



Nesting attempts and annual fecundity in a population of the yellow-chinned spinetail (*Certhiaxis cinnamomeus*), with a review on Neotropical passerines

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Abstract

Knowledge on nesting attempts and annual fecundity are essential to understand avian population dynamics, viability, and life history adaptations, yet this type of information is scarce for most Neotropical species. Here, we addressed reproductive phenology, nesting attempts, nest parasitism by striped cuckoos (*Tapera naevia*), nest survival, and the number of offspring produced per female in the yellow-chinned spinetail (*Certhiaxis cinnamomeus*). We observed nine marked couples during the 2018/2019 breeding season, which exhibited mate fidelity, initiated the construction of 1–4 nests (mean \pm SD = 2.89 ± 0.93), and completed the construction of 0–3 nests (2.11 ± 1.05), and they initiated 0–3 clutches (2.11 ± 1.05). Of 19 initiated clutches, nine were depredated, three drowned after heavy rains, one successfully fledged yellow-chinned spinetails (three young), and six fledged one striped cuckoo each, with an annual reproductive output of 0.33 ± 1.0 yellow-chinned spinetails fledglings per pair, or 1.0 ± 1.12 fledglings when considering both host and parasitic broods. The maximum number of successful broods produced by a pair was two, and two pairs ceased reproduction in the middle of the breeding season after producing only one successful brood. Our data and information on other Neotropical and northern temperate passerines gathered from the literature contradicted the premise of the “bet-hedging strategy” that longer breeding seasons in the tropics imply in more clutches per season than in temperate species.

Keywords Bet-hedging strategy · Brood parasitism · Double-brooding · Multiple brooding · Nest predation · Mate fidelity · Renesting · Reproductive output

Introduction

Annual fecundity is a key parameter for the understanding of avian population dynamics, viability, and life history adaptations (Martin 1996; Ricklefs 2000; Lima and Roper 2009;

Machado et al. 2020). It is defined as the number of offspring produced per female per reproductive season (Grzybowski and Paese 2005) and it results from a combination of factors, including clutch sizes, nest survival, and number of nesting attempts in a season (Cooper et al. 2005; Grzybowski and Paese 2005). Although clutch size and nest survival information are available for many taxa and habitats (Jetz et al. 2008; Freeman et al. 2020), nesting attempts data are scarce due to the difficulty to mark and to follow females throughout an entire breeding season (Walk et al. 2004; Cooper et al. 2005; Grzybowski and Paese 2005; Styrsky and Brawn 2011).

The lack of breeding information on marked individuals hampered the interpretation of important life history theories. One such theory is the “bet-hedging strategy,” which infers that the smaller clutch sizes typical of tropical species (Martin 1995; Jetz et al. 2008) occur because in tropical latitudes, breeding seasons are longer and nest predation rates are higher than in temperate habitats, and under these conditions, smaller broods are favored to permit more breeding attempts after

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nest failure (Foster 1974; Martin 1995, 1996; Jetz et al. 2008; Griebeler et al. 2010). However, the main predictions of this theory still need clarification because some tropical and northern temperate passerines can have similar annual numbers of broods and reneating rates (Martin 1996), and a recent review indicated that nest predation rates are not generally higher in the tropics (Freeman et al. 2020). The idea of the “bet-hedging strategy” focuses on the maximization of reproductive effort within breeding seasons, but alternatively, tropical birds also could have limited numbers of nesting attempts and lower annual fecundity even when they succeed, spreading reproductive effort between years across a longer life (Martin 1996, 2004). Yet, data on nesting attempts and annual fecundity of tropical passerines are still limited and more species should be studied.

The yellow-chinned spintail (*Certhiaxis cinnamomeus*) is a small Furnariidae passerine (14–14.5 cm) widely distributed across all the east portion of South America. It inhabits freshwater marshes and mangroves (Remsen-Jr. and de Juana 2019), being often one of the most common elements in these habitats. Reproductive biology was well studied in Argentina (Di Giacomo 2005; de la Peña and Salvador 2016), where the species forms stable pairs during the reproductive season that lasts from October to February. Its nest is a globular structure (15–29 cm in width and 16–32 cm in height), built with twigs, thorns, and leaves, and presents an elongated tubular entrance (Euler 1900; Sick 1997; Di Giacomo 2005; de la Peña and Salvador 2016; Remsen-Jr. and de Juana 2019; Murcia et al. 2020). They are often built slightly above humid ground or water, being supported by shrubs or by grassy vegetation. Estimated incubation and nestling periods are 15–16 days and 16 days, respectively (Di Giacomo 2005; de la Peña and Salvador 2016), and they are frequently parasitized by the striped cuckoo (*Tapera naevia*, Cuculidae) (de la Peña and Salvador 2016; Murcia et al. 2020).

