# Additional breeding data for Ceará Gnateater Conopophaga cearae, with a review of the breeding biology of the Conopophagidae

Authors: Vieira, Odilon, Crozariol, Marco Aurélio, Ferreira, Talita de Andrade, Capdevile, Tomás Gonçalves, Caetano, Carlos Augusto, et al.

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# Additional breeding data for Ceará Gnateater *Conopophaga cearae*, with a review of the breeding biology of the Conopophagidae

*by Odilon Vieira, Marco Aurélio Crozariol, Talita de Andrade Ferreira, Tomás Gonçalves Capdevile, Carlos Augusto Caetano, Fábio de Paiva Nunes, Francisco Werlyson Pinheiro & Ileyne Tenório Lopes*

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*http://zoobank.org/urn:lsid:zoobank.org:pub:6B1122FE-E7C5-4A6C-B913-CBC65C37F8A5*

Summary.—We present data on the breeding biology of Ceará Gnateater *Conopophaga cearae* obtained during field work in the Serra de Baturité region, Ceará, Brazil, between 2017 and 2023: five nests, nine eggs, one nestling, one fledgling and a broken-wing display were documented. We also searched for specimens in two Brazilian ornithological collections, which resulted in an additional nest, two eggs and five specimens with evidence of breeding condition. Finally, we review available breeding data for the Conopophagidae, revealing that breeding biology information for the family is largely confined to two of the 11 currently recognised species.

The Conopophagidae is a small family of Neotropical birds that comprises two genera, *Pittasoma* and *Conopophaga*, and 11 species (Remsen *et al*. 2023) that inhabit the forest understorey from Costa Rica to northern Argentina (Greeney 2018, Winkler *et al*. 2020). The shared history between these genera is supported by molecular analysis (Rice 2005a,b, Moyle *et al*. 2009, Ohlson *et al*. 2013, Harvey *et al*. 2020), as well as similarities in morphology, bioacoustics and aspects of breeding (Rice 2005b).

In common with many bird taxa in the Neotropics, the breeding biology of the Conopophagidae is poorly known (Xiao *et al*. 2017, Greeney 2018) despite that basic information (e.g., nest and egg descriptions) exists for almost all species (Whitney 2003, Greeney 2018, del Hoyo *et al*. 2020, Lizarazo & Londoño 2022, Pereira *et al*. 2022). Recent studies have contributed by adding new data or improving existing information for the breeding biology of some of the family (e.g., Studer *et al*. 2019, Bodrati & Di Sallo 2020, Lizarazo & Londoño 2022, Pereira *et al*. 2022, Alarcón *et al*. 2023), although there are still many knowledge gaps, especially for the restricted-range species. Ceará Gnateater *Conopophaga cearae* represents one such gap, as there is, for example, no formal descriptions of the nest, eggs, nestling or fledgling (Greeney 2018, del Hoyo *et al*. 2020, Pereira *et al*. 2022). Formerly considered a subspecies of Rufous Gnateater *C. lineata* (Whitney 2003, Batalha-Filho *et al*. 2014), it is endemic to north-east Brazil, where it occurs in several disjunct populations, in northern Ceará (type locality, Serra de Baturité), Rio Grande do Norte, Alagoas and north-central Bahia (Chapada Diamantina), generally in humid regions and montane forests (*Brejos de altitude*) (Greeney 2018). Habitat loss and isolation of its populations are major threats to this species, which in Brazil is currently treated as Endangered (EN), with an Area of Occupancy estimated at just 144 km$^2$ (ICMBio 2018). Only recently its global conservation status was reclassified from Least Concern to Near Threatened (BirdLife International 2022), and it is listed as EN for the state of Ceará (Ceará 2022). This underscores the urgent need for life history data for this threatened and still poorly known endemic.



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We provide the first descriptions of the nest, eggs, nestling, fledgling and 'broken-wing' distraction display for *C. cearae*. In addition, we present an updated review of the breeding biology of the Conopophagidae, to reflect what is known and to highlight characteristics shared between species.

## Methods

All nests, eggs and young (nestling and fledgling) described here were found in the Serra de Baturité, Guaramiranga and Pacoti municipalities, Ceará, Brazil. The Serra de Baturité is an enclave of evergreen, montane forest within the semi-arid Caatinga biome. It encompasses approximately 20,000 ha of forest remnants (Bencke *et al*. 2006), with elevation averaging between 600 and 800 m but reaching 1,115 m at Pico Alto (Pinheiro & Silva 2017). The region is considered an Important Bird Area (IBA CE03) under BirdLife International criteria and one of the most biodiverse areas in north-east Brazil. It harbours both Amazonian and Atlantic Forest species, as well as endemics and endangered taxa (Bencke *et al*. 2006, Albano & Girão 2008).

We obtained data on active nests of *C. cearae* in the field, and searched for additional material (nests, eggs, young, or adults with gonad or brood-patch data recorded on the tags) in two Brazilian ornithological collections: Museu de História Natural do Ceará Prof. Dias da Rocha, Universidade Estadual do Ceará, Pacoti (MHNCE) and Museu Nacional, Universidade Federal do Rio de Janeiro (MN). Following Crozariol *et al*. (2016), for specimens without gonadal measurements, the representations (drawings) of the gonads on their labels were measured using callipers accurate to 0.01 mm.

Species taxonomy follows Greeney (2018) for nomenclature and distribution, which was used also to identify *C. cearae* specimens at MN that were still labelled *C. lineata*. Nests were classified according to Simon & Pacheco (2005) and the coloration of two eggs was compared to a standard colour guide (Smithe 1975). Some nests and eggs could not be measured or followed in the field, but one nest was collected, after it was abandoned by the adults, and is now at MHNCE.

To review breeding biology of the Conopophagidae, we searched Google Scholar, Scielo, Biodiversity Heritage Library and Web of Science using the keywords 'description', 'nest', 'eggs', 'nestlings', 'fledglings', 'incubation', 'breeding', 'gnateater', 'antpitta', 'Conopophaga' and 'Pittasoma' in English and Portuguese. We also searched specialised literature (e.g., Sick 1997, Whitney 2003, Greeney 2018, Winkler *et al*. 2020). Data were organised in six categories: (i) breeding period; (ii) nest architecture; (iii) eggs, clutch size and incubation period; (iv) nestling, fledgling and parental care; (v) reproductive success; and (vi) mating system. To better compare nests and eggs between genera, photographs of a Black-crowned Antpitta *Pittasoma michleri* nest and eggs at the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) were obtained. These specimens constitute the main breeding data available for *Pittasoma*, but images of the nest and eggs were not presented in the original description (Wetmore 1972) and other sources that analysed this material (e.g., Greeney 2018). To compare measurements between species, we calculated the mean, standard deviation, range and sample size in R (R Core Team 2022). For each measurement, the respective sample included the values from each study; averages, isolated values presented separately for each object, or total ranges. For elliptical / oblong nests, in which diameters (internal and external) are usually measured at two perpendicular angles, we calculated the mean of these two values for the sample. Measurements are summarised in Table 1, and the data and scripts used are available for download at https://github.com/OdilonVieira/conopophagidaeNesting.



