

Effects of Sarcophagid Fly Infestations on Green Anole Lizards (*Anolis carolinensis*): An Analysis across Seasons and Age/Sex Classes

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ABSTRACT.—A largely unresolved ecological issue concerns why normally rare parasites become common within reptile and amphibian populations. We gathered demographic data on incidence of infection and demographic consequences of a normally rare sarcophagid fly parasite (*Lepidodexia blakeae*) on a population of Green Anole Lizards (*Anolis carolinensis*). These sarcophagid flies primarily larviposit on adult male Green Anoles during the winter. Sampling by age and sex classes during two years (2003 and 2004) revealed that adult male anoles were infected at an unusually high rate (up to 16%) compared to other populations (only a few documented cases over the past 60 years) and relative to conspecific juveniles and females. Male anoles at Tulane exhibited high mortality compared to other nonparasitized populations, suggesting that parasitism negatively affects survivorship. Although the underlying cause of the high parasitism in the Tulane population remains unclear, several lines of evidence suggest that high and stressful levels of male competition may be a key factor.

Parasites may play a key role in influencing mortality and reproductive opportunity within animal populations generally and reptiles and amphibians in particular (for a recent review, see Moore, 2002). One largely unresolved issue for reptile and amphibian populations concerns why normally rare parasites are common within some populations, especially if highly deleterious, and a major source of mortality. In a related vein, for populations that experience high rates of normally rare parasites, there is little temporal data (i.e., data across different seasons) on how the parasite affects different age/sex classes (i.e., males, females, juveniles).

We attempt to fill this void by integrating demographic data on the incidence of infection by a normally rare sarcophagid fly parasite (*Lepidodexia blakeae*, Diptera: Sarcophagidae) with mark-recapture data on a lizard population (the Green Anole, *Anolis carolinensis*). *Lepidodexia blakeae* is a medium-sized (total length about 6 mm) parasitic fly that was first described by Blake (1955) as infecting Green Anoles. These flies larviposit on live Green Anoles, and the larvae develop inside the lizard until they emerge from a wound (see Fig. 1) and pupate into adult flies in sediment. Green Anoles are small (2–6 g), arboreal, and insectivorous lizards that have been a model system for studies of behavioral ecology (e.g., Greenberg and Crews, 1990; Jenssen et al., 2000, 2001; Lovern and Jenssen, 2003; Lailvaux et al., 2004). Despite the use of anoles in general, and Green Anoles specifically, as model systems for systematics, behavioral ecology, and neuroethology (Losos, 1994; Roughgarden, 1995), sarcophagid fly infections have been documented in only a few individuals over the past 60 years (Blake, 1955; Dial and Roughgarden, 1996, see also Crump and Pounds, 1985; Pounds and Crump, 1987; Smith et al. 1994). Our data hold importance for the general field of herpetology because little is known of how parasitic flies affect reptile or amphibian populations, and we are aware

of no data that compare infection rates across different seasons, or among age/sex classes. Indeed, based on our data, we suggest that certain populations that are typically rarely examined by herpetologists (e.g., urban populations) may show higher incidences of such normally rare parasites.

We had two primary goals: (1) to describe the incidence of both “active” (i.e., infections with live sarcophagid larvae inside the lizard) and “past” infections within different age/sex classes of Green Anoles across different seasons; and (2) to determine whether the mortality in adult male Green Anoles was unusually high in the affected population compared to other, noninfected populations examined by previous authors. We focused on adult males because the sarcophagid fly *L. blakeae* appears to target them. To achieve these goals, we captured 1363 Green Anoles (males, females and juveniles) across several seasons (spring, fall, and winter) in two populations. One of the populations (Tulane University) shows an abnormally high incidence of sarcophagid fly infection, whereas the other sampled population (Good Hope Field) showed no evidence of sarcophagid fly infection.

MATERIALS AND METHODS

Our primary field site (Tulane) was located on Tulane University (Orleans Parish, Louisiana) within the city of New Orleans. We sampled along a 380-m transect (a road with clumps of vegetation on either side) that was relatively isolated from the rest of the campus. The vegetation of the Tulane campus was dominated by clumps of relatively short (< 2 m) palmetto leaves (*Aspidistra elatior*), with few large trees or bushes. The Tulane population is watered regularly, and, thus, lizards are not exposed to drought. We sampled a second, more natural swamp population (Good Hope Field, St. Charles Parish, Louisiana) as a point of comparison. We sampled along a linear 755-m transect that consisted of an access road, with vegetation running along either side of the road, and open swamp water isolating each of the rows of vegetation.

