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Breeding biology of the Critically Endangered Cherry-throated Tanager *Nemosia rourei*

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Summary

The "Critically Endangered" Cherry-throated Tanager *Nemosia rourei* is endemic to the Atlantic Forest of south-eastern Brazil, and extremely rare for reasons that are not yet fully understood. We monitored reproductive activities of the only known individuals of the species, at two sites, between October 2018 and November 2023. The birds foraged in social groups of 5–8 individuals. Ten nests, built in trees at heights of 12–26 m, were monitored through continuous direct observation. Most reproductive activity occurred between October and end of November, with one further nest found in March. Clutch size was 3–4 eggs, the incubation and nestling periods were 16 days, and the chicks were fed mainly on invertebrates. Up to six nest helpers, likely young from previous seasons, assisted with the collection of nest material, feeding the chicks, and defending the nest. Reproductive success was 50%, with losses due to climatic conditions (rain and cold) and predation, but may have been enhanced by the efforts of the researchers in scaring away potential predators including Spot-billed Toucanet *Selenidera maculirostris* and Black Capuchin *Sapajus nigritus.* These findings reinforce the value of detailed observation of social groups and their nests, and continuing efforts to deter predators. Further research could address how parental care and nest helpers affect reproductive success. The availability of large trees with abundant lichens may be a limiting factor for the reproductive success of species in the long term, and so protecting and restoring habitat with such features is crucial for the long-term conservation of this species.

Introduction

The Atlantic Forest of eastern South America, in Brazil, Paraguay, and Argentina, is an important global biodiversity hotspot (Mittermeier et al. 2004; Myers et al. 2000). This biome is under considerable anthropogenic pressure across its range, with only about 12% of its original cover remaining in small, isolated fragments (Ribeiro et al. 2009). Within this context, the Atlantic Forest is home to a large number of endemic bird species (Vale et al. 2018), many of which are under some degree of threat (IUCN 2024; Jenkins et al. 2015). Regarding reproductive biology, Neotropical birds have been identified as having the largest knowledge gaps (Xiao et al. 2017), information that is crucial for the development of conservation and management strategies.

Among the threatened species with limited biological information, the Cherry-throated Tanager *Nemosia rourei* is among the rarest and least known. This bird is endemic to the Atlantic Forest and has a very restricted distribution in a small and narrow area in the state of Espírito Santo, south-eastern Brazil (BirdLife International 2018). Described over 150 years ago (Cabanis 1870), there were fears in the twentieth century that the species might have gone extinct, although it was never formally declared as such (Collar et al. 1992, 1994). After more than 50 years without confirmed sightings, the species was rediscovered between 1995 and 1998 in Conceição do Castelo municipality, southern Espírito Santo (Bauer et al. 2000). In 2003, a group of eight individuals was found by Ana C. Venturini in Caetés, Vargem Alta municipality, approximately 30 km from the site in Conceição do Castelo. Additionally, between 2002 and 2003, Guy M. Kirwan observed at least two individuals in the Augusto Ruschi Biological Reserve, in Santa Teresa municipality (Venturini et al. 2005). Since then, the species has been recorded relatively frequently in Vargem Alta and Santa Teresa, either in small groups or as solitary individuals, with a known population of 20 individuals divided between these two sites by the end of 2023 (Lourenço and Rocha 2023). Limited available information about the Cherry-throated Tanager's biology includes observations of foraging (Bauer et al. 2000; Venturini et al. 2005) and nest-building (Venturini et al. 2002).

Owing to its small population size and inferred continuing decline based on habitat loss and fragmentation, the species has been classified as "Critically Endangered" since 1994 on the global Red List (BirdLife International 2018) and is also listed as "Critically Endangered" on the national and state Red Lists (Silveira et al. 2023). There is an urgent need for better information on its ecology and natural history to support the development of conservation strategies. Independent researchers, including one of the authors, G.R.M., began field data collection in 2018. In 2020, the non-profit Instituto Marcos Daniel (IMD) initiated the "Programa de Conservação da Saíra-apunhalada" (PCSA) to organise available data and gather new field information to promote effective conservation actions.

In 2021 IMD, with the support of partners (see Acknowledgements), organised a workshop with 40 participants to develop an action plan for the conservation of the species (Santos et al. 2021). The group identified research priorities and key conservation actions. Among the knowledge gaps identified was the lack of detailed information on the basic ecology and natural history of the Cherry-throated Tanager. Fundamental information such as distribution, home range size, habitat use, breeding season, nest-site, clutch size, reproductive success, sex ratio, and other aspects of social, dispersion, reproductive, and foraging behaviour are essential to inform conservation efforts. Moreover, these data may also help address another knowledge gap related to the taxonomic classification of the species. The genus *Nemosia* comprises two species, with the Hooded Tanager *Nemosia pileata* being relatively better known regarding its reproductive biology (Lindenblatt and Burns 2020; Penard and Penard 1910; Renaudier et al. 2008; Studer et al. 2021). There have been suggestions that the two species may not be very closely related, and may not even be each other's closest relative, because of vocal and other differences (Hilty 2011).

This paper focuses on the first detailed description of the reproductive biology of the Cherry-throated Tanager, based on observations of nests. We present information on nest-site characteristics, eggs, clutch size, breeding success, and incubation and nestling periods. This contributes to filling important knowledge gaps regarding its social and reproductive behaviour. We discuss the implications of these findings for the conservation of the species.

Methods

Study area

The study was conducted in the Mata dos Caetés (MC), a forested area partially protected in a private reserve at the border of Vargem Alta and Castelo municipalities (20°29'45"S, 41°1'45"W, 1,200 m a.s.l., 3,000 ha), and in the Augusto Ruschi Biological Reserve in Santa Teresa (ST) municipality (19°54'20"S, 40°33'45"W, 810 m a.s.l., 3,598 ha), both located above 800 m altitude in the mountainous region of Espírito Santo, south-eastern Brazil, and approximately 85 km apart (Figure 1). Both areas consist of large blocks of mountainous, dense ombrophilous forest, with tall trees and the presence of epiphytic plants, juçara palm *Euterpe edulis*, and other species characteristic of this environment (Bencke et al. 2006). The area has a