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TABLE 1

Clutches and measurements of nests and eggs for some Conopophagidae spp.: ED = external diameter (mm); ID = internal diameter (mm); H = height (mm); D = depth (mm); HAG = height above ground (cm); L = length (mm); W = width (mm); FW = fresh weight (g); CS = clutch size (mean). Notation: mean (± standard deviation, range, sample size). Sources: 1 = Nehrkorn (1899), 2 = von Ihering (1900), 3 = Oates & Reid (1903), 4 = Velho (1932), 5 = Frisch & Frisch (1964), 6 = Schönwetter (1967), 7 = Kreuger (1968 *apud* Greeney 2018), 8 = Wetmore (1972), 9 = Hilty (1975), 10 = Willis *et al*. (1983), 11 = Fraga & Narosky (1985), 12 = Straube (1989), 13 = Begazo & Valqui (1998), 14 = Alves *et al*. (2002), 15 = Dreyer (2002), 16 = Hillman & Hogan (2002), 17 = Whitney (2003), 18 = Sánchez & Aponte (2006), 19 = Marini *et al*. (2007), 20 = Lima & Roper (2009), 21 = Leite *et al*. (2012), 22 = Lopes *et al*. (2013), 23 = Maurício *et al*. (2013), 24 = Londoño (2014), 25 = Stenzel & Souza (2014), 26 = Greeney (2018), 27 = Studer *et al*. (2019), 28 = Bodrati & Di Sallo (2020), 29 = Lizarazo & Londoño (2022), 30 = Pereira *et al*. (2022), 31 = Alarcón *et al*. (2023). (*) estimated by Greeney (2018). (**) statistics taken from source.

| Species | Nest cup | | | | | Eggs | | | | Source |
|---|---|---|---|---|---|---|---|---|---|---|
| | ED | ID | H | D | HAG | L | W | FW | CS | |
| *P. michleri* | 200–240* (*n* = 1) | 90 (*n* = 1) | - | 60* (*n* = 1) | 100 (*n* = 1) | 31.75 (± 0.64, 31.3–32.2, *n* = 2) | 23.25 (± 0.35, 23.0–23.5, *n* = 2) | - | 2 (*n* = 1) | 8, 26 |
| *C. melanops* | 123 (± 18.38, 110–136, *n* = 2) | 64.53 (± 13.88, 55–85, *n* = 4) | 83.67 (± 17.62, 65–100, *n* = 3) | 43.2 (± 5.06, 37.8–50.0, *n* = 4) | 87.84 (± 69.36, 20–265, *n* = 10) | 22.24 (± 0.78, 21.0–23.1, *n* = 8) | 17.05 (± 0.21, 16.8–17.5, *n* = 8) | 3.4 (± 0.16, 3.21–3.6, *n* = 4) | 1.99 (± 0.09, 1–2, *n* = 137) | 2, 6, 12, 14, 17, 20, 25, 27 |
| *C. aurita* | 123 (*n* = 1) | 66.5 (± 12.02, 58–75, *n* = 2) | 96 (*n* = 1) | 30 (± 2.83, 28–32, *n* = 2) | 68 (± 16.97, 56–80, *n* = 2) | 22.55 (± 0.49, 22.2–22.9, *n* = 2) | 17.5 (*n* = 2) | - | 1.5 (± 0.71, 1–2, *n* = 2) | 17, 21 |
| *C. peruviana* | 89.12 (± 15.84, 68.0–102.5, *n* = 4) | 59.38 (± 3.54, 55.0–62.5, *n* = 4) | 65.67 (± 4.04, 62–70, *n* = 3) | 38 (± 2.45, 35–40, *n* = 4) | 52.5 (± 20.83, 30–84, *n* = 6) | 21.14 (± 0.53, 20.5–21.9, *n* = 5) | 16.3 (± 0.23, 16.1–16.7, *n* = 5) | 2.93 (± 0.32, 2.7–3.3, *n* = 3) | 2 (*n* = 19) | 13, 15, 16, 26 |
| *C. cearae* | 100.52 (± 13.84, 85.0–111.6, *n* = 3) | 65.2 (± 4.85, 60.0–69.6, *n* = 3) | 74.5 (± 21.23, 50.0–87.5, *n* = 3) | 44.33 (± 0.95, 43.65–45.0, *n* = 2) | 42 (± 3.46, 40–46, *n* = 3) | 21.65 (± 1.04, 20.0–22.8, *n* = 6) | 17.32 (± 1.02, 16.0–18.05, *n* = 6) | - | 1.83 (± 0.41, 1–2, *n* = 6) | this study |
| *C. roberti* | 89.55 (± 14.78, 79.1–100.0, *n* = 2) | 64.7 (± 7.5, 59.4–70.0, *n* = 2) | 105 (*n* = 1) | 42.8 (± 3.11, 40.6–45.0, *n* = 2) | 39.9 (± 25.63, 15–75, *n* = 4) | 20.43 (± 0.75, 20.0–21.3, *n* = 3) | 17.07 (± 0.12, 17.0–17.2, *n* = 3) | 3.1 (± 0.1, *n* = 23)** | 2 (*n* = 18) | 4, 17, 30 |
| *C. lineata* | 121 (± 17.07, 99–150, *n* = 9) | 63.89 (± 5.84, 55–74, *n* = 9) | 73 (± 18.92, 50–100, *n* = 6) | 38.33 (± 8.96, 29–55, *n* = 9) | 59.56 (± 48.16, 9–200, *n* = 16) | 22.36 (± 0.88, 20–24, *n* = 32) | 17.38 (± 0.52, 16.4–18.25, *n* = 32) | 3.36 (± 0.38, 2.8–3.9, *n* = 10) | 2.14 (± 0.6, 1–4, *n* = 35) | 1–3, 5–7, 10, 11, 17, 19, 22, 23, 28 |
| *C. castaneiceps* | 112.31 (± 14.12, 91.75–122.15, *n* = 4) | 62.85 (± 9.35, 50–70.6, *n* = 5) | 75.97 (± 37.86, 50.8–131.0, *n* = 4) | 44.83 (± 5.28, 39.1–49.5, *n* = 3) | 69.6 (± 21.76, 50–100, *n* = 5) | 22.5 (± 1.1, *n* = 3)** | 17.9 (± 0.9, *n* = 3)** | 3.9 (± 1.5, *n* = 3)** | 2 (*n* = 5) | 9, 29, 31 |
| *C. ardesiaca* | 90 (*n* = 1) | 75 (*n* = 1) | 85 (*n* = 1) | 60 (*n* = 1) | 110 (*n* = 1) | 22.1 (± 1.13, 21.3–22.9, *n* = 2) | 16 (± 0.85, 15.4–16.6, *n* = 2) | - | 2 (*n* = 2) | 18, 24 |



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## Results

The search of museum collections resulted in one nest, two eggs, at least five specimens of *C. cearae* in breeding condition and seven others with gonad drawings on their tags. The field work resulted in five nests, nine eggs (four of which were measured) and one nestling being discovered. All the nests presented here are of the type low cup / base, placed on tree branches or saplings in the understorey of forest remnants, open on top and close to the ground (Table 1). Constructed of dry leaves, twigs and other vegetable fibres, like a pile of debris, their exteriors were formed of larger leaves and thicker sticks, and interiors were lined with thin sticks or petioles. Eggs were ovoid, pale cream with a darker area concentrated near or on the larger pole. See below for details.