Here, we addressed annual fecundity in the Neotropical yellow-chinned spintail. Specifically, we investigated reproductive phenology, nesting attempts, nest parasitism, nest survival, and the number of offspring produced per female based on marked pairs that could be observed during an entire breeding season. By comparing our findings with information from other Neotropical and northern temperate passerines, we gathered evidence that contradicts the traditional premise that tropical birds lay and fledge more clutches per year due to the longer reproductive seasons.

Methods

Study area

The study area was a well-preserved freshwater marshland from the municipality of Santa Barbara d’Oeste (22°51’S;

47°26’W, altitude 590–610 m), São Paulo state, southeastern Brazil. We searched for nests in two perennial lakes of 14 and 45 ha, and in their surrounding marshy areas (Fig. 1). These lakes were 800 m apart, were about 1 m deep, and were characterized by abundant emergent vegetation (mainly of *Rhynchosporae* sp. and *Cyperus* sp.). At the edges, lakes were surrounded by a 50 to 150 m belt of humid grassy and shrubby vegetation, where *Andropogon bicornis* was abundant. These humid areas were surrounded by a reforestation of arboreal species in late regeneration stage. The climate was mesothermic, with a rainy season from October to March (average temperature 22.8 °C and average precipitation 1100 mm), and a dry season from April to September (average temperature 18 °C, and precipitation 300 mm) (Alvares et al. 2013).

Field procedures

We conducted field work during two reproductive seasons, 2017/2018 and 2018/2019, but we collected annual fecundity data only in the 2018/2019 season. We captured birds with mist nets and we used playback trials to increase capture efficiency. We marked the birds with unique combinations of two to three PVC colored rings for individual identification, and we captured them during the entire 2017/2018 breeding season, and also in September during the 2018/2019 season.

We initiated nest searches in September, before any nesting activity could be observed, and we ceased observations in late February, when pairs were no longer involved in breeding activities. We inspected the territorial marked couples for breeding activities every 3–7 days, during 30–40 min focal observation sessions. We searched for individuals carrying nest material or delivering food to the nestlings, and we also thoroughly checked the surrounding vegetation looking for nests (Martin and Geupel 1993). Once found, we checked the nests every 3–7 days, but we intensified monitoring near laying and fledging periods. We observed nest contents and we inspected whether nests were parasitized by striped cuckoos with a portable Endoscope Inspection Camera (Model AN97 novadigital) through nest tubular entrance, and we observed and stored the images in a smartphone.

We considered nest predation when nest contents disappeared before fledging age, and we confirmed successful fledging by the observation of fledglings being fed by the parents nearby the nests (Martin and Geupel 1993). We opted for reporting only “apparent nest survival” (the simple percentage of nests surviving to fledging stage) rather than nest survival estimates based on exposure time (e.g., Mayfield 1961). This is because parasitized and non-parasitized nests can suffer different predation rates and can have different incubation and nestling periods (nest exposure times), meaning that with the use of exposure



Fig. 1 Study area in the municipality of Santa Barbara d’Oeste, state of São Paulo, southeastern Brazil

time methods, nest survival probabilities should be estimated separately for each nest category (parasitized and non-parasitized) (see for instance Hauber 2000). However, many nests were depredated during incubation stage, when brood identity could not be established because of the close similarities between host and parasitic eggs in shape, size, and color (Murcia et al. 2020). Then, we considered apparent survival as a more adequate method to provide an overall estimate of nest survival, which did not affect the main objective of our work of recording the numbers of nesting attempts and offspring production by marked pairs that could be followed during the whole breeding season.

