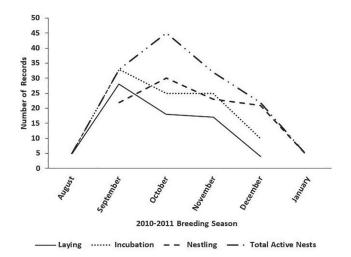
excavated (Heneberg, 2008; Meireles *et al.*, 2018). Harder substrates are more difficult to dig and demand greater time and energy expenditure, while very loose substrates can result in the collapse of the nesting cavity (Meireles *et al.*, 2018). Thus, burrowing birds need to find a trade-off between cavity stability and ease of excavation, a principle known as the Heneberg compromise (Smalley *et al.*, 2013). By contrast, the different substrates in which the nesting cavity may be located respond differently to radiation, influencing the cavity microclimate (Mersten-Katz *et al.*, 2012; Maziarz & Wesolowski, 2013) and possibly nest site selection. Clay is an ideal substance for the construction of nests, as it is thermally insulating, as pointed out by Figueiredo (1995) for *Furnarius rufus* (Gmelin, 1788). It seems likely in our study that cavities in clay substrates were selected because of their thermal insulation, high moisture content (especially in drier times), and softness (making it easy to excavate) as well as their strength (offering stability and protection). This suggestion is supported by the fact that nest cavities were not observed on road cuts with soil profiles consisting of Oxisols and Ultisols. Both these soil types are well-drained with a low water storage capacity and contain little to no clay. Therefore, they are very porous, friable, and highly susceptible to



Figure 7A-7D. Nestlings of *Cinclodes pabsti* recorded in the breeding season of 2010-2011 in Campos de Cima da Serra, southern Brazil. (7A and 7B) istribution of brown, natal, down feathers (neossoptiles) in the semi-covered body, with closed eyes and opened ears in the new hatchling; (7C and 7D) body covered by feathers, except for the neossoptiles in the feather cannons of the wings and tail at 11 days of age.



**Figure 8.** Breeding chronology of *Cinclodes pabsti* during the breeding season of 2010-2011 based on the monitoring of eight nests in three nesting cavities in Campos de Cima da Serra, southern Brazil. Scheme of phenophases based on Faria *et al.* (2008), evidencing: 08/15/2011 – Beginning of the 2010-2011 breeding season with the laying of the first egg in the nest of nesting cavity NC09 [Nesting Cavity 09]; 08/18/2010 – Beginning of the incubation phase of three eggs in the nest of the nesting cavity NC09 [Nesting Cavity 09]; 08/18/2010 – Beginning fieldgling from the nesting cavity NC10 [Nesting Cavity 10].



**Figure 9.** Number of *Cinclodes pabsti* nests in laying, incubation, and nestling phenophases, and the total number of active nests out of 52 nesting cavities monitored in the 2010-2011 breeding season in Campos de Cima da Serra, southern Brazil.

erosion (Vieira & Dortzbach, 2017) and are highly unstable and unsafe for the excavation of cavities, which may be the reason why they are avoided by cavity nesters.

Cinclodes pabsti constructed most of its nests in cavities located in road cuts in the present study, although nests on other substrates such as rock walls at the base of a bridge and house roofs were also recorded. Belton (1984) noted that this species usually constructed nest holes in extremely hard, rock-like materials that would take a long time to excavate. In general, Cinclodes spp. build their nests on several different substrates (Table 3). However, horizontal cavities independent of the substrate type are consistently used as breeding sites across all species of the Cinclodes genus (Vaurie, 1980; Narosky et al., 1983; Sick, 1997; Ojeda, 2016). Generally, nests of C. pabsti are described as underground, with a chamber that widens towards its end to form a bowl (Sick, 1997), or as a cavity/with-tunnel/low cup type with a horizontal tunnel (Simon & Pacheco, 2005). However, individuals of this species in the present study were found to be nested in cavities in which the tunnel sloped slightly upwards, and in abandoned C. campestris nesting cavities, where the cavity depth (minimum of 15 cm) was represented only by the nesting chamber. They are classified as cavity/without-tunnel/simple/[lined]-type nests in this case (Simon & Pacheco, 2005).