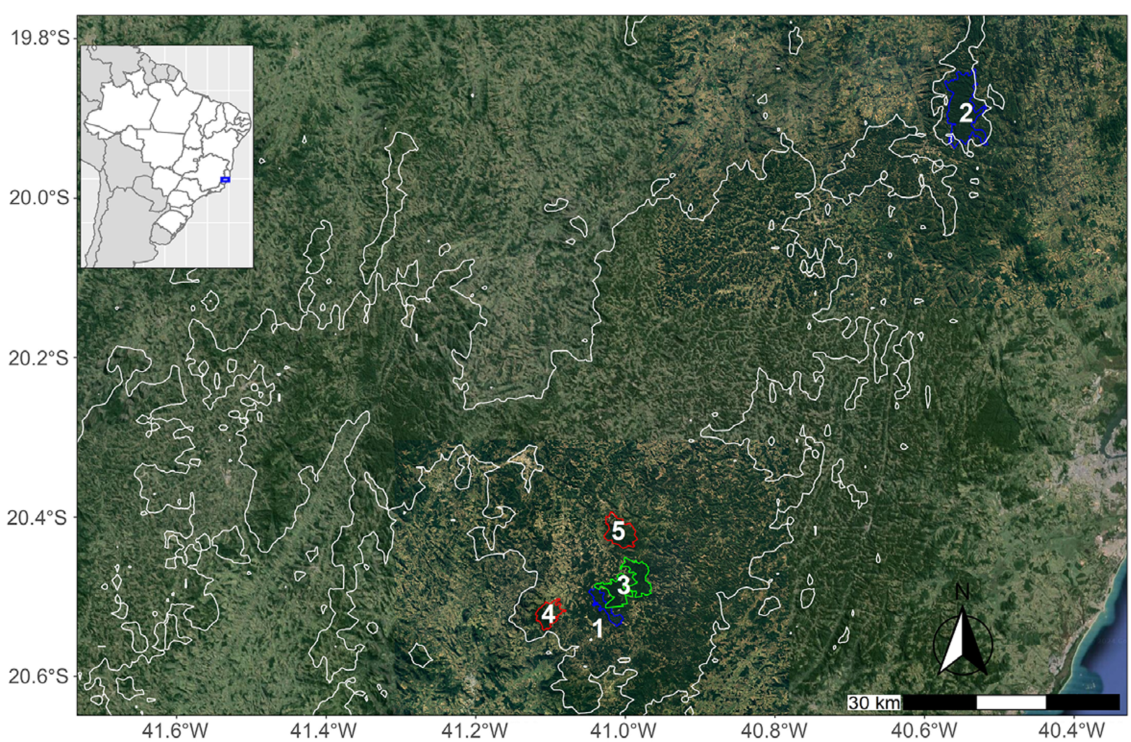

Figure 1. Map showing the Kaetés Reserve at Mata dos Caetés (1) and Augusto Ruschi Biological Reserve in Santa Teresa (2), the two areas (in blue) where we monitored nests of Cherry-throated Tanager. The Águia Branca Private Reserve (3) is highlighted in green, where one of the monitored groups has been recorded visiting. Forno Grande State Park (4) and Pedra Azul State Park (5) are in red, two protected forest areas where the species has not yet been recorded. The 800 m altitudinal contour, above which the species has been recorded, is outlined in white. (Photograph: D. Hoffmann)

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humid subtropical climate with no dry season (Alvares et al. 2013). Both MC and the ST are part of important ecological corridors and are designated as Important Bird and Biodiversity Areas (IBAs), known for endemic and endangered species (Bencke et al. 2006).

Field study

Fieldwork was conducted from October 2018 to November 2023. Between 2018 and 2020, nest searches were conducted during field trips in the months of October, November, and December. From 2020 to 2023, weekly surveys for Cherry-throated Tanager individuals were conducted throughout the year, with special attention to nesting signs in the last quarter. Once nests were located, they were monitored daily, except in 2018, before the beginning of the PCSA, when visits were not systematic. Given the perilously small population of this species, a conscious decision was made to intervene by deterring predators that came close to nests, in addition to collecting observational data.

Nest monitoring

In the field, Cherry-throated Tanagers were located along transects (trails and roads) through spontaneous vocalisations or playback. Playback was primarily used between 2018 and 2020 during field surveys to detect individuals and locate territories. Once territories were identified, playback was no longer necessary, and individuals were located through spontaneous vocalisations. Once located, individuals or social groups were followed for as long as possible, and nests were found by observing adult behaviour. Nests were monitored through *ad libitum* direct observation with continuous recording (Altmann 1974), to the extent permitted by the rugged terrain and weather conditions, such as rain and fog. Observations were made from ~25 m distance to avoid disturbing the birds. In some cases, low platforms of 2–3 m height were built with scaffolding materials to facilitate observations (see Supplementary material Figure S1) that were made using binoculars and cameras (with zoom or telephoto lens).

Arrival and departure times of one individual or group at the nest surroundings during construction, egg incubation (duration of stay), brooding, and feeding of nestlings were recorded. The period between each arrival and departure was termed a session. During each session, information on various actions, such as food provisioning (number and types of food items) and care of the young, as well as intra- and interspecific interactions, were noted. Individuals could not be identified as there is little variation in plumage, no sexual dimorphism, and the birds were not marked (Phalan et al. 2024). Video recordings were used to confirm the number of feeds and food types. All information was documented in field notebooks, audio recordings, photographs and videos, later transcribed into digital spreadsheets.

The presence and number of eggs were determined using a camera drone (model: DJI Mavic) when adults were spontaneously absent. For nests where aerial imagery was not feasible, minimum clutch size was inferred from the number of nestlings subsequently observed and may have been underestimated if some eggs did not hatch. Egg colour was described based on aerial imagery. Food items provided to the nestlings were identified visually or through video and photograph analysis when possible.

The incubation period was defined as the time between the laying of the last egg and the hatching of the first egg. The nestling period was defined as the time between the hatching of the first egg and the departure of the last chick from the nest. Nests were considered failed on the death of all eggs or chicks, or when visits by adults ceased before the nestlings had reached a stage that likely allowed them to fledge. Reproductive success was evaluated by the percentage of nests that produced at least one fledgling (= apparent nest success), by the number of eggs that hatched in nests with confirmed clutch size (= hatching success), and by the number of hatchlings that fledged (= fledging success) (Mayfield 1961; Ricklefs and Bloom 1977). To describe the breeding period, we generated circular histograms based on breeding activity data (i.e. nest building, incubation, nestling) using the circular package (Agostinelli and Lund 2024) in R 4.4.0 (RStudio Team 2020).

Nest descriptions, including height above ground, were made using binoculars, drones, and material collected after nesting had finished. The structure of the nest was described according to Simon and Pacheco (2005). After the breeding period, only one nest could be collected with the assistance of a drone. Collected material was deposited in the collection of eggs and nests of the Museu Nacional, Universidade Federal do Rio de Janeiro. The collected nest was measured for its internal and external diameter, the external height of the nest walls, and the depth of the incubatory chamber.

Results

Social groups

Encounter rates with the species during the surveys conducted between 2020 and 2023 were not estimated. However, in ST, encounters were less frequent, likely because parts of the protected area were inaccessible, with rugged terrain, and so detections relied on individuals passing close to trails to which there was access. Over the years of the study, the two known populations of the Cherry-throated Tanager varied in group size as new individuals were born, and others disappeared. Initially, in 2018, only two adults were recorded in MC (Table 1). Their nest was monitored, and after this and other successful breeding events, the group expanded. It is likely that the group split around the end of 2021, as the number observed went from seven adults plus three fledglings (10 individuals) in September, to six birds in March. The largest number of adult birds seen together was eight, but if we assume all fledglings survived, the size of this population would have reached 15 individuals. In ST, group size was consistently five fully grown individuals across breeding seasons, even after the production of two fledglings. As of the end of 2023, the known population was between 10 (the number directly observed) and 20 adult birds (the number accounting for fledglings produced since 2020, minus two fledglings believed not to have survived).