***Museum specimens***.—Three adult males taken in October to December at MHNCE had gonad measurements (MHNCE 200, 201, 341). Only MHNCE 341 was collected away from the Serra de Baturité (Itatira municipality). Two specimens with brood patches are held at MN, both males (MN 42745, MN 42746) collected at Chapada Diamantina, Ibicoara, Bahia, on 7 December 1995. Another seven specimens at MN have drawings on their tags indicating that the gonads were visible when prepared, but without measurements: MN 34554, 34555, 35001, 36378, 36938, 43276 and 43309, collected in February to July (see Table 2).

***Nest 1***.—A nest at MHNCE (480) was collected on 22 February 1994 at Sítio São José (04°13'57.78"S, 38°57'8.02"W), Batalha, Guaramiranga. It was 40 cm from the ground, with broad leaves at the base, many petioles of which the finest were in the lining, and some long bamboo leaves around the egg cup, on the edge and externally. It was supported by the

TABLE 2
Specimens of Ceará Gnateater *Conopophaga cearae* in Museu de História Natural Prof. Dias da Rocha, Universidade Estadual do Ceará, Pacoti (MHNCE) and Museu Nacional / Universidade Federal do Rio de Janeiro (MN) with information about gonad or brood patch (*measured from drawings on labels).

| Voucher | Locality | Date | Sex | Skull | Brood patch (mm) | Gonad (mm) |
|---|---|---|---|---|---|---|
| MHNCE 200 | Guaramiranga, Ceará | 10 October 1987 | Male | Ossified | - | 3.0 × 2.8 |
| MHNCE 201 | Aratuba, Ceará | 23 December 2005 | Male | Ossified | - | 7.0 × 2.5 |
| MHNCE 341 | Itatira, Ceará | 24 January 2007 | Male | Ossified | - | 6.5 × 5.0 |
| MN 34554 | Guaramiranga, Serra de Baturité, Ceará | 9 February 1986 | Female | Ossified | - | * Ovary: 4.6 × 3.25 |
| MN 34555 | Guaramiranga, Serra de Baturité, Ceará | 9 February 1986 | Male | Ossified | - | * Testes: right, 2.85 × 1.68; left, 4.13 × 2.73 |
| MN 35001 | Fazenda Riachão, Quebrangulo, Alagoas | 24 February 1987 | Male | - | - | * Testes: right, 4.63 × 3.05; left, 5.43 × 3.47 |
| MN 36378 | Gama, Sítio São Luiz, Pacoti, Ceará | 3 April 1989 | Female | - | - | * Ovary: 5.0 × 3.63 |
| MN 36938 | Pacoti, Ceará | 26 February 1990 | Female | Ossified | - | * Ovary: 3.92 × 3.52 |
| MN 42745 | Chapada Diamantina, Ibicoara, Bahia | 7 December 1995 | Male | Ossified | 20.0 × 18.6 | * Testes: right, 8.70 × 5.69; left, 9.17 × 5.08 |
| MN 42746 | Chapada Diamantina, Ibicoara, Bahia | 7 December 1995 | Male | Semi-ossified | 20 × 17 | * Testes: right, 8.18 × 3.83; left, 8.14 × 3.43 |
| MN 43276 | Vale do Rio do Cabelo, João Pessoa, Paraíba | 5 May 1997 | Male | Ossified | - | * Testes: right, 4.0 × 2.47; left, 4.0 × 2.66 |
| MN 43309 | Vale do Rio do Cabelo, João Pessoa, Paraíba | 2 July 1997 | Female | Ossified | - | * Ovary: 3.88 × 3.47 |


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fresh branches of a recently pruned tree and measured 111.6 mm (external diameter) and 50 mm (height). Two eggs in this nest were both Pale Pinkish Buff (Color 121D) but darker at the large pole (Robin Rufous, Color 340): MHNCE 495, 22.8 × 18.0 mm, and MHNCE 496, 21.7 × 18.0 mm.

***Nest 2***.—Parque das Trilhas (04°15′55″S, 38°55′55″W, 856 m), Guaramiranga, 6 February 2017, found by FN with one young (Fig. 1A) that fledged sometime prior to 20 February 2017 (no measurements taken).

***Nest 3***.—Hotel Remanso (04°14′35″S, 38°55′49″W; 812 m), Guaramiranga, 30 January 2019: also found by FN, it was *c*.60 mm in internal diameter, and held two eggs (Fig. 1B) one of which subsequently disappeared, whilst the other hatched on an unknown date, and the nestling was observed last on 10 February. On this date, the nestling (Fig. 1C) had its eyes open and appeared well grown and feathered, occupying almost the entire nest cavity, and was well camouflaged. Its bill was grey, darker at the tip and edges, paler at the base, with a yellowish-white rictus. A bare periophthalmic region contrasted with its dark brown plumage, albeit with irregular paler (ochre) stripes evident on the back and wing-coverts, giving the plumage a mottled appearance.

***Nest 4***.—RPPN Sítio Lagoa (04°12′20.4″S, 38°57′49.4″W; 923 m), Guaramiranga, 17 March 2020, found with two eggs at 06.40 h by MAC & OV (Fig. 1D). On 18–19 March the female was observed at the nest but the eggs disappeared four days later (on 23 March). The nest was then collected (MHNCE 470). It was sited 46 cm above ground, measured from the nest's upper edge, and had a large base of longer sticks that supported the cup between the branches of an unidentified shrub. Including the base of sticks, it measured 170 × 235 mm in diameter, and its height varied between 65 and 110 mm to the upper edge of the nest. The nest's cup measured 85.9 × 124.0 mm (external diameter), 64.25 × 74.95 mm (internal diameter) and 43.65 mm (depth in the centre). Materials were mainly sticks, dry leaves and petioles in the lining, with a layer of leaves and tree bark above the base of sticks. The nest was collected on a rainy day, when it weighed 158 g, but its dry weight (assessed on 29 May 2020) was 45 g. Several invertebrates were found among the nest materials, including diplopods, annelids and unidentified larvae. The eggs measured 22.64 × 18.05 mm and 21.75 × 17.85 mm, were ovoid, pale ivory or slightly pink in colour, with a darker, reddish (salmon-coloured) larger pole, in which were concentrated a few small, irregular and discrete, paler or darker speckles (Fig. 1D).

***Nest 5***.—RPPN Sítio Lagoa, Guaramiranga, 6 February 2022, found by FN while the male was incubating two eggs (Fig. 1 E–F); it was not visited again until 10 March, when the nest was empty.