The distance of the nest entrance from the ground and/or from the top of the vertical structure in which it is located is also a determinant of nest site selection. Nests located farther from the ground or the cliff top greatly decrease predation risk (Graves & Arango, 1988; Hahn et al., 2005; Ojeda, 2016). Our results for C. pabsti showed that most cavity entrances were located up to 1 m from the cliff top and from 1-2 m off the ground. At least one-third of the cavity entrances close to the cliff top were present in the superficial layer of the soil (organic layer). This is similar to the results of another study on C. excelsior (Graves & Arango, 1988) in which the authors hypothesized that the consistent selection of the upper quartile of the road cut was influenced by the presence of a layer of pumice, which facilitated digging and provided protection against predation. Our data on the substrate type, physical characteristics of the nest, and nesting materials used by C. pabsti are also consistent with those of the nests of other Cinclodes spp., besides those of C. excelsior (Table 3). As 98% of the cavities in our study were in road cuts, changes in the road level due to road maintenance or engineering activities could alter the distance of the nest cavity entrance from the ground between breeding seasons owing to the extraction or deposition of materials. Our records of nesting cavity dimensions (depth, entrance height, and width) are consistent with those of the nests of other Cinclodes spp. (Table 3). However, at least four nesting cavities had depths greater than 1.08 m, which is unusual for species in this genus, and were therefore considered as outliers. The entrance width was generally 0.08-0.10 m; wider entrances were mostly due to erosion caused by the continuous movement of birds into and out of the nest. The tunnel depth and inclination and the distance of the cavity entrance from the cliff top are critical to the stability of the nest (to avoid collapse of the chamber ceiling – Faria et al., 2008; Heneberg, 2008; Smalley et al., 2013) and to reduce access for predators from the cliff top. Indeed, several nest predation events were recorded for cavities in the upper layer of soil, where predators had dug out the cavities from above (unpublished data). The

steepness of the road cuts (usually greater than 80° and in some cases greater or equal to 90°), distance from the cliff top, distance from the ground, and the narrow entrance diameter make the burrows generally inaccessible to terrestrial predators, except for snakes (Zocche *et al.*, 2017). Additionally, overhanging vegetation conceals the burrow entrance to some degree in some instances, offering protection against aerial predators.

*Cinclodes pabsti* in this study used nesting materials similar to those used by other species of the genus (Table 3). The owl pellets, fresh sheep droppings, pieces of mammal skin with fur, and pellets of wool from sheep and wild mammals recorded around the nests of *C. pabsti* suggest that besides the function of thermoregulation, these materials are used for their strong and characteristic smell to mask the birds' scent from predators.

The eggs of species that nest in enclosed nests are generally white in color because they do not require camouflage (Oniki, 1985). The eggs of C. pabsti, along with congeneric and most other Furnariidae species, are consistent with this observation (Narosky et al., 1983; Sick, 1997; De La Peña, 2016). This species has pure white, somewhat translucent eggs (De La Peña, 2016), and our data showed that the mean length, breadth, and mass of these eggs were higher than those of other species in the genus for which data are available (Table 6). The clutch size ranged from 1 to 3 eggs, which is consistent with that of other species in the genus (Table 6). Cinclodes fuscus is an exception with a clutch size of 2-4 eggs (Ojeda, 2016). The incubation period of C. pabsti is slightly higher, with the fledging period shorter, than that of its congeneric species (Table 6). Hatching is highly synchronous within each clutch, with the nestlings hatching not more than 4 h apart. This reinforces the hypothesis that the female does not incubate until the entire clutch is laid, an observation also recorded for C. a. antarcticus by Cawkell & Hamilton (1961).

The onset of breeding in the 2010-2011 breeding season was highly synchronous (except for three pairs, which began laying early in mid-August), beginning in the first week of September in 14 out of 52 monitored nesting cavities. The breeding season was longer than that of congeneric species (Table 6). However, synchronization decreased with time, mainly owing to nest failures for various reasons. *Cinclodes pabsti* began breeding in winter, an observation also recorded by Sick (1997), and the chicks were found ready to leave the nest on September 21, 2010, corroborating the observations by Belton (1984) and Repenning *et al.* (2010). Our results indicate an extension of the breeding season of the species from mid-August to mid-January.

Nesting cavities were often reused by *C. pabsti*, both within the same breeding season and in subsequent years, a fact also recorded for *C. excelsior* by Graves & Arango (1988) and for *C. fuscus* by Ojeda (2016). Sometimes, a nesting cavity would be abandoned between reproductive events or breeding seasons but reused in subsequent reproductive events or breeding seasons. The pair was absent from the nesting cavity during these abandonment periods and roosted in other cavities or sites in the vicinity. This behavior may be an

adaptation to prevent infestation by parasites, to avoid septic conditions resulting from the build-up of feces in the nest, or a predator avoidance strategy.

*Cinclodes pabsti* pairs generally clean a nesting cavity before reusing it, moving all the old contents of the nest to the front of the cavity (Belton, 1984). Images in Vizcarra *et al.* (2018) suggest that *C. taczanowskii* adopts the same behavior between reproductive events. Although it could not be concluded for *C. espinhacensis*, Costa *et al.* (2019) reported the presence of feathers, nesting materials, and eggshell fragments on the ground below nesting cavities, indicating that they had been cleaned. Therefore, this seems to be a common behavior within the genus. In fact, the entanglement of these materials in the vegetation below road cuts, along with the strong green coloration of moss that grows below the entrance tunnel, was highly effective for locating nesting cavities.