Nests

A total of 10 nests (N1 to N10) were found and monitored (Table 1): six in MC (from 2018, and 2020–2023) and four in ST (in 2021–2023). All nests were discovered by observing the behaviour of adult birds and subsequent active searches. During the breeding season, group behaviour facilitated nest detection: when the group repeatedly returned to the same area, this gave an indication of the nest's location. The nests were monitored from discovery until their outcome (success or failure), totalling 218 days of sampling with approximately 12 hours of daily observation (Table 1).

The nests have a low cup shape, supported at the base. They were located on horizontal branches of the main trunk or in forks. Nest heights ranged from 12 m to 26 m (mostly 20–25 m) above the

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Table 1. Characteristics of 10 nests of two groups of Cherry-throated Tanager *Nemosia rourei* monitored in Mata dos Caetés (MC) and Santa Teresa (ST). Nest-building sessions are periods during which material collection, material insertion into the nest, and shaping were observed. During nest-building sessions, the group's provision of food to one of the constructing individuals was observed, with items offered during material insertion or nest shaping. (-) = absence of information; (?) = impossibility of precise determination

Nest	Area	Group size (*n*)	Nest discovered (date)	Final monitoring (date)	Total samples (days)	Nest height (m)	Nest-building (days)	Nest-building sessions (*n*)		*N* material gathering (*n* sessions)	*N* material insertion (*n* sessions)*	*N* nest shaping (*n* sessions)	*N* food items (*n* sessions)	
								Morning	Afternoon				Insertion	Shaping
N1	MC	2	2018/10/22	2018/11/12	21	23	1	2	-	?	2 (2)	?	-	-
N2	MC	5	2020/11/01	2020/11/26	26	21	-	-	-	-	-	-	-	-
N3	MC	7	2021/09/16	2021/09/30	15	25	-	-	-	-	-	-	-	-
N4	ST	5	2021/09/24	2021/10/13	19	21	-	-	-	-	-	-	-	-
N5	ST	5	2021/10/18	2021/11/27	41	20	8	23	19	12 (3)	29 (15)	27 (24)	0	20 (12)
N6	MC	6	2022/03/10	2022/03/16	7	12	-	-	-	-	-	-	-	-
N7	MC	8	2022/09/14	2022/10/25	41	24	11	71	15	?	217 (44)	47 (42)	6 (6)	13 (10)
N8	ST	5	2022/10/27	2022/11/15	16	26	9	30	12	?	239 (30)	13 (12)	10 (9)	1 (1)
N9	MC	5	2023/08/11	2023/08/21	5	16	-	-	-	-	-	-	-	-
N10	ST	5	2023/09/05	2023/10/02	27	23	12	?	?	?	?	?	?	?
Total / mean					218	22	41	126	46	12 (3)	487 (91)	87 (78)	16 (15)	34 (23)

*The average number of material insertions may be greater than the number of individuals in the group because some individuals deposit an item and quickly return with new material.

ground (Table 1), always in large, mature trees with many epiphytes and lichens (Figure 2B–F). Only one nest (N2) was collected and measured (MN 53004) (Figure 2C). It was primarily made of lichens *Usnea* sp., with the following dimensions: external height of 51.6 mm, internal height (incubation cup) of 36.5 mm, external diameter of 121.1 mm, internal diameter of 44.8 mm, and a weight of 21 g (dry). Spider webs were not found in nest N2, but birds were observed collecting and deploying webs in nests N1 and N5.

Five nests were found and monitored from the construction stage (Table 1), which took up to 12 days. Nest construction, with the collection, insertion of material, and shaping the nest was observed in 172 sessions, which was the interval between the arrival of an individual or group until all individuals left the vicinity of the nest. Collection of nest materials was observed in three sessions, in the nest tree, by groups of three, four, and five individuals, where each individual brought one piece of material, totalling 12 items (Figure 2A and Table 1). Insertion of material was observed in 91 sessions, with 487 insertion actions recorded (individuals could make multiple insertion actions in a session). Non-participating individuals remained in the same or nearby trees, foraging and vocalising frequently. Nest shaping was observed in 78 sessions, with individuals seen sitting in the cup, totalling 87 shaping actions (in a building session an individual could shape the nest more than once).

In all monitored nests, two individuals were apparently more active in deploying material and shaping the nest, while the others provided occasional assistance. This observation was possible because two individuals repeatedly left and returned with material, whereas the non-participating individuals remained in the same or nearby trees, foraging and vocalising frequently, without leaving the researchers' field of observation. The individual most active in nest shaping was often fed by the less active participants. We recorded 34 food items being offered across 23 sessions before the individual settled and shaped the nest, and 16 food items (in 15 sessions) while the individual was already sitting. Some shaping actions may include egg-laying, as these actions sometimes lasted several minutes, and due to the nest height, it was not possible to determine whether the individual was shaping the nest or laying eggs. Most nest-building sessions occurred in the morning (126), with fewer in the afternoon (46).

Eggs and clutch size

The eggs were ovoid in shape, with a white background colour extensively covered with variable-sized spots in grey and light grey, interspersed with small black spots (Figure 2C). Three complete clutches consisted of 3, 4, and 4 eggs (mean 3.7) (Figure 2C and Table S1). However, it is possible that some clutches may have been complete with only two eggs, as three nests were observed with only two nestlings (Table S2).

Incubation

The pattern of arrivals and departures indicated that only one individual incubates the eggs, although the sex of this individual was unknown. We observed 497 incubation sessions, at six of the monitored nests (Figure 2D and Table S1). In 380 instances, incubation sessions began with the group arriving at the nest tree along with the incubator. Of 497 incubation sessions, the duration of 358 sessions was measured, averaging 1:00:52 (range 0:01:00–3:43:00). Overnight incubation sessions often began or ended during the period of observation and are not considered here. The interval between incubation sessions, when the eggs were left exposed, averaged 0:24:53 (n = 366, ranging from 0:01:00 to 2:09:00). The incubator was frequently fed by other group members when it arrived at the nest and less frequently during incubation sessions (Figure S2A). Provisioning behaviour was observed in 251 sessions, with the incubator being fed one or more times, totalling 526 feeding interactions. The food offered to the adult was identified in less than 5% of cases, consisting exclusively of invertebrates, such as crickets, spiders, larvae, small moths, and beetles. In 133 instances, the incubation session was interrupted by the group's arrival near the nest, at which point the

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Figure 2. Cherry-throated Tanager with *Usnea* sp. lichens (A) for nest construction (red circle), always located in large emergent trees (N3) (B). The nests contained three to four eggs (N2) (C), which were apparently incubated by only one individual (N5) (D). Individuals of the species obtained a large part of the food items from the trees surrounding the nest (N2) (E) and offered them to the nestlings (N2) (F). (Photographs: (A) C.H.R. Noia; (B) T.D. Fiorotti; (C) G.R. Magnago; (D) G.S. Bonfa; (E, F) D. Hoffmann)

incubator left and joined the group. The complete incubation period was monitored for two nests, lasting 16 days.

Nestlings

Nestlings hatch with sparse down, closed eyes, and whitish gape flanges (labial commissure). Within a few days, they are covered in long tufts of white down. As they develop, they acquire the adult plumage pattern. After the tenth day, nestlings begin to stretch and exercise their wings in the nest (49 records). When they fledge, they have pinkish legs, a light reddish patch on the throat (coloration less intense than in adults), shorter tail and wing feathers, and some remnants of the characteristic nestling down (Figure S2C and D). The complete nestling phase was monitored for three nests, with an average duration of 16 days (15–17 days) (Table S2).