***Nest 6***.—Queijo (04°16′30.02″S, 38°58′21.87″W; 956 m), Guaramiranga, 11 February 2022, found by FWP with two eggs (Fig. 1G). It was 40 cm above ground, sited in a shrub fork, surrounded by young branches. It measured 45 mm deep, 86 mm tall, 66 mm internal diameter and 85 mm external diameter; and was lined with thin petioles and twigs, darker than the exterior, which was constructed of large dry leaves (bamboo and other plants) around the cup, and sticks at the base. The eggs measured 20 × 16 and 21 × 16 mm, and were whitish, with brown spots concentrated at the larger pole.

***Fledgling and 'broken-wing' display***.—At Sítio Boa Vista (04°12′55″S, 38°54′00″W; 855 m), Pacoti, 2 January 2023, a fledgling was found by MAC, perched 1.5 m above ground on a horizontal branch. It was noticed due to the restless behaviour of an adult female nearby, which vocalised frequently and occasionally fluttered its wings while singing. The fledgling remained motionless and silent, permitting a photo to be taken (www.wikiaves.com.br/5236285). It eventually flew, still with evident difficulty. Its plumage was brown, mottled with irregular darker and paler stripes, a bare dark grey periophthalmic region,


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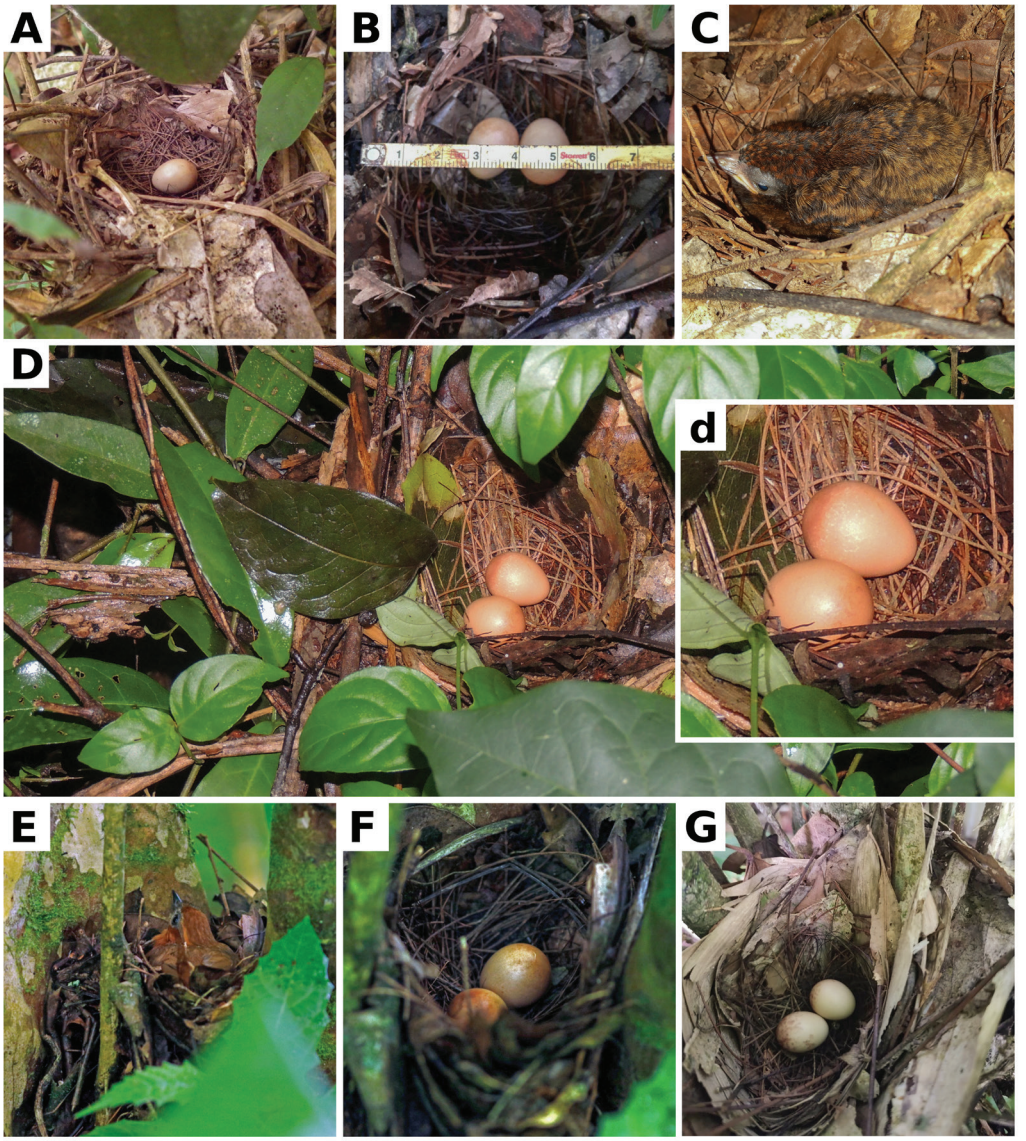


Figure 1. Breeding data for Ceará Gnateater *Conopophaga cearae* in the Serra de Baturité, Ceará, Brazil: (A) nest and egg at Parque das Trilhas, Guaramiranga, 6 February 2017; (B) nest and eggs at Hotel Remanso, Guaramiranga, 30 January 2019, and the nestling (C) on 10 February; (D) nest (now MHNCE 0470) and eggs (d) at RPPN Sítio Lagoa, Guaramiranga, 17 March 2020; (E–F) the other nest at RPPN Sítio Lagoa with male incubating, 6 February 2022; (G) nest and eggs at Queijo, Guaramiranga, 11 February 2022 (A–C, E–F: Fábio de Paiva Nunes; D: Odilon Vieira; G: Francisco Werlyson Pinheiro)

dark brown eyes and a yellowish gape. When it flew, the young gave two or three calls, whereupon the female approached, even more agitated. While MAC was searching for the young, the female landed on the ground in a clear area of a narrow trail, 6 m away, and performed a 'broken-wing' distraction display, wings drooping and body lowered, recalling a wounded animal, before starting to jump slowly on the ground away from where the juvenile was hiding silently. The display ceased immediately after MAC took just two steps towards the female.