Our data on the complete set of cavities monitored over the course of three years showed that the reuse of cavities between breeding seasons ranged from 14.7% between the 2008-2009 and 2010-2011 seasons and 34.6% between the 2008-2009 and 2009-2010 seasons. Alternatively, the reuse percentage ranged from 26.9% in the 2008-2009 breeding season to 40.4% in the 2010-2011 breeding season, if the reuse between reproductive events within the same breeding season is considered. This is lower than the proportion of nesting cavities reused by C. fuscus (72.2%) across multiple seasons, recorded by Ojeda (2016), but higher than that used by C. espinhacensis (25.0% (one of four)) in both 2009 and 2012 (Costa et al., 2019). The reuse of nesting cavities, both within and between breeding seasons, could be a strategy to reduce the amount of time and energy spent excavating new cavities (Vergara et al., 2010). However, reusing previously successful nesting sites could also be a way of maximizing individual fitness because of the greater assurance of success (Aitken et al., 2002; Styrsky, 2005; Tobolka et al., 2013), a feature termed as an "ecological magnet" by Hickey (1942). Indeed, Ojeda (2016) recorded that birds did not reuse four cavities located near the ground in which nesting had been unsuccessful in three previous years. Burrows in the southern Brazilian highland grasslands persist for many years until the road cut erodes, making them suitable for use for many years. In fact, the use of several nesting cavities has been recorded continuously for over 12 years, and several pairs marked with colored bands have used the same cavities over multiple years (unpublished data).

Hatchlings of *C. pabsti* are similar to their congeneric species with respect to the eyes, ears, skin color, distribution of natal down feathers (neossoptiles), and reliance on parental care. This includes *C. comechingonus*, *C. olrogi* (Salvador & Salvador, 2012), and *C. espinhacencis* (Costa *et al.*, 2019). The body mass of *C. comechingonus* nestlings ranged from 4.0 to 4.3 g. This is lower than the average egg mass  $(5.1 \pm 0.3 \text{ g})$  and mean mass of *C. pabsti* nestlings recorded in this study  $(6.0 \pm 1.0 \text{ g})$ . Similar to the onset of incubation, hatching and fledging seemed to be highly synchronized. The high degree of similarity in the body mass of nestlings observed across several

growth stages, even though they may initially be different at hatching, reinforces the hypothesis of synchrony in the hatching and development of nestlings. This agrees with the findings reported for other species in the genus of Cawkell & Hamilton (1961).

*Cinclodes pabsti* exhibit biparental care at all stages of the breeding cycle, similar to other species in the genus (Cawkell & Hamilton, 1961; Hahn *et al.*, 2005; Avalos & Gómez, 2014; Ojeda, 2016; Costa *et al.*, 2019). However, the time spent in the cavity by the parents decreased as the days passed, and on no occasion were the parents recorded feeding the young. This was similar to the observation recorded in *C. aricomae* (Avalos & Gómez, 2014). A pair foraging with three juveniles was recorded in a field of low grass on two occasions in our study. However, fledglings were not recorded in their parents' territory in either of the cases, as identified by using colored bands in adults and fledglings. Similarly, foraging family groups in *C. o. baeckstroemii* usually consist of two adults and two to three juveniles (Hahn *et al.*, 2005).

Recent studies in the southern Brazilian highland grasslands have shown that approximately 50% (Fontana et al., 2016) to 60% (Andrade et al., 2015) of the original grassland areas have been lost in the past decade (Andrade et al., 2015). Land use has led to losses in species richness and the biotic homogenization of grassland remnants (Staude et al., 2018). The conversion of highland grassland habitats is the most important predictor of the extinction risk of grassland birds (Machado & Loyola, 2013; Fontana et al., 2016). The areas to which C. pabsti is endemic cover only 125,000 km<sup>2</sup> (BirdLife International, 2021a, b) and are under high anthropic pressures due to the replacement of natural grasslands by agriculture, cultivated pastures, and forestry plantations (Nabinger et al., 2000; Overbeck et al., 2007; Repenning et al., 2010; Azpiroz et al., 2012; Fontana et al., 2016). The agrochemicals used for the crops of grassland areas are another problem that affect the quality of bird habitats (Rivera-Milán et al., 2004). Nevertheless, the effects of habitat modification on C. pabsti remain unclear, as information about their life history patterns is still incipient.

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# **AUTHORS' CONTRIBUTIONS**

JJZ: Conceptualization, Methodology, Field work, Visualization, Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. FC: Field work, Visualization, Investigation, Data curation, Formal analysis, Writing – original draft. APCN: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review. All the authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper.

## **CONFLICTS OF INTEREST**

Authors declare there are no conflicts of interest.

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