Breeding phenology

The onset of reproductive activities, as well as the duration of nest building, incubation, and nestling periods, indicate a seasonal pattern. Seasonality can be assessed through a visual analysis of daily frequency histograms (Figure 3). The breeding season lasted approximately four months, beginning in the first week of August (with the onset of nest building) and extending to the end of

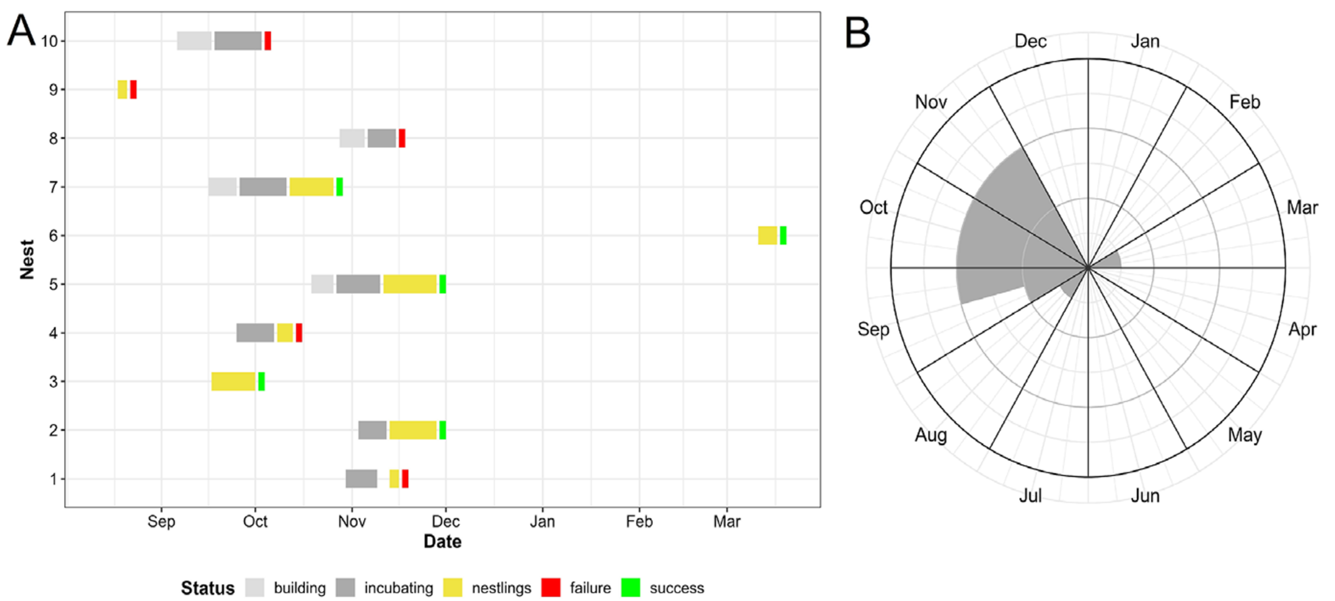

Figure 3. Breeding activity (A) during nest monitoring of two groups of Cherry-throated Tanager in Mata dos Caetés and Santa Teresa, in south-eastern Brazil between October 2018 and November 2023. Circular histogram (B) of frequency of nest in breeding activity concentrated between the months of September and November indicates high seasonality. Grey bars represent breeding activity frequency on each of the two halves of the month.

November (when the last nest was completed). Atypical breeding activity was observed in 2022, when an active nest was found in March (Figure 3A), following three months (December–February) of exceptionally high rainfall, with total precipitation in February 2022 exceeding 400 mm (M.R.S., unpublished data). This nest represents an outlier rather than a sampling failure in previous years, as weekly searches for adults have been conducted year-round since 2020, without any prior signs of reproduction, additional nests or changes in group size due to the addition of new fledglings.

Parental care

Of the 10 monitored nests, three did not reach the nestling phase (N8–N10). Some brooding was observed on all days of the nestling period. The average brooding duration was 0:27:46 (n = 407, ranging from 0:01:00 to 3:17:00) and the average interval was 0:44:42 (n = 403, ranging from 0:01:00 to 9:45:00) (Table S2), from a total of 542 brooding sessions. The duration of brooding was longer in the first days of nestling and during periods of rain and low temperatures. The intervals between sessions of staying with the chicks were longer in the final phase of nestling development or on dry or sunny days, for which we recorded two intervals of nine hours and one of seven. All brooding was apparently done by the same individual, usually after the nestlings had been fed. During brooding, some group members approached to feed the nestlings. On these occasions, when the brooder repositioned laterally to allow feeding and then returned to brooding, it was not considered a new brooding session. A total of 2,846 nestling feeding sessions were observed, offering 9,231 food items (Figure 2F and Table S2). The number of food items offered daily gradually increased as the nestlings developed (Figure S3), being higher for nests N3 and N7, which had three nestlings. Each session lasted less than a minute and was usually preceded by the pair or group arriving vocalising in a nearby tree. From this tree, the feeders flew in silently to feed the nestlings.

In most sessions, nestlings were fed more than once, by one or more individuals, depending on the group size (569 sessions just one feed; 506 two; 624 three; 454 four; 388 five; 195 six; 98 by seven or more feed items). In some sessions, the feeders returned to offer a second food item. The highest number of food offerings per section coincided with nests that had three nestlings (N3 and N7) (Figure S3) and reproductive seasons where groups were composed of seven and eight individuals, respectively. In 476 sessions (1,372 food items), an individual stayed behind to brood the nestlings, and in 434 sessions (877 food items), feeding occurred while an individual was brooding. In 230 sessions, feeders passed food to the brooding adult, who then fed the nestlings. Food passing occurred mainly in the early days. Removal of faecal sacs was observed on 547 occasions (Table S2), sometimes being consumed by an adult and other times carried away from the nest.

Food items offered to nestlings were unidentified in 98% of cases (9,057). Identified items included caterpillars of moths or butterflies (Lepidoptera) (95), crickets and katydids (Orthoptera) (22), insect larvae and chrysalids (13), adult Lepidoptera (5), winged termites (Blattodea) (4), spiders (3), fruits (3), bees (Hymenoptera) (1), beetles (Coleoptera) (1), and stick insects (Phasmida) (1) (Figure 2E and Table S3).

Interspecific interactions/reactions

A total of 235 interspecific interactions or reactions were recorded during the construction phase (10), incubation (70), nestling period (151), and after the nestlings fledged (4). In 142 instances, the species involved were identified. In 14 cases, only the family was identified, in 15 situations the interaction occurred with mixed-species flocks, and in 64 cases the species was not determined. The interactions involved 43 species, with Spot-billed Toucanet *Selenidera maculirostris* (39), Black Capuchin *Sapajus nigritus* (8), Gilt-edged Tanager *Tangara cyanoventris* (7), Brassy-breasted Tanager *Tangara desmaresti* (7), and Golden-chevroned Tanager *Thraupis ornata* (6) being the most frequent (Table S4).