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## Breeding biology of the Conopophagidae

***Breeding period.***—Reports of breeding (active nests, eggs, nestlings / fledglings, gonadal data and brood patches) for the Conopophagidae are sparse, with a few exceptions among species subject long-term studies: Hooded Gnateater *C. roberti* (Pereira *et al*. 2022), Black-cheeked Gnateater *C. melanops* (e.g., Studer *et al*. 2019) and *C. lineata* (e.g., Willis *et al*. 1983, Bodrati & Di Sallo 2020). For *C. lineata* reports are available from September to November in northern Argentina (e.g., Bodrati & Di Sallo 2020) and August–January in southern and south-east Brazil (Greeney 2018). Similarly, in southern and south-east Brazil, *C. melanops* nests from August to February (*C. m. melanops*; Greeney 2018) and September–June in north-east Brazil (*C. m. nigrifrons*; Studer *et al*. 2019; and at least January in *C. m. perspicillata*; Greeney 2018). For *C. roberti*, in northern (Pará) and north-eastern (Maranhão) Brazil, the season ranges from November to April (Whitney 2003, Pereira *et al*. 2022). Other species in northern and / or north-west South America nest apparently year-round, with reports from July–March or May, e.g., for Chestnut-belted Gnateater *C. aurita* (Oniki & Willis 1982, Tostain *et al*. 1992, Leite *et al*. 2012, Greeney 2018), Ash-throated Gnateater *C. peruviana* (Parker 1982, Dreyer 2002, Hillman & Hogan 2002, Greeney 2018) and Chestnut-crowned Gnateater *C. castaneiceps* (Hilty 1975, Greeney 2018, Lizarazo & Londoño 2022, Alarcón *et al*. 2023). The season for Slaty Gnateater *C. ardesiaca* lasts from June to November (Remsen 1984, Sánchez & Aponte 2006, Greeney 2018), with most of these records involving *C. a. ardesiaca* (Greeney 2018). For Black-bellied Gnateater *C. melanogaster*, there is only an observation of an inactive nest presumed to belong to this species in Amazonas, northern Brazil, in July (Greeney 2018). In the case of *Pittasoma*, active nests and observations of fledglings of Black-crowned Antpitta *P. m. michleri* are available from Panama in April and July (Karr 1971, Wetmore 1972). Our study found out that *C. cearae* breeds at least in December to March, possibly until April (see Fig. 2).

***Nest architecture.***—Nests of most species in the family have been formally described, except Rufous-crowned Antpitta *Pittasoma rufopileatum*, *Conopophaga melanogaster* and, until now, *C. cearae* (Greeney 2018, Winkler *et al*. 2020). However, Greeney (2018) commented on an unpublished report by B. M. Whitney of two large, inactive,

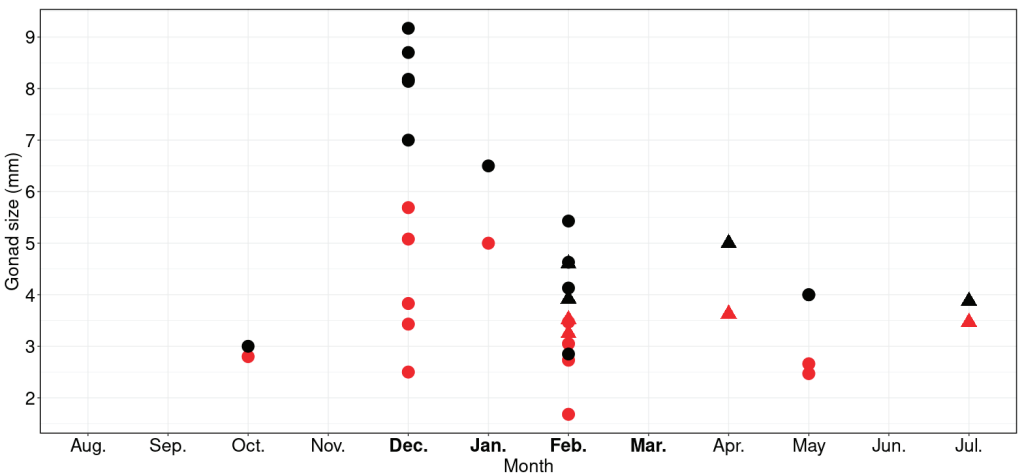


Figure 2. Gonad size of specimens of Ceará Gnateater *Conopophaga cearae* held in Museu de História Natural Prof. Dias da Rocha, Universidade Estadual do Ceará, Pacoti (MHNCE) and Museu Nacional / Universidade Federal do Rio de Janeiro (MN), testes (dots) and ovary (triangles), length (black) and width (red); in bold (December–March), the breeding period with evidence (nests, eggs, nestlings and brood patch).



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Figure 3. Nest (A) and eggs (B) of Black-crowned Antpitta *Pittasoma michleri* collected by A. Wetmore and W. M. Perrygo on the upper Jaqué River, Panama, 14 April 1947, housed in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM B40975) (© Jacob Saucier)

*Conopophaga*-like nests found in July on the Aripuanã River, Amazonas, Brazil, just 10 m from where a juvenile *C. melanogaster* was photographed. For the other nine species, nests were described using different terms (e.g., cup, bowl, semisphere, bulky or 'low / cup base' *sensu* Simon & Pacheco 2005), placed on a base of dry leaves and sticks, near the ground or >1.5 m above it as in *C. melanops* and *C. lineata* (Table 1). Nest materials can be dry leaves, rootlets, petioles, twigs, lichens, vegetable fibres and rhizomorphic fungi, lined with some of these same materials, e.g., dry leaves, twigs and grass stems (Greeney 2018; Figs. 1–3). Rhizomorphic fungi are mentioned as nest material of *C. ardesiaca* (Sánchez & Aponte 2006), *C. peruviana* (Greeney 2018), *C. castaneiceps* (Lizarazo & Londoño 2022), *C. aurita* (Tostain *et al*. 1992), *C. lineata* (Greeney 2018, Bodrati & Di Sallo 2020) and *C. melanops* (Sick 1957, Straube 1989), identified as *Marasmius* for the last three species. Conopophagidae nests are exposed or sometimes concealed by the surrounding vegetation, fixed to a diversity of substrates, such as palm trunks or leaves (Wetmore 1972, Whitney 2003), saplings (Dreyer 2002, Whitney 2003, Lopes *et al*. 2013, Lizarazo & Londoño 2022), shrubs (Snethlage 1935, Marini *et al*. 2007, Stenzel & Souza 2014), bamboo (Fraga & Narosky 1985, Sánchez & Aponte 2006), pteridophytes (Hilty 1975, Hillman & Hogan 2002, Leite *et al*. 2012, Maurício *et al*. 2013), epiphytic plants (Alarcón *et al*. 2023), bromeliads (Alves *et al*. 2002, Lizarazo & Londoño 2022, Pereira *et al.* 2022), heliconids (Straube 1989), broken tree trunks, liana accumulations, and fallen branches (Studer *et al*. 2019, Pereira *et al.* 2022). Measurements of nests are similar among almost all *Conopophaga* spp., with range overlap and close averages, mainly in internal diameter and depth. However, in the version of Lizarazo & Londoño (2022) available at the time of writing, two nests of *C. castaneiceps* were reported as being just 3.9 and 4.95 mm deep. Nevertheless , we have confirmed that this was a mistake and the correct measurements


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were 39.1 and 49.5 mm, respectively (J. Lizarazo *in litt*. 2023), which perfectly align with the pattern otherwise observed in this genus.