Comparative data

To compare the data obtained for the yellow-chinned spintail with that of other Neotropical passerines, we performed a literature search in the indexing base Web of Science, using the keywords “nesting attempts”, “annual fecundity”, “re-nesting”, “double-brooding”, “multiple

Table 1 Identities (ID) of nine marked pairs of the yellow-chinned spintail (*Certhiaxis cinnamomeus*, Furnariidae), and numbers of nest construction initiations (Construction), numbers of nests for which construction was concluded (Nests), numbers of clutch initiations (Clutches), and numbers of successful broods of yellow-chinned spintails and of striped cuckoos (*Tapera naevia*)

| Pair ID | Construction | Nests | Clutches | <i>C. cin-namomeus</i> Successful broods | <i>T. naevia</i> Successful broods |
|---------|--------------|-------|----------|--|------------------------------------|
| 02 | 3 | 3 | 3 | 0 | 2 |
| 03 | 4 | 3 | 3 | 0 | 0 |
| 07 | 3 | 2 | 2 | 0 | 1 |
| 09 | 4 | 3 | 3 | 0 | 0 |
| 10 | 3 | 3 | 3 | 0 | 1 |
| 11* | 1 | 1 | 2 | 0 | 2 |
| 12 | 2 | 2 | 2 | 0 | 0 |
| 13 | 3 | 2 | 1 | 1 | 0 |
| 14 | 3 | 0 | 0 | 0 | 0 |

*Only pair for which one nest reuse was observed

brooding”, “Neotropics”, and “Neotropical region”. Our search considered the title, abstract, and keywords of the potential manuscripts, and we used “OR” as the Boolean operator, except for the words “Neotropics” and “Neotropical region”, for which we used “AND.” Then, we refined the search to journals from the areas of Ecology, Zoology, and Ornithology. We selected works reporting numbers of nesting attempts and/or annual fecundity for Neotropical passerines that were based on the observation of marked individuals that could be followed across entire breeding seasons, and we considered nesting attempts only when clutch initiations occurred (see also Grzybowski and Paese 2005). We did not consider studies reporting the occurrence of multiple nesting attempts or multiple brooding without providing quantifications, and we eliminated studies that considered only females having at least one breeding attempt to address annual fecundity, as they could overestimate population rates. We also discarded works providing theoretical estimates obtained with equations that use breeding season and nesting cycle durations to derive maximum annual fecundity, and we averaged the data when information for multiple breeding seasons were provided. For the interpretation of latitudinal life history theories (i.e., the bet-hedging strategy), we also compiled the nesting attempts and annual fecundity data from the review provided by Grzybowski and Paese (2005), and therein references, for New World temperate passerines, as providing a thorough review for the latter is beyond the scope of the present manuscript. For comparative purposes, we compiled information on breeding season duration, nesting attempts, and annual fecundity.

Results

We captured and marked 26 individuals, among which were nine territorial couples that could be observed one to three times a week during the entire 2018/2019 reproductive season. These couples were stable within the breeding season, but of the five couples marked in the 2017/2018 season, one couple remained together in 2018/2019, and the others changed partners, suggesting low mate fidelity between years. The first clutch initiations ($n = 3$) of the nine marked pairs we observed in the 2018/2019 season occurred in the first week of October 2018, with nest constructions that started in September. We recorded the last active nest on 13 February 2019, with a nestling of the striped cuckoo in late developmental stage.

The nine marked couples we observed in 2018/2019 breeding season initiated the construction of 1–4 nests (2.89 ± 0.93) and completed the construction of 0–3 nests (2.11 ± 1.05), and they initiated 0–3 clutches (2.11 ± 1.05) (Table 1). Of the 19 nests with initiated clutches, nine

were depredated during incubation or nestling stages, three drowned after heavy rains, one successfully fledged yellow-chinned spintails (three young), and six fledged one striped cuckoo each. Parasitized nests never fledged more than one striped cuckoo. Then, the annual reproductive output was 0.33 ± 1.0 yellow-chinned spintails fledglings per pair, or 1.0 ± 1.12 fledglings when considering host and parasite clutches together (Table 1). The maximum number of successful broods produced by a pair was two, and in the two cases in which it happened, only striped cuckoos were produced. We observed nest reuse only once, with the subsequent production of two striped cuckoos.