The responses of Cherry-throated Tanagers varied, with demonstration (151), alarm calls (17), silent departure (12), indifference (10), and pursuit (8) being the most common. Demonstration involved approaching the other species, by one or more individuals,

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emitting calls and half-opening wings, ruffling feathers to increase body size. On 11 occasions, in addition to the response of Cherry-throated Tanagers, the researchers intervened using playback of the predator's vocalisations to attract them away from the nest or shouting to drive away potential nest predators like the Spot-billed Toucanet and Black Capuchin (Figure S4B).

Other reactions included individuals moving away while emitting alarm calls, the incubator/brooder crouching in the nest, showing restlessness, or remaining nearby on guard until the other species left. Alarm sounds or silent departures were mainly in response to the presence and overflight of species from Accipitridae, Falconidae, and Cathartidae families. In one instance, a Grey-capped Tyrannulet *Phyllomyias griseocapilla* was observed trying to pluck down from unattended nestlings until the adults returned and chased off the intruder (Figure S4C and D). Another nest was visited once by a pair of Yellow-green Grosbeaks *Caryothraustes canadensis*, which fed the nestlings while adult Cherry-throated Tanagers perched nearby. For nest N3, the 15-day-old nestlings fled silently from the nest after a female Spot-billed Toucanet arrived. They stayed in the canopy of midstorey trees and did not return to the nest, being located later by the adults who remained nearby (Figure S2C and D).

Cooperative breeding

Although the individuals were not ringed, continuous observation of the groups throughout the year suggests that juveniles from the previous year remain in the area with their parents. All individuals participate in nest construction, provisioning of the incubator, nestling feeding, and nest-site defence, indicating cooperative breeding in this species (Figure S2B).

Reproductive success

Of the 10 monitored nests, the estimated nest survival was 50%. Two nests (N1 and N4) failed during the nestling phase. The day before their failure was confirmed, there was heavy rain and strong winds combined with low temperatures, indicating that adverse weather conditions may have influenced the loss of the nestlings. Dead nestlings from N4 were carried away from the nest by two adult Cherry-throated Tanagers. A third nest (N8) was abandoned on the seventh day of incubation, possibly related to ants, many of which were observed on the nest branch. Nest N9, also in the incubation phase, was predated, probably during the night or early morning hours before the researchers arrived. Nest N10, also in the incubation phase, had its four eggs predated by a Black-necked Aracari *Pteroglossus aracari* (Figure S4E and F). Of the 11 eggs in the three nests where clutch size was confirmed (N2, N5, and N10), three failed to hatch, four were predated as mentioned, and four hatched successfully (Tables S1 and S2). Of the 17 chicks known to have hatched, 12 fledged successfully (Table S2). Overall productivity was 1.2 fledglings per nesting attempt.

Of the successful nests, three produced two fledglings (N2, N5, and N6) and two produced three (N3 and N7). Nest N2 contained three eggs, of which one did not hatch, and at least one nestling was parasitised by botfly larvae (likely *Philornis* sp.; Figure S4A). After fledging, the parasitised nestling struggled to keep up with the group in the first week after which it improved and could not be distinguished from the other individuals. Fledglings from N2 were monitored for three consecutive days after fledging and opportunistically (when they could be located) for another 21 days between December 2020 and March 2021. Fledglings from N3 were monitored for five consecutive days. Fledglings from nests N5, N6, and N7 were monitored for two, three, and five consecutive days, respectively, after leaving the nest. On the first day after leaving the nest, the fledglings remained close to the nest, 30–50 m away and were recorded up to 100 m away after three days, using the middle to upper stratum of vegetation.

Discussion

This work represents the first detailed description of the breeding biology of the Cherry-throated Tanager. The only prior published information on breeding biology of this species consists of some observations of nest-building at one nest (Venturini et al. 2002). A better understanding of natural history provides an essential basis for conservation efforts, including interventions at or near the nest, as well as providing further clues as to the taxonomic position of this bird.

Particularly notable is the confirmation of cooperative breeding in the Cherry-throated Tanager. Cooperative breeding might be facultative in this species, as the first monitored nest involved only the breeding pair. If helpers are birds hatched in the previous breeding season, the absence of helpers would indicate that there was no successful nest in the previous breeding season. Nest helpers have been observed in other Thraupidae (Skutch 1961), such as White-banded Tanager *Neothraupis fasciata* (Alves 1990; Manica and Marini 2012) and Yellow Cardinal *Gubernatrix cristata* (Beier et al. 2017) but have not been reported for the other *Nemosia* sp., Hooded Tanager (Lindenblatt and Burns 2020). In these species, helpers typically defend the nest and care for nestlings but do not assist in construction. Helpers may reduce the cost of reproduction for breeding birds (e.g. Manica and Marini 2012; Paquet et al. 2013) and increase reproductive success (e.g. Schaub et al. 1992). The importance of the social group was evident in instances where other species were driven away by more than three individuals, such as the Grey-capped Tyrannulet, which attempted to pluck down from the nestlings, and multiple occasions of group actions against individuals of Spot-billed Toucanets, a potential predator, from near nests.

Our observations of diet may be biased towards larger and more recognisable prey, as 98% of the recorded food items could not be visually identified. Many invertebrates are very small, making them difficult to see from a distance. In this context, our observations included the first records of fruit in the diet of the Cherry-throated Tanager, which previously had been proposed to eat only invertebrates (Venturini et al. 2005). We recorded provision of fruit to nestlings on just three occasions (2% of the 148 identified food items), and it is clear from these data with identified items and from observations of the tanagers foraging that invertebrates are the main food items. The Hooded Tanager is also largely insectivorous (Lindenblatt and Burns 2020), but may eat a higher proportion of fruit (Studer et al. 2021).

The breeding period and duration align with patterns observed in other Thraupidae (Winkler et al. 2020). Incubation in Cherry-throated Tanager appears to be performed by a single individual, similar to the pattern in other tanager species, with the incubation period slightly longer than the 12–14 days observed in other non-cavity-nesting species in the family (Winkler et al. 2020). The nestling period, 15–17 days, also aligns with the family's pattern (Winkler et al. 2020), suggesting that the presence of nest helpers does not expedite nestling departure through increased food provision and consequently faster development.

Half of the monitored nests were successful in producing fledged young, which might be considered high for a tropical region where predation rates tend to be elevated (Stutchbury and Morton 2001). However, this success rate should be interpreted with care, given that only 10 nests were monitored. Moreover, our active intervention in deterring potential predators influenced (positively) this success. There were indications of inviable eggs due to hatching failure, and of an impact of parasites on fledgling health. Hatching failure can be considered common in birds, especially in endangered species (e.g. Heber and Briskie 2010). The main causes of failure are infertility and embryo mortality, which can be caused by male quality/health, copulation failure, female conditions, environmental factors, and inbreeding depression (Hemmings et al. 2012). Parasites can decrease post-fledging survival (Streby et al. 2009) and may be of particular concern as an additional stressor for species with very small and vulnerable populations, as is the case here (Bulgarella et al. 2019).