Biparental partitioning of nestbuilding and maintenance have been reported in *Conopophaga*, including *C. roberti* (Whitney 2003, Pereira *et al*. 2022), *C. peruviana* (Greeney 2018) and *C. melanops* (Stenzel & Souza 2014), although Lima & Roper (2009) observed only males of the last-named species constructing the nest. The duration of nestbuilding varies among the few available reports: eight days for *C. roberti* in north-east Brazil (Pereira *et al*. 2022) and 4–5 (Stenzel & Souza 2014) or 14–20 days (Lima & Roper 2009) for *C. melanops* in south-east and southern Brazil, respectively. For *C. melanops* the nest cycle (egg-laying to fledging) ranged from 38–44 days in southern Brazil (three nests reported by Lima & Roper 2009) and a max. of 32 days in the north-east (two nests: Studer *et al*. 2019). For *C. roberti* (Pereira *et al*. 2022) the pair bond is maintained after a failed nesting attempt (also in *C. melanops*: Lima & Roper 2009), but nest reuse or pairs successfully raising two broods in a season have not been reported. Nest site selection is unknown for all species (Greeney 2018), but the habit of starting to build during rain has been reported for *C. melanops*, perhaps to facilitate the use of dry leaves in the nest (Stenzel & Souza 2014).

***Eggs, clutch size and incubation period***.—Until now, three species lacked egg descriptions: *Pittasoma rufopileatum*, *Conopophaga melanogaster* and *C. cearae*. However, Greeney (2018) commented on three eggs described by Kreuger (1968) from Bahia (without precise locality) as belonging to *C. l. lineata*, which possibly pertain to *C. cearae*. They measured 22.15–23.0 × 17.2–17.85 mm and were reddish cream with a few, small pale speckles, mostly at the large end (Greeney 2018). The eggs of the other species were variously described as ovoid, elliptical, conical, oval, or spheroidal. Measurements are quite similar, except *Pittasoma michleri*, which has the biggest eggs (*c*.10 mm longer than most *Conopophaga* spp., Table 1, Fig. 3). Egg fresh weight is rarely recorded (see Table 1) and, as it must vary with the embryo's development, would be even more difficult to compare. Coloration is usually pale, but can vary within species or clutches, ranging from near-white to cream-beige or buffy brown, with a few spots and a darker region at the large pole—sometimes referred to as the 'cap' or 'ring' (Greeney 2018).

Clutch size is most frequently reported as two (Table 1), with some cases of fewer or more (3–4) eggs or nestlings in a nest, all of the latter in *C. lineata* from south-east Brazil (Frisch & Frisch 1964, Marini *et al*. 2007, Maurício *et al*. 2013) to northern Argentina (Bodrati & Di Sallo 2020). The incubation period is known only for *C. melanops* and *C. lineata*, 17–18 days (Alves *et al*. 2002, Whitney 2003, Stenzel & Souza 2014, Studer *et al.* 2019) and 14 days (Whitney 2003), respectively, with contributions from both sexes, but males spend more time incubating diurnally than females, which are responsible for nocturnal incubation, as also reported for *C. peruviana* (Greeney 2018).

***Nestling, fledgling and parental care***.—Information exists regarding nestling development of some *Conopophaga*, e.g., *C. castaneiceps* (Hilty 1975, Lizarazo & Londoño 2022), *C. lineata* (Willis *et al*. 1983, Bodrati & Di Sallo 2020), *C. peruviana* (Hillman & Hogan 2002), *C. melanops* (Studer *et al*. 2019) and *C. roberti* (Pereira *et al*. 2022). Like other passerines nestlings hatch naked, with eyes closed and regions bordering (e.g., rictus) or inside the bill (e.g., inner surface and throat) brightly coloured (e.g., white, yellowish or orange), contrasting with the dark bill. Based on nestling development of *C. lineata* (Willis *et al*. 1983, Bodrati & Di Sallo 2020) and *C. castaneiceps* (Lizarazo & Londoño 2022), feather sheaths are visible at 3–4 days, start to open over the body at 6–7 days, and on the wings at 9–10 days; the eyes are open / half-open after 6–8 days; at 10–12 days plumage is well distributed on the body and head, and the eyes are completely open. Development in *C. roberti* is similar, except the eyes start to open at four days old, when feather sheaths are visible over the body


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(Pereira *et al*. 2022). Similarly, in *C. peruviana* the contour feathers start to open in the first week, and they are rather well covered in overall downy plumage at 8–10 days (Greeney 2018).

Nestling period is known for *C. lineata* (Willis *et al*. 1983, Whitney 2003, Bodrati & Di Sallo 2020), *C. melanops* (Stenzel & Souza 2014, Studer *et al*. 2019), *C. roberti* (Pereira *et al*. 2022) and *C. castaneiceps* (Lizarazo & Londoño 2022), in all of these species being *c*.2 weeks or a little more. In *C. lineata*, *C. melanops* and *C. castaneiceps* both sexes contribute to nestling care (brooding and feeding) and nest maintenance (faecal sac removal and structural repairs), with the female primarily responsible for nocturnal brooding (Willis *et al*. 1983, Studer *et al*. 2019, Lizarazo & Londoño 2022). Nocturnal brooding by males has been reported only for *C. castaneiceps* (Lizarazo & Londoño 2022). Partitioning of parental care is known for *C. aurita* (Willis 1985), *C. peruviana* (Greeney 2018) and *C. roberti* (Pereira *et al*. 2022), but the difference in effort, if any, is unrecorded. Distraction displays may be given near active nests, such as 'broken-wing' displays, accompanied by alarm calls. Both *Pittasoma* (*P. michleri*: Wetmore 1972) and *Conopophaga* (many species: Schunck & Mix 2021) are reported to give displays that could be interpreted as distraction displays, but formal descriptions like those of Leite *et al*. (2012) and Schunck & Mix (2021) are scarce. Our observations of adult female *C. cearae* expand the occurrence of this behaviour in the family. As noted by Greeney (2018), at least in *C. aurita* the postocular feathers can be used during this behaviour (see Leite *et al*. 2012 for images).

Descriptions of fledglings or juveniles exist for *C. melanops*, *C. castaneiceps*, *C. ardesiaca*, *C. peruviana*, *C. lineata*, *C. roberti*, *Pittasoma rufopileatum* (see Greeney 2018, Bodrati & Di Sallo 2020, Lizarazo & Londoño 2022, Pereira *et al*. 2022) and now for *C. cearae*. Based on fledgling development of *C. castaneiceps* (Hilty 1975, Lizarazo & Londoño 2022), *C. lineata* (Willis *et al*. 1983) and *C. roberti* (Pereira *et al*. 2022), nestlings fledge smaller and lighter than adults (Willis *et al*. 1983, Lizarazo & Londoño 2022, Pereira *et al.* 2022), when still unable to undertake long-distance flights (Pereira *et al.* 2022), attaining near-adult size in *c*.2 weeks, but still with a short tail and small head and bill (Willis *et al*. 1983). The young may remain with its parents for *c*.45 days post-fledging (Hilty 1975, Willis *et al*. 1983) when the plumage is still streaked but the tail reaches full length (Willis *et al*. 1983). During this phase young occasionally try to forage on the ground independently until they reach complete independence, and then forage alone on the same home territory for up to another 80 days (Willis *et al*. 1983).