After applying the manuscript selection criteria, and after checking therein references, our literature search returned 20 studies on 18 Neotropical passerine species containing nesting attempts and/or annual fecundity information (Table 2). For the temperate New World passerines, we gathered information on six thoroughly studied North American species, as reported by Grzybowski and Paese (2005) and therein references (Table 2).

Discussion

Annual fecundity in our investigated population of the yellow-chinned spintail was low compared to other Neotropical passerines, and the main reason was the combined effect of nest predation and brood parasitism by the striped cuckoo. In a study considering nests of both marked and unmarked pairs conducted in the same population of yellow-chinned spintails in southeastern Brazil, the frequency of parasitism by striped cuckoos was 75% (Murcia et al. 2020). In a population from Suriname, parasitism frequency was 66.7% (Haverschmidt 1961), and in a population from Argentina, it was 26.6% (Di Giacomo 2005), suggesting that annual fecundity can vary greatly across populations of yellow-chinned spintails as a result of striped cuckoo parasitism and that the low annual fecundity we observed may not be a general rule. Other studies have reported that the association of nest predation with brood parasitism can result in very low passerine fecundity rates (Paese and Grzybowski 1995; Hargrove and Unitt 2017). The social monogamy observed within the breeding season agreed with the reports of de la Peña and Salvador (2016), although they did not report the methods used to follow the individuals and sample sizes. On the other hand, the high parasitism and the low apparent nest survival rates could have contributed to the increased number of divorces between breeding seasons, as divorces are often influenced by low breeding success (Culina et al. 2015).

The theory that longer breeding seasons in the tropics allow more nesting attempts and more broods per year

Table 2 Annual fecundity components of Neotropical passerines for which marked reproductive pairs could be thoroughly investigated throughout entire breeding seasons. The parameters included breeding season duration, numbers of clutch initiations per season, relevant observations emphasized by the authors, annual fecundity (number of offspring produced per pair in a breeding season), latitude in which the study was conducted, and references. English and scientific nomenclature followed American Ornithological Society (AOS) checklists

| Species | Breeding season | Clutch initiations | Author's notes | Annual fecundity | Latitude | Reference |
|---|-----------------|--------------------|--|-------------------|----------|------------------------------|
| Neotropical species | | | | | | |
| Puerto Rican vireo (<i>Vireo latimeri</i>) | 2.5–3.5 months | 3.15 (1–6) | Pairs fledging two broods never initiated another clutch | 0.78 (0–5) | 17°N | Woodworth (1997) |
| Montserrat oriole (<i>Icterus oberi</i>) | 4–5 months | - | - | 1.26 - | 16°N | Oppel et al. (2013) |
| Rufous-and-white wren (<i>Thryophilus rufalbus</i>) | ~3–4 months | - | Pairs fledging one brood rarely initiated another clutch | - | 11°N | Ahumada (2001) |
| Buff-breasted wren (<i>Cantorchilus leucotis</i>) | ~2 months | - | Pairs fledging one brood rarely initiated another clutch | - | 11°N | Ahumada (2001) |
| Song wren (<i>Cyphorhinus phaeocephalus</i>) | 7 months | 2.14 ± 0.6 (1–3) | Pairs fledging one brood rarely initiated another clutch | 1.4 ± 0.03 | 9°N | Robinson et al. (2000) |
| Spotted antbird (<i>Hylophylax naevioides</i>) | 4 months | 4.7 ± 0.2 (2–8) | Pairs fledging two broods never initiated another clutch | 1.5 ± 0.2 | 9°N | Styrsky and Brawn (2011) |
| Buff-breasted wren (<i>Cantorchilus leucotis</i>) | ~5.5 months | 2.1 ± 0.17 - | - | - | 9°N | Gill and Haggerty (2012) |
| White-banded tanager (<i>Neothraupis fasciata</i>) | ~4 months | - | - | 0.62 - | 16°S | Duca and Marini (2014) |
| Tropical mockingbird (<i>Mimus gilvus</i>) | 6–7 months | (1–4) | Pairs fledging one brood never initiated another clutch | - | 20°S | Morais et al. (2019) |
| Tropical kingbird (<i>Tyrannus melancholicus</i>) | 6 months | 1.15 ± 0.42 (1–3) | - | - | 20°S | Daros et al. (2018) |
| Yellow-chinned spintail (<i>Certhiaxis cinammomeus</i>) | ~4.5 months | 2.11 ± 1.05 (0–3) | Pairs fledging two broods (of the parasite) never initiated another clutch | 0.33 ± 0.33 (0–3) | 23°S | Present study |
| Black-cheeked gnateater (<i>Conopophaga melanops</i>) | 3 months | 1.5 ± 0.7 (1–3) | Pairs fledging one brood never initiated another clutch | 0.72 | 25°S | Lima and Roper (2009) |
| Star-throated antwren (<i>Rhopias gularis</i>) | 4 months | (1–4) | Pairs fledging one brood never initiated another clutch | 1.0 ± 0.3 | 25°S | Lima and Roper (2016) |
| Tawny-bellied seedeater (<i>Sporophila hypoxantha</i>) | 4 months | - | Pairs fledging one brood never initiated another clutch | - | 28°S | Franz and Fontana (2013) |
| Tropeiro seedeater (<i>Sporophila beltoni</i>) | 3.8 months | - | Only 15% of females having one successful brood attempted to renest | - | 28°S | Repenning and Fontana (2016) |
| Rusty-collared seedeater (<i>Sporophila collaris</i>) | ~7 months | 1.28 ± 0.46 (1–2) | Only 3% of females having one successful brood attempted to renest | - | 29°S | Rosoni et al. (2019) |
| Yellow cardinal (<i>Gubernatrix cristata</i>) | ~5 months | 2.2 ± 0.42 (1–3) | - | - | 30°S | Beier and Fontana (2019) |
| Red-crested cardinal (<i>Paroaria coronata</i>) | 5 months | 4.4 ± 0.2 (2–8) | - | - | 35°S | Segura et al. (2015) |
| Firewood gatherer (<i>Anumbius annumbi</i>) | 9 months | 2.84 (1–6) | - | - | 38°S | Delhey et al. (2010) |