Our observations provide further evidence of differences between the Cherry-throated Tanager and Hooded Tanager, extending beyond morphology. The two species differ substantially in aspects such as nest material, nest-site, nest structure, egg characteristics, and clutch size, along with morphological and behavioural differences observed in the field. The nests of Cherry-throated Tanager observed in this study are similar to the only previously known nest of the species (Venturini et al. 2002). Nest materials and structure are different to those of the nest of Hooded Tanager (Penard and Penard 1910; Studer et al. 2021; Teixeira 2009) (see for comparison https://www.wikiaves.com/4606900). Cherry-throated Tanager constructs a low cup of lichens supported by the base, whereas Hooded Tanager builds a low cup of plant fibres supported laterally in forks. The nest of Cherry-throated Tanager more closely resembles the nests of other unrelated birds, such as the Swallow-tailed Cotinga *Phibalura flavirostris* in the family Cotingidae (Silva 2019). The availability of suitable *Usnea* lichens, particularly those restricted to humid and elevated forest areas (see Gerlach 2017) might limit the species' distribution.

The two species of *Nemosia* also differ in other characteristics of reproductive biology. The Cherry-throated Tanager lays up to four white eggs with grey blotches and some black spots and has cooperative breeding, with the breeding pair assisted by up to six non-breeding individuals. The Hooded Tanager lays clutches of two shiny, bluish eggs with varying shades of brown, has no nest helpers and nest-building is by the female, with the male standing guard (Penard and Penard 1910; Renaudier et al. 2008; Studer et al. 2021).

The Cherry-throated Tanager was not included in molecular phylogenetic studies by Barker et al. (2013) or Burns et al. (2014). Hooded Tanager was placed in the subfamily Nemosiinae, the "flock-dwelling tanagers", together with three monotypic genera: *Cyanicterus*, *Sericossypha*, and *Compsothraupis* (Burns et al. 2014). All these species, including Hooded Tanager, can be observed in monospecific small flocks. Breeding is poorly known in these other genera, but cooperative breeding has been described in the case of the White-capped Tanager *Sericossypha albocristata* (Greeney et al. 2007), an indication that the placement of Cherry-throated Tanager in this subfamily is appropriate.

Our observations provide some clues as to factors influencing the timing of breeding in the Cherry-throated Tanager. The observed breeding season is consistent with the timing of the only previously recorded nest (Venturini et al. 2002) and with that of most passerine species breeding in the Atlantic Forest of south-eastern Brazil, predominantly between September and November (Marini and Durães 2001). This is generally the period with highest rainfall (INMET 2024). Breeding during the rainy season might be linked to resource availability, as shown for other forest insectivores (Wikelski et al. 2000). Understanding the factors governing the breeding period of such a small and restricted population is crucial for its conservation, particularly in the face of climate change altering ecosystem structures and resilience (Hoegh-Guldberg et al. 2018; Newell et al. 2023). La Fuente et al. (2023) found significant impacts of warming and extreme precipitation patterns on bird communities in montane tropical forests in Australia. We speculate that similar dynamics might be affecting Cherry-throated Tanager, as evidenced by the loss of nestlings (N1 and N4) after heavy rains and unseasonably low temperatures (in October).

Our observations can help to inform conservation strategies for the Cherry-throated Tanager. The species nests in tall trees with abundant lichens and epiphytes, characteristics of mature forest. Such trees were relatively abundant in the study area but are not found in younger secondary forests and are usually found at higher altitudes, where mist promotes the growth of lichens and epiphytes. This highlights the importance of well-preserved forests at suitable altitudes for the successful reproduction of this species.

As noted elsewhere, we found toucans (including aracaris and toucanets) to be important nest predators (Costa et al. 2021; Cove et al. 2017; Martínez 2021). Five species of toucans can be found in the study area. Of these, Spot-billed Toucanet and Black-necked Aracari were frequently heard and seen during monitoring, and one individual was seen preying four eggs of Cherry-throated Tanager. On multiple occasions, we consider that our interventions spared nests from predation, and efforts to deter predators from approaching active nests should be continued.

Further work is needed to better understand the natural history, ecology, habitat use, distribution, and conservation management needs of the Cherry-throated Tanager. Unsuccessful surveys of the species in other areas with similar habitats were conducted by the PCSA team in previous years. However, new surveys in these and additional areas may be crucial for locating and understanding the movements of individuals from the large group that split in MC. Understanding habitat use and movement patterns could provide valuable insights into the species' spatial dynamics. This information is important to help with directing efforts for reserve expansion and community engagement. Currently, the two monitored populations are located in protected areas, as IMD established a new private reserve in 2024, the Kaetés Reserve in MC. Ecological niche models, already in development, could help guide fieldwork to identify suitable habitats to where individuals may have dispersed, as well as to locate areas with potential for conservation expansion. Individual marking, with colour ringing, would be helpful to understand social dynamics, sex ratio, and the identity of the incubator and nest helpers, but is not without risk. The PCSA team has so far been able to capture and colour-ring four adult birds without problems, which will be helpful in understanding dispersal and local movements (details will be published elsewhere). Visual identification of food items was not possible in most cases, and metagenomic methods, analysing faeces, could help to reveal more details of the birds' diet. Studies on egg viability, the impact of parasites on post-nestling survival (and identification of these parasites), and more detailed information on parental care and the role of nest helpers can contribute to conservation of the species. Sequencing of genetic material will help to resolve the question of how closely related it is to the Hooded Tanager.

Conclusions

This study provides important new data on the natural history of the Cherry-throated Tanager, which will directly contribute to

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effective conservation actions for one of the world's rarest and most endangered birds. The number of nests, eggs, and chicks observed indicate that both known groups of Cherry-throated Tanager have reproductively healthy individuals. The apparent increase in size of the known population over three years can be attributed at least in part to the interventions of the field team in deterring diurnal nest predators. For now, given the initial indications that such interventions are beneficial, and given the urgency of increasing population size to reduce the risk of extinction, we suggest that predator deterrence continues.

Although it is demanding in terms of time and resources, continuing the monitoring and protection of the Cherry-throated Tanager population will be important in securing the future of the species as well as providing additional information to inform conservation strategies.

In the long term, habitat availability, with large trees and abundant lichens, will likely limit population growth and carrying capacity. The impacts of climatic changes are as yet unquantifiable but might be substantial. Protecting and restoring forests in the region may buffer some of the effects of climate change as well as providing nesting and foraging habitat, and continue to be a priority for this charismatic species.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/S0959270925100117.

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SUPPLEMENTARY INFORMATION

Research Article

Breeding biology of the "Critically Endangered" Cherry-throated Tanager *Nemosia rourei*

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Table S1. Information on the incubation phase, such as start date, number of incubation days, number of eggs, number of incubation sessions (time intervals in which an adult individual was with the eggs), average duration of incubation sessions (h:mm:ss), average interval between incubation sessions (h:mm:ss), and number of feedings of the incubator while it was incubating. Monitoring of ten nests of two groups of the Cherry-throated Tanager *Nemosia rourei* in Mata dos Caetés (MC) and Santa Teresa (ST). (-) absence of information; (?) impossibility to determine precisely; (*) the value does not represent a complete period of incubation or nestlings.