***Reproductive success***.—The few species with information about reproductive success, *C. melanops*, *C. lineata* and *C. roberti*, evidently experience low survival rates.

For *C. lineata* in the Atlantic Forest, Willis *et al*. (1983) reported one successful nest (at least one nestling fledged and survived until the end of the study) in four that were monitored (25%) in a 21-ha forest fragment in south-east Brazil (São Paulo), Marini *et al*. (2007) and Marini (2017) reported three successful nests of nine monitored (33%; survival rate 0.966 $day^{-1}$) in fragments of 50–200 ha also in south-east Brazil (Minas Gerais), and Bodrati & Di Sallo (2020) observed one successful nest among five monitored (20%) in a large protected area in northern Argentina (Misiones). For *C. melanops*, Stenzel & Souza (2014) noted three successful nests of 13 monitored (23.07%) in a human-modified forest fragment in south-east Brazil (Rio de Janeiro), Lima & Roper (2009) reported four successful nests of 18 monitored (22%; survival rate 0.966 $d^{-1}$) in a large protected area in south Brazil (Paraná), and Studer *et al*. (2019) 23 successful nests of 114 monitored (20.2%; survival rate 0.883 $d^{-1}$, Mayfield nest success 12.9%) in a 4,469 ha protected area in north-east Brazil (Pernambuco / Alagoas). For *C. roberti*, Pereira *et al*. (2022) witnessed nine successful nests among 22 monitored (40.9%) in a 3,500-ha protected area in north-east Brazil (Maranhão).


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In these species, nest success is low mainly due to predation, desertion and environmental factors (Willis *et al*. 1983, Marini *et al*. 2007, Lima & Roper 2009, Stenzel & Souza 2014, Marini 2017, Studer *et al*. 2019, Bodrati & Di Sallo 2020, Pereira *et al*. 2022), but at least Willis *et al*. (1983) also mentioned infertile eggs. Total production of young is usually low, 0.36 per adult in *C. melanops* in south Brazil (Lima & Roper 2009) and 0.58 per adult female for *C. roberti* in north-east Brazil (Pereira *et al*. 2022). Studer *et al*. (2019) reported daily survival rates for *C. melanops* during the incubation and nestling periods in north-east Brazil (0.922 $d^{-1}$ and 0.958 $d^{-1}$), with predation the only cause of failure during the latter period.

***Mating system***.—*Conopophaga* are presumably monogamous, being frequently recorded in pairs year-round (Whitney 2003). *Pittasoma* are recorded in pairs too, at least when foraging (Krabbe & Schulenberg 2003). However, the specific mating system is still unknown for either genus. In *C. melanops* the pair bond may break after a nesting failure (Lima & Roper 2009). One or both pair members can disappear from the home territory, with no sign of predation, which Lima & Roper (2009) interpreted as territory / mate abandonment, suggesting that monogamy may not be permanent.

## Discussion

The nest of *Conopophaga cearae* described here conforms to the basic pattern in this genus: a cup of dry leaves and twigs placed over a base of debris, relatively close to the ground, surrounded by leaves, but sometimes very exposed above. Measurements are similar to almost all other descriptions of, e.g., *C. castaneiceps*, *C. roberti*, *C. peruviana* and others (see Table 1). An open nest sited relatively close above ground seems to be the rule in Conopophagidae, perhaps related to their foraging habits (see Willis 1991), with some species known to follow ants and forage both on the ground and from perches (Willis 1985, Alves & Duarte 1996).

The eggs described here are similar to those reported by Greeney (2018) and described by R. Kreuger from Bahia, at least in size. However, this is the basic egg pattern in other *Conopophaga* that occur there (*C. melanops* and *C. lineata*), making it impossible to know (given the lack of precise locality) if these eggs really belonged to *C. cearae*, as Greeney (2018) supposed. Lizarazo & Londoño (2022) compared the egg pattern in some *Conopophaga* spp. based on field data for *C. castaneiceps* and literature for the other seven species. They reported extensive variation in egg coloration between species, from shells with scattered markings (*C. peruviana*, *C. lineata* and *C. aurita*) to intermediate (*C. ardesiaca* and *C. roberti*) or dense markings (*C. castaneiceps* and *C. melanops*). At least two factors challenge such comparisons. Firstly, the lack of standardisation in descriptions of eggs of Conopophagidae (as in nest measurements) makes some information subjective, e.g., egg coloration / shape and the density, distribution and shape of markings, especially without photographs or specimens in ornithological collections; secondly, egg coloration and shape can vary considerably within species / clutches, as already noted by Greeney (2018) for some *Conopophaga*. Indeed, our data document colour variation in *C. cearae* eggs, from more cinnamon to pale and whitish, with some profusely spotted at the large pole (see Fig. 1), despite localities being relatively close to each other.

Based on nestling development in other *Conopophaga*, the nestling of *C. cearae* found on 10 February 2019 (Fig. 1C) was probably 9–11 days old, suggesting that the nest was first found during the final days of the incubation period. Mottled plumages (streaked, spotted, 'V-shaped' markings) are also recorded in nestlings / fledglings of other *Conopophaga*, e.g., *C. lineata*, *C. peruviana*, *C. ardesiaca*, *C. roberti* and *C. castaneiceps* (see Greeney 2018, Bodrati & Di Sallo 2020, Pereira *et al*. 2022, Alarcón *et al*. 2023).


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Almost all species tend to breed during the wet season or at the end of the dry season. Species with large ranges present some variation in season duration, e.g., *C. melanops* has a period of 100 days in southern Brazil (*C. m. melanops*; Lima & Roper 2009) but 269 days in north-east Brazil (*C. m. nigrifrons*; Studer *et al*. 2019). Lima & Roper (2009) noted that the short reproductive period at their study locality is uncommon among tropical species, and they struggled to identify a causal link between climate and breeding season in this population. They suggested that climate might not be the only factor providing cues for nesting, but that day length could be more important. Another difference between these two populations of *C. melanops* is nest-cycle interval, 41 days on average (Lima & Roper 2009) or a max. of 32 days (Studer *et al*. 2019). Studer *et al*. (2019) suggested that shorter nesting periods might be a response to high levels of nest predation pressure at their study locality, enabling adults to prolong post-fledging care and minimise predation. Nevertheless, the discrepancies between these two geographically distant *C. melanops* populations merit further study, including long-term or experimental approaches and larger samples.

*C. cearae* breeds during the wet season, December–March, as evidenced herein. The species' breeding period is probably longer, but more work is necessary to discover if the species could have a breeding period similar to *C. melanops* in north-east Brazil as reported by Studer *et al*. (2019).

Predation seems to be an important factor in the low reproductive success in *Conopophaga*, encompassing all stages of the nesting cycle, but abandonment and environmental conditions (e.g., rain and treefalls) are relevant too. The open nest relatively close to the ground may facilitate predation or abandonment in areas subject to much human disturbance, although Marini (2017) found little difference in nest success between closed and open-cup nests (22 species analysed, including *C. lineata*), or even between open-cup nests at different heights above ground or different distances from forest borders, but there is a tendency for reduced success in open-cup nests closer (<50 m) to borders. It is important to note that there is much variation in nest success among *Conopophaga* spp. (20–40%), possibly because of variation in sample sizes and environments, making comparison between studies difficult. Successful nests in *C. lineata* vary between 20–30% in small and large fragments in the southern and south-east Atlantic Forest, but sample sizes are small (4–9 nests in each study). Also in the Atlantic Forest, *C. melanops* exhibits little variation in breeding success between small and large fragments (20–23%), with greater but varied sample sizes (13–114 nests) across eastern Brazil. *C. roberti* is unique in having nest success of *c*.40% (albeit not higher than other understorey species in Marini 2017) in a large protected area and a reasonable sample of 22 nests (Pereira *et al*. 2022). Small sample sizes and studies conducted solely in small forest fragments or human-modified environments can bias reproductive success (Oniki 1979, Martin 1996). At least *C. lineata* appears to respond well to forest fragmentation, surviving in small fragments without significant changes in sex ratio (Dantas *et al*. 2009) or nesting capacity (Marini *et al*. 2007, Marini 2017) despite morphological alterations being reported (Anciães & Marini 2000, Dantas *et al*. 2009). However, in a small forest fragment, Willis *et al*. (1983) found three infertile eggs in two of four monitored nests of the species; inbreeding and insecticides used in nearby crop fields were hypothesised as possible causes. More data on reproductive success are needed for all Conopophagidae, to facilitate meaningful comparison between different geographical areas, environments and levels of habitat degradation.

Being dimorphic mainly in plumage, the presumed monogamy in Conopophagidae raises questions about the influence of this type of mating system on sexual selection and reproductive success in the group, as polygynous and lekking / promiscuous species tend to be more dimorphic than monogamous taxa in plumage, body mass and length of


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wing and tail (Dunn *et al*. 2001). Recently, Gaiotti *et al*. (2020) reinforced the importance of testing assumptions regarding mating systems in Neotropical birds, to reveal any potential divergence among closely related genera, possibly due to different ecological pressures. They investigated the mating system of Araripe Manakin *Antilophia bokermanni*, a threatened bird endemic to north-east Brazil with clearly dichromatic plumage, finding evidence for polyandric females and males that defend territories and do not aggregate at display arenas (leks), a pattern atypical in Pipridae, where most species are polygynous and form leks (Gaiotti *et al*. 2020). There is no evidence for biparental care in this species; males do not incubate the eggs or provision the nestlings (Gaiotti *et al*. 2020). This is not the case for some Conopophagidae (see Nestling, fledgling and parental care), making monogamy a plausible assumption, but lack of genetic analysis could mask the existence of cryptic mating systems (see Johnson & Burley 1998, Pechacek *et al*. 2005). Thus, studies like Gaiotti *et al*. (2020) are necessary to know the real diversity of mating systems, which certainly will help to understand breeding dynamics in the group.

In comparing *Pittasoma* and *Conopophaga*, Greeney (2018) noted that the subelliptical eggs of *Pittasoma michleri* do not resemble the eggs of any *Conopophaga* or other antpittas (Myrmotheridae *sensu* Gaudin *et al*. 2021) in size or shape (Table 1, Fig. 3). Although the available data indicate that *Pittasoma* and *Conopophaga* at least share a type of 'cap' at the larger pole, the eggs of *P. michleri* are strongly marked with larger and darker brown markings at the larger pole, and small dark dots distributed over the rest of the pale shell (Fig. 3). In many *Conopophaga* this pattern tends to be more subtle, but there is variation between clutches even in those species with some eggs that are more densely marked (e.g., *C. castaneiceps*, *C. melanops* and *C. cearae*). More study is needed to assess variation in egg pattern in *Pittasoma*, as the only information available comes from a single clutch of *P. michleri* (Wetmore 1972; Fig. 3). Concerning nest architecture in these genera, *Conopophaga* have smaller nests than *P. michleri* (Table 1), but this seems directly proportional to differences in body size between the genera. In addition to similarities in materials used, both genera appear to prefer to construct their nests in areas with a natural accumulation of debris, enhancing nest camouflage and reducing nestbuilding effort compared to other types of understorey nests (e.g., suspended or enclosed). Nest architecture in the Conopophagidae is thus quite conservative.

In a global review of avian breeding biology (Xiao *et al*. 2017), Conopophagidae (not including *C. cearae*) appears as poorly known (six species) or partly known (four species), based on the three topics analysed by these authors (clutch size, incubation period and nestling period). Our review included more information about the family's breeding biology, and took into account differences in methodology, but most of the species could be classified as partly known according to our results. Only *Pittasoma rufopileatum* and *C. melanogaster* lack any basic breeding biology data, e.g., formal descriptions of nest, eggs and nestlings, but information for other species vary in quantity and quality. Most information summarised here pertained to two Atlantic Forest *Conopophaga* spp., *C. lineata* and *C. melanops*. Recent exceptions are studies by Lizarazo & Londoño (2022) for *C. castaneiceps* in Colombia and Pereira *et al*. (2022) for *C. roberti* in north-east Brazil. Nevertheless, breeding data for most species were the result of mainly casual encounters, and are thus not necessarily representative of the species concerned, making generalisations difficult.

The nest, egg, nestling, fledgling and 'broken-wing' distraction display of *C. cearae* described here fill a gap in knowledge of the species' life history, but much remains to be discovered about several other species in the family. In general, the breeding biology of the Conopophagidae can be considered still only partially known, despite some evidence of common patterns between most species in the family (e.g., nest and eggs, clutch size,


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biparental care, etc.). However, focusing only on these aspects could mask the lack of data on other facets of breeding biology, such as overall period, incubation / nestling period, nest site selection, mating system, reproductive success, parental care, prey diversity, seasonality, and others. We encourage long-term studies of all Conopophagidae, especially the *Pittasoma* spp., given the chronic lack of breeding data for these two, and of *C. cearae*, due to its conservation status.

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*Addresses*: Odilon Vieira, Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Museu Nacional/UFRJ, Quinta da Boa Vista s/n, São Cristóvão, Rio de Janeiro, RJ, 22290-040, Brazil, e-mail: odilon.vieira95@gmail.com. Odilon Vieira, Talita de Andrade Ferreira, Tomás Gonçalves Capdevile & Carlos Augusto Caetano, Setor de Ornitologia, Departamento de Vertebrados, Museu Nacional/UFRJ, Quinta da Boa Vista s/n, São Cristóvão, Rio de Janeiro, RJ, 22290-040, Brazil. Marco Aurélio Crozariol, Museu de História Natural do Ceará Prof. Dias da Rocha/UECE, Rua Divino Salvador 225, Centro, Pacoti, CE, Brazil. Fábio de Paiva Nunes & Francisco Werlyson Pinheiro, Associação de Pesquisa e Preservação de Ecossistemas Aquáticos, Av. Pintor João Figueiredo, SESC, Iparana, Caucaia, CE, 61627-250, Brazil.


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