Table 2 (continued)

| Species | Breeding season | Clutch initiations | Author's notes | Annual fecundity | Latitude | Reference |
|---|-----------------|---------------------------|---|---------------------|----------|---------------------------|
| Yellow cardinal (<i>Gubernatrix cristata</i>) | 3 months | 1.38 ± 0.60 (1–4) | Pairs fledging one brood never initiated another clutch | - | 38/39°S | Domínguez et al. (2015) |
| Northern temperate species | | | | | | |
| Black-throated blue warbler (<i>Setophaga caerulescens</i>) | ~3 months | 1.7 ± 0.7 (1–4) | - | 4.3 ± 2.3 | 44°N | Holmes et al. (1992) |
| Hooded warbler (<i>Setophaga citrina</i>) | ~3 months | (1–2) | - | - | 41°N | Ogden et al. (1996) |
| Song sparrow (<i>Melospiza melodia</i>) | ~3.5 months | 3.25 ± 0.45 (3–4) | - | 4.3 ± 2.5 (0–10) | 40°N | Nice 1937 |
| Prairie warbler (<i>Setophaga discolor</i>) | ~3 months | 3.2 ^a (1–7) | - | 2.5 (0–7) | 39°N | Nolan (1978) |
| Dickcissel (<i>Spiza americana</i>) | ~3 months | 1.4 ± 0.1 (1–2) | - | 2.5 ± 0.3 | 39°N | Walk et al. (2004) |
| Wrentit (<i>Chamaea fasciata</i>) | ~2 months | 1.2 ± 0.4 (1–2) | - | - | 38°N | Geupel and DeSante (1990) |

^aIncludes completed nests without egg laying (four of 70 nests)

is important because it is a fundamental prediction of the “bet-hedging strategy,” which infers that the reduced clutch sizes observed for tropical birds would result from the distribution of nest predation risks across multiple smaller broods in a long breeding season (Foster 1974; Martin 1995, 1996; Jetz et al. 2008; Griebeler et al. 2010). Here, we did not aim to present a complete review that includes, for instance, Old World species, but the data on the yellow-chinned spinetail and other tropical and temperate New World passerines for which marked pairs were thoroughly investigated throughout breeding seasons confirmed the idea that breeding seasons are longer in the Tropics (2–9 months) than in temperate habitats (2–3.5 months). However, our review did not provide clear evidence for the prediction of the “bet-hedging strategy” that numbers of nesting attempts could be higher in the tropics (see also Martin 1996). The most common pattern of up to three or four nesting attempts (clutch initiations) observed in tropical species also was observed in northern temperate taxa, e.g., the song sparrow (*Melospiza melodia*) and the black-throated blue warbler (*Setophaga caerulescens*), and cases of up to seven or eight nesting attempts per season seemed to be associated to exceptional pairs that occurred in both tropical and temperate species, e.g., the spotted antbird (*Hylophylax naevioides*) and the prairie warbler (*Setophaga discolor*), respectively.

For the yellow-chinned spinetail, although the last striped cuckoo nestling was observed on 13 February (pair 10), pairs that lost their clutches or successfully fledged young after 11 January never attempted to reproduce again, likely because of the proximity to the end of the reproductive season. Pairs 7 and 13, however, stopped reproducing after fledging young on 05 and 17 December, respectively, which suggests that

they would have enough time for laying a further clutch. This was consistent with the findings that most Neotropical passerines studied so far were not willing to fledge more than one clutch per season, such as the song wren (*Cyphorhinus phaeocephalus*), the tropical mockingbird (*Mimus gilvus*), the black-cheeked gnatcatcher (*Conopophaga melanops*), the buff-breasted wren (*Cantorchilus leucotis*), the star-throated antwren (*Rhopias gularis*), the yellow cardinal (*Gubernatrix cristata*), the tawny-bellied seedeater (*Sporophila hypoxantha*), and the rusty-collared seedeater (*Sporophila collaris*), or two clutches in a season, e.g., the spotted antbird and the Puerto Rican vireo (*Vireo latimeri*) (see Table 2), even when they succeeded and had enough time for producing further clutches, suggesting that there were parameters other than only nest predation and breeding season duration constraining multiple brooding in tropical passerines. Associated to the smaller clutch sizes, it could explain the reduced annual fecundity of the tropical songbirds, and this pattern is more consistent with a model in which tropical species spread their reproductive efforts between breeding seasons across a longer life (Martin 1996, 2004; Duca and Marini 2014), rather than within long breeding seasons.

Analyses that controlled for the phylogenetic non-independence of the data were useful to prove that smaller clutch sizes in southern tropical birds than in northern temperate species were not merely an effect of the phylogenetic distances of the taxa from different hemispheres (Jetz et al. 2008). Performing statistical tests involving multiple taxa was not in the scope of our work, but the data gathered for comparative purposes indicated that the patterns of reproductive effort could be similar even across representatives of phylogenetically distant passerine families, distributed throughout both hemispheres and habitats.

Although the tendencies depicted by our comparisons contradicted some of the components of a classical bird life-history theory, it is important to consider that empirical studies on annual fecundity based on marked individuals are still scarce, especially for Neotropical species. Understanding the broad geographic reproductive patterns have never been so important, as they could contribute to the comprehension of how the different species will respond to the increasing climatic and land-use changes (Mattsson et al. 2011), meaning that basic field work based on marked individuals still should be in the agenda of ornithologists.

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Author contribution AM and MRF conceived the study design; AM, MCC, CABM, and MRF carried out data collection; AM and MRF analyzed the data and wrote the first version of the paper; AM, MCC, CABM, and MRF contributed with the elaboration of the final version of the manuscript.

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Data availability Data is available from the authors upon request.

Code availability Not applicable.

Declarations

Ethics approval Field work procedures were following the Brazilian legislation. Birds capture and marking, and nest checking were approved by Ministério do Meio Ambiente, Instituto Chico Mendes de Conservação da Biodiversidade, SISBIO/ICMBio (permit #60880–1), and by the Ethical Committee for the Use of Animals (CEUA: permit #8369111217) from Universidade Federal de São Carlos, UFSCar. Field work at the private property was authorized by the company owning the farm (RADAR/Nova Amaralina S.A. Propriedades Agrícolas).

Consent to participate All of the authors have approved the final version of the manuscript and have agreed to participate of this publication.

Consent for publication All authors have agreed with the publication of this manuscript in Ornithology Research.

Competing interests The authors declare no competing interests.

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