Nest	Lo-cal	Incubation Start (date)	Incubation period (days)	Eggs (n)	Incubation sessions (n)	Average incubation duration (n)	Average interval between incubation sessions (n)	N of incubator feeds (n sessions)
N1	MC	-	11*	?	19	0:54:15 (8)	?	1 (1)
N2	MC	-	10*	3	94	0:51:07 (67)	0:19:40 (73)	38 (30)

Nest	Local	Incubation Start (date)	Incubation period (days)	Eggs (n)	Incubation sessions (n)	Average incubation duration (n)	Average interval between incubation sessions (n)	N of incubator feeds (n sessions)
N3	MC	-	-	?	-	-	-	-
N4	ST	-	13*	?	86	1:21:13 (71)	0:25:15 (76)	194 (75)
N5	ST	2021/10/26	16	4	99	1:20:37 (75)	0:27:24 (82)	92 (52)
N6	MC	-	-	?	-	-	-	-
N7	MC	2022/09/25	16	?	137	0:50:16 (96)	0:23:26 (100)	97 (57)
N8	ST	2022/11/05	10*	?	62	0:47:41 (41)	0:28:39 (35)	104 (36)
N9	MC	-	-	?	-	-	-	-
N10	ST	2023/09/17	15*	4	?	?	?	?
Total/mean			16	3.7	497	1:00:52 (358)	0:24:53 (366)	526 (251)

Table S2. Information on the nestling phase, such as the hatching date of the eggs, the number of days of the nestling period, the number of nestlings (when possible to determine), the number of brooding sessions (time intervals in which an adult individual was with the nestlings), the average duration of brooding sessions (h:mm:ss), the average interval between brooding sessions (h:mm:ss), the number of feeding sessions (time interval, with the arrival of an individual or group to offer one or multiple food items), the number of food items offered to the nestlings. Some food offerings to the nestlings occurred before the start of a brooding session and even during brooding sessions, with the brooder moving aside to allow other individuals of the group to offer food to the nestlings. After feeding sessions, fecal sac removal was recorded, and after the nestling phase, the nest status and the number of fledglings were verified in ten nests of two groups of the Cherry-throated Tanager *Nemosia rourei* in Mata dos Caetés (MC) and Santa Teresa (ST). (-) absence of information; (?) impossibility to determine precisely; (*) the value does not represent a complete period of incubation or nestlings.

Nest	Local	Nestling start	Nest-lings period (days)	Nestlings (n)	Brood-ing ses-sions (n)	Average brooding du-ration (n)	Average in-terval be-tween brooding sessions (n)	Feeding sessions (n)	Food items (n)	Food items upon arrival to brood (n sessions)	Food items during brooding (n ses-sions)	Fecal sacs re-moval (n)	Nest status	Fledglings (n)
N1	MC	?	4*	≥2	21	0:45:30(14)	0:19:17 (14)	24	32	21 (14)	5 (5)	5	Failure	0
N2	MC	11/11/2020	16	2	132	0:31:01(102)	0:28:18(101)	503	1319	296 (116)	223 (117)	141	Success	2
N3	MC	?	15*	3	109	0:15:42 (88)	0:39:36 (86)	984	3281	285 (95)	205 (97)	169	Success	3
N4	ST	07/10/2021	6*	3	58	0:41:17 (48)	0:17:25 (48)	129	264	116 (47)	126 (73)	13	Failure	0
N5	ST	12/11/2021	17	2	110	0:30:28 (78)	0:50:48 (78)	451	1461	300 (113)	175 (85)	76	Success	2
N6	MC	?	7*	2	6	0:11:30 (4)	1:51:40 (3)	212	769	16 (4)	9 (5)	32	Success	2
N7	MC	11/10/2022	15	3	106	0:18:52 (73)	0:45:50 (73)	543	2105	338 (87)	134 (52)	111	Success	3
N8	ST	-	-	-	-	-	-	-	-	-	-	-	Failure	0
N9	MC	?	4*	?	-	-	-	-	-	-	-	-	Failure	0

N10	ST	-	-	-	-	-	-	-	-	-	-	-	Failure	0
Total / mean			16.0	17	542	0:27:46 (407)	0:44:42 (403)	2846	9231	1372 (476)	877 (434)	547	50%	12

Table S3. Table S3. List of types of food items offered to the nestlings of ten nests of two groups of the Cherry-throated Tanager *Nemosia rourei* in Mata dos Caetés (MC) and Santa Teresa (ST). (-) absence of information.

Item	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	Total
Undetermined	28	1267	3269	239	1426	755	2073	-	-	-	9057
Caterpillars of moths or butterflies (Lepidoptera)	2	37	10	13	7	9	17	-	-	-	95
Crickets and katydids (Orthoptera)		5		8	2	1	6	-	-	-	22
Insect larvae and chrysalis	1	7		2		2	1	-	-	-	13
Adult Lepidoptera							5	-	-	-	5
winged termites (Blattodea)	1	1			1		1	-	-	-	4
Spiders (Araneae)						1	2	-	-	-	3
Fruits			2			1		-	-	-	3
Bees (Hymenoptera)		1						-	-	-	1
Beetles (Coleoptera)				1				-	-	-	1
Stick insects (Phasmida)					1			-	-	-	1
Total	32	1318	3281	263	1437	769	2105	-	-	-	9205

Table S4. List of species that provoked agonistic reactions in individuals of the Cherry-throated Tanager *Nemosia rourei* during the monitoring of ten nests of two groups, in Mata dos Caetés (MC) and Santa Teresa (ST).

Species	Family / Group	Construction phase			Incubation phase						Nestling phase						Nestlings fledged	Total
		N5	N7	N8	N2	N4	N5	N7	N8	N10	N2	N3	N4	N5	N6	N7	N2	
Indefinite	INDETERMINATE	1	1	1	1	3	8	2	1			29	1	7	3	6		64
Selenidera maculirostris	RAMPHASTIDAE			1		4	6		3			10	6	2	4	3		39
Mixed flock	MIXED FLOCK	1			2		1		3			4		3	1			15
Sapajus nigritus	MAMMALIA		1		2									2	1	2		8
Dendrocolaptidae	DENDROCOLAPTIDAE					1	1					1		3		1		7
Tangara cyanoventris	THRAUPIDAE				1		1					4		1				7
Tangara desmaresti	THRAUPIDAE											7						7
Thraupis ornata	THRAUPIDAE											6						6
Accipitridae	ACCIPITRIDAE		1			1						2					1	5
Elanoides forficatus	ACCIPITRIDAE				2						2						1	5
Anabacerthia lichtensteini	FURNARIIDAE					3					1			1				5
Melanerpes flavifrons	PICIDAE											4						4
Ramphastos vitellinus	RAMPHASTIDAE					2					1					1		4
Dacnis cayana	THRAUPIDAE							1	1			2						4