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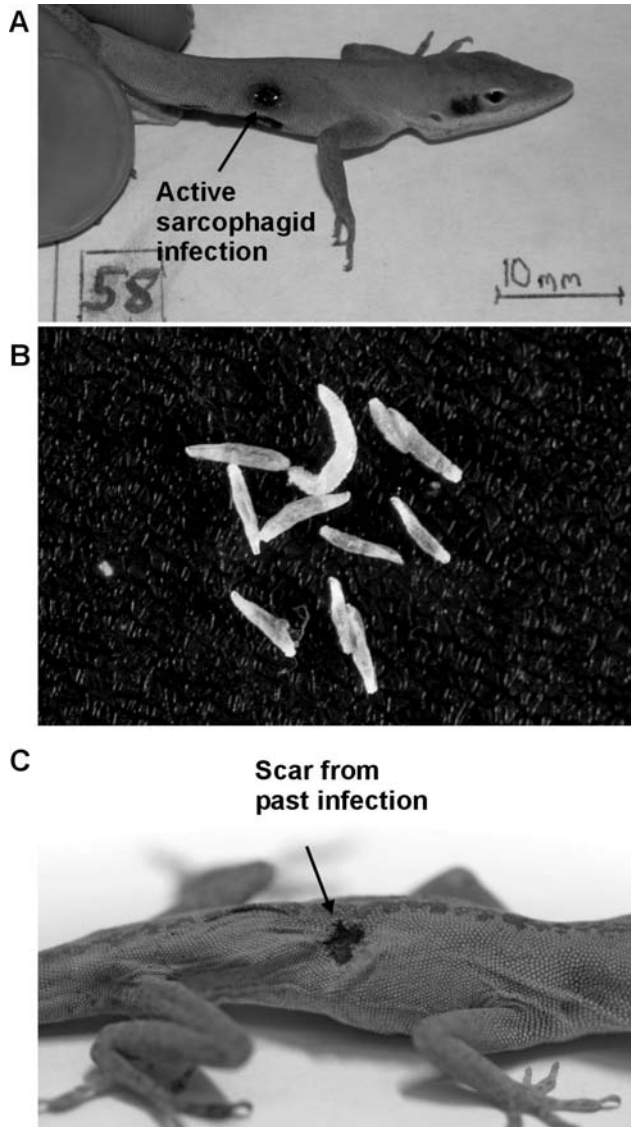


FIG. 1. Panel A shows a typical “active” sarcophagid infection (larvae inside lizard) on an adult male Green Anole as observed during the winter (Table 1). Panel B shows 11 sarcophagid larvae taken from an adult male green anole lizard during the winter of 2003/2004 (combined mass = 0.023 g). Panel C shows a scar from a lizard captured during the spring of 2004 indicating a “past” sarcophagid infection (the fly larvae have left the lizard). These parasite scars were prevalent during the spring (Table 1).

Therefore, both populations were linear transects of isolated vegetation (for details, see Irschick et al., 2005). The Good Hope Field site was relatively undisturbed, and contains complex vegetation (e.g., cypress trees), and a typical Southern Louisiana community of potential anole predators (e.g., herons, snakes).

At Tulane, we collected anoles (for sample sizes, see Table 1) during the winter of 2003/2004 (10 December to 10 January), the spring of 2004 (1 April to 30 May), and the fall of 2004 (15 September to 31 October). Thus, we sampled for about the same number of human-hours per season. Beginning in the winter of 2003/2004,

we recorded signs of parasite infection from sarcophagid flies, which are distinguished by a hole (live infection), or a scar (old infection; Fig. 1). For Good Hope Field, we gathered samples of anoles during the fall of 2002 ($N = 403$, including juveniles, adult females, and adult males, $N = 220$ adult males), and the spring of 2004 ($N = 180$, including juveniles, adult females, and adult males, $N = 103$ adult males). Although we did not detect the sarcophagid parasite until the winter of 2003/2004, we maintained digital images of the fall 2002 Good Hope Field sample, and determined that this population was not infected. We

measured snout-vent length (SVL; to 0.01 mm with digital Mitutoyo calipers) and mass (to 0.001 g on a Mettler scale) on all lizards. To determine the condition of anoles in the two populations, we regressed (linear least-squares) log-transformed SVL (x-axis) versus log-transformed mass (y-axis) from pooled data for both populations, and calculated residuals.

To assess whether parasitism negatively affected mortality at Tulane, we began to gather mark-recapture data during the spring of 2003. We defined adult (sexually mature) males as being equal to or larger than 45 mm SVL. We focused on males because they were most heavily parasitized (see Results) and conspicuous and, hence, were more readily recaptured. We captured lizards during normal activity hours (0900–1700 h) and distinguished males by their enlarged postanal scales. For each season (spring 2003, winter 2003/2004, and spring 2004), we permanently marked adult males using a VIE tag (visual implant elastomer tag), that was injected under the ventral skin (Nauwelaerts et al., 2000). We placed tags in unique color (red, green, yellow), and body position (forelimb, hind limb) combinations. Lizards were returned to their point of capture within 48 h. These marks are easy to detect and are unseen by most potential predators or congeners because they were placed ventrally. We sampled the population for each season until approximately 80% of the adult males were marked. Because of the isolated nature of the clumps of low bushes, we were confident that each sampling period we captured and marked the majority of the population. The sample sizes of total number of marked males were: spring 2003 ($N = 86$), winter 2003/2004 ($N = 56$), spring 2004 ($N = 73$), and fall 2004 ($N = 23$). We note that of the 56 “marked” adult males in the winter 2003/2004 sample, nine were already marked (i.e., were recaptured from the spring of 2003), and hence 47 were “new” marked animals. Similarly, of the 73 “marked” males for the spring 2004 sample, 27 were already marked in the winter of 2003/2004, meaning that 46 “new” adult males were marked.

RESULTS

Anoles in the Tulane population exhibited relatively large numbers of live sarcophagid infections and parasite scars across different seasons (Table 1), but we did not detect any parasitized lizards at Good Hope Field. Sarcophagid infections were seasonal within the Tulane population; we only observed “active” infections (Fig. 1) in the winter of 2003/2004 (6.0% of all lizards sampled), and fall 2004 (7.6% of all lizards sampled). However, we observed only parasite scars, indicating “past” infections (4.8% of all lizards sampled), in the spring of 2004, with the exception of one lizard with a parasite scar in the fall of 2004 (1.0% of all lizards sampled; Table 1). The pattern of parasite infections was also unequal among age/sex classes (Table 1). During the winter of 2003/2004, adult males were 5–8 times more likely to exhibit live infections compared to adult females and juveniles. This pattern persisted to the spring of 2004, which consisted of animals with parasite scars from winter infections (Table 1, Fig. 2). Active parasite infections were present at significantly higher levels in adult males compared to adult females or juveniles in the winter of 2003/2004 (live infections, $\chi^2 = 189.7$, $P < 0.001$) and the spring of 2004 (parasite scars, $\chi^2 = 5.9$, $P = 0.05$). The pattern of

TABLE 1. Frequencies of Tulane lizards of different age/sex classes (adult females, adult males, juveniles) with both “active” sarcophagid infections (i.e., larvae inside them) and “past” infections (i.e., larvae have left the lizard) across several seasons. Numbers outside parentheses are the total numbers of individuals per age/sex class that show either active infections or past infections. Numbers in parentheses represent percentages of the sample sizes in the “Season column” (i.e., the 2.3% for the juveniles from the winter 2003/2004 frequent infections row represents the percentage of juveniles parasitized relative to the total sample of 126 juvenile lizards).

Season	Frequent active infections	Frequent past infections
Winter 2003/2004 ($N = 210$)	13 (6.2%)	0
Juveniles ($N = 126$)	3 (2.3%)	0
Adult females ($N = 28$)	1 (3.6%)	0
Adult males ($N = 56$)	9 (16.1%)	0
Spring 2004 ($N = 210$)	0	10 (4.8%)
Juveniles ($N = 11$)	0	0
Adult females ($N = 125$)	0	3 (2.4%)
Adult males ($N = 74$)	0	7 (9.5%)
Fall 2004 ($N = 118$)	9 (7.6%)	1 (0.8%)
Juveniles ($N = 61$)	4 (6.6%)	0
Adult females ($N = 34$)	4 (11.8%)	0
Adult males ($N = 23$)	1 (4.3%)	1 (4.3%)

parasite infection during the fall of 2004 was more complex; unlike the winter, most of the infections were in juveniles (6.6%), and adult females (11.8%), with only one adult male showing an active infection (Table 1), resulting in a significant difference among age/sex classes ($\chi^2 = 25.9$, $P < 0.001$).

During the fall of 2004, we acquired an adult sarcophagid fly that emerged from a pupae. The fly was identified as *L. blakeae* by G. Gentry (a synonym of *Anolisimymia blakeae* as identified by Blake, 1955; see Pape, 1996). Unlike the two other accounts of *Anolisimymia* parasitizing anoles (Blake, 1955; Dial and Roughgarden, 1996), some lizards we observed survived infection (Figs. 1, 2). Of the 13 lizards (all age/sex groups) with active infections documented in the winter of 2003/2004, only one individual persisted until fall of 2004 (Fig. 2). The adult male pattern is noteworthy; 16.1% of the winter adult males had active parasite infections, but only 9.5% and 4.3% of the spring 2004 and fall 2004 adult males exhibited parasite scars.

Based on data across four seasons, adult male Green Anole mortality at Tulane is extremely high. We only recaptured nine of 86 marked spring 2003 males in the winter of 2003/2004 (90.0% mortality), and only one and zero individuals from the spring of 2004 (99.0% mortality) and the fall of 2004 (100% mortality). Overwintering mortality was lower, with 27 of the 56 marked winter 2003/2004 males surviving (52.0% mortality), although only two of these survived to the fall of 2004 (96.4% mortality). Finally, we only recaptured three marked males from the spring 2003 cohort

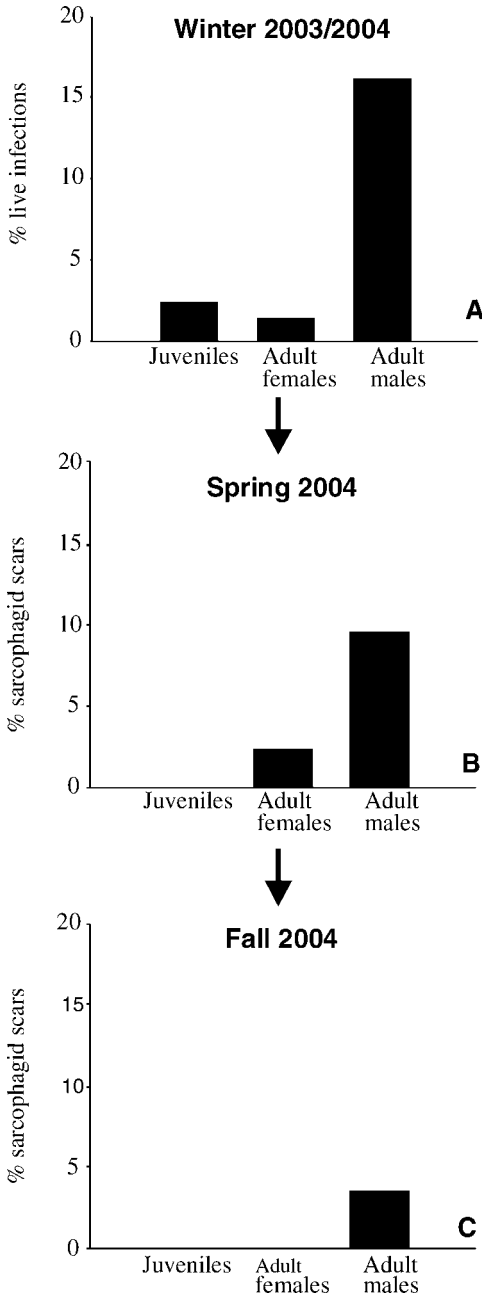


FIG. 2. Frequencies of parasitized green anole lizards from population samples taken during the (A) winter of 2003/2004 (active infections only), (B) spring of 2004 (past infections only shown), and (C) fall 2004 (past infections only shown). Of the relatively large number of adult males with active infections in the winter (16.1%), fewer remain each following season (spring: 9.5%, fall: 4.3%), suggesting mortality caused by the infections.

(73 males marked, 95.9% mortality). By comparison, annual recapture rates for Green Anole males in other habitats (i.e., Bahamas) range from 10–30% (Schoener and Schoener, 1982). Hence, Tulane adult male survivorship (about 1% annual survival) is low compared to other Green Anole populations. In agreement with this comparison, adult male condition (residual mass) was significantly lower for Tulane Green Anole adult males during both the nonreproductive (Winter 2003/04 for Tulane, Fall 2002 for Good Hope Field) and reproductive seasons compared to Good Hope Field Green Anole adult males (nonreproductive season; $F_{1,268} = 62.8, P < 0.001$; reproductive season; $F_{1,174} = 130.1, P < 0.001$).

DISCUSSION

We documented a high incidence of a normally rare sarcophagid fly parasite infecting a population of Green Anoles. We detected live sarcophagid infections during the winter and fall and scars from prior infections during the spring. The pattern of sarcophagid infections differed greatly among age/sex groups. During the winter, adult male Green Anoles were 5–8 times more likely to be parasitized compared to juveniles or adult females, a pattern persisting into the spring of 2004. On a cautionary note, during the fall of 2004, only one male exhibited a live parasite wound, suggesting that the full-blown pattern of sarcophagid infections may not take place until late in the winter season. However, the fall 2004 sample was relatively small compared to the other samples ($N = 118$ animals total, $N = 23$ males), in large part because of the scarcity of lizards. Nevertheless, mark-recapture data indicates that annual adult male mortality (about 