Species	Family / Group	Construction phase			Incubation phase						Nestling phase						Nestlings fledged	Total
		N5	N7	N8	N2	N4	N5	N7	N8	N10	N2	N3	N4	N5	N6	N7	N2	
Hemithraupis ruficapilla	THRAUPIDAE					1						1	1			1		4
Leptodon cayanensis	ACCIPITRIDAE										1						2	3
Lepidocolaptes squamatus	DENDROCOLAPTIDAE						1							2				3
Myiodynastes maculatus	TYRANNIDAE		1								1			1				3
Amadonastur lacernulatus	ACCIPITRIDAE						1		1									2
Caryothraustes brasiliensis	CARDINALIDAE						1							1				2
Sittasomus griseicapillus	DENDROCOLAPTIDAE						1	1										2
Xiphocolaptes albicollis	DENDROCOLAPTIDAE													2				2
Micrastur ruficollis	FALCONIDAE														2			2
Oxyruncus cristatus	OXYRUNCIDAE											1			1			2
Picidae	PICIDAE											2						2
Veniliornis maculifrons	PICIDAE					2												2
Pyrrhura frontalis	PSITTACIDAE											2						2

Species	Family / Group	Construction phase			Incubation phase						Nestling phase						Nestlings fledged	Total
		N5	N7	N8	N2	N4	N5	N7	N8	N10	N2	N3	N4	N5	N6	N7	N2	
Tangara cyanocephala	THRAUPIDAE					2												2
Thraupis cyanoptera	THRAUPIDAE											2						2
Harpagus diodon	ACCIPITRIDAE					1												1
Rupornis magnirostris	ACCIPITRIDAE										1							1
Cathartes burrovianus	CATHARTIDAE											1						1
Milvago chimachima	FALCONIDAE								1									1
Euphonia pectoralis	FRINGILLIDAE						1											1
Dendroma rufa	FURNARIIDAE					1												1
Philydor rufum	FURNARIIDAE					1												1
Callithrix flaviceps	MAMMALIA														1			1
Dryocopus lineatus	PICIDAE											1						1
Piculus aurulentus	PICIDAE		1															1
Pteroglossus aracari	RAMPHASTIDAE									1								1
Pteroglossus bailloni	RAMPHASTIDAE											1						1

Species	Family / Group	Construction phase			Incubation phase						Nestling phase						Nestlings fledged	Total
		N5	N7	N8	N2	N4	N5	N7	N8	N10	N2	N3	N4	N5	N6	N7	N2	
Ramphastos dicolorus	RAMPHASTIDAE											1						1
Sclerurus scansor	SCLERURIDAE						1											1
Chlorophanes spiza	THRAUPIDAE											1						1
Coereba flaveola	THRAUPIDAE													1				1
Pachyramphus castaneus	TITYRIDAE						1											1
Tityra inquisitor	TITYRIDAE						1											1
Phyllomyias griseocapilla	TYRANNIDAE										1							1
Sirystes sibilator	TYRANNIDAE		1															1
Total		2	6	2	8	22	25	4	10	1	8	82	8	26	13	14	4	235

Figure S1. Researchers in the field, with binoculars and cameras, monitoring individuals of the Cherry-throated Tanager *Nemosia rourei* (A), near the platform used for nest monitoring (B). Photos by G. Magnago (A) e D. Hoffmann (B).

Figure S2. During the monitoring of the nests of the Cherry-throated Tanager *Nemosia rourei*, it was observed that group individuals fed the incubator (N5) (A) and that the species has nest helpers (N5) (B). After the chicks leave the nest, they are closely monitored by adults, remaining alone for only a few minutes (N3) (C, D). Photos by C.H.R. Noia (A), G.S. Bonfa (B) e T.D. Fiorotti (C, D).

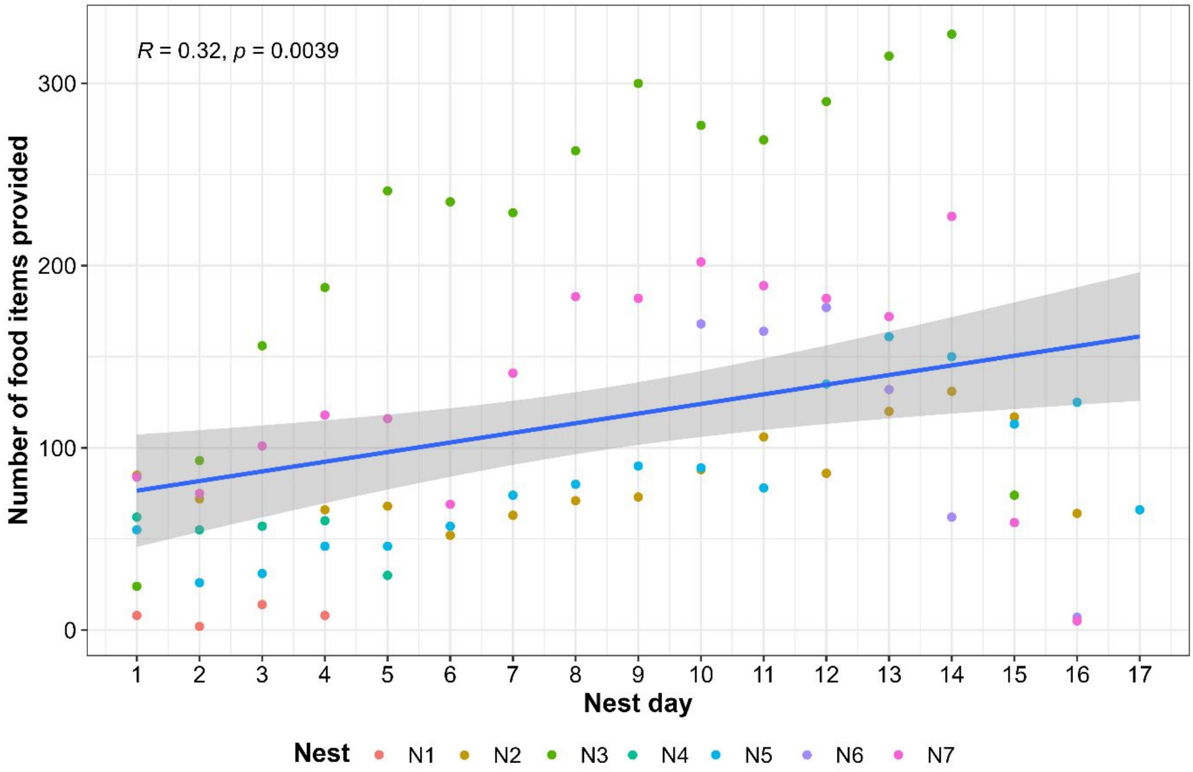

Figure S3. Relation of Number of food items provided by adults of Cherry-throated Tanager to nestling by nest day, for seven nests that have reached the nestling phase. The blue line represent the linear trend with the 95 percent confidence interval. At the top left is the result of the Pearson correlation.

Figure S4. During the monitoring of the nests of the Cherry-throated Tanager *Nemosia rourei*, it was observed that some chicks were parasitized by botfly larvae (N2) (A), which affected their flight ability in the first days after leaving the nest. The individuals became agitated when hawks, toucans, and monkeys were near the nests (N2) (B). On one occasion, the approach (C) and attempt to pluck feathers from the nestlings (D) by a Gray-capped Tyrannulet *Phyllomyias griseocapilla* were filmed (N2). On another occasion, a Black-necked Aracari *Pteroglossus aracari* was filmed removing (E) and eating four eggs (N10) (F). Images C-F are stills taken from video footage. Photos by G. Magnago (A, C, D), D. Hoffmann (B) e A.J.R Souza (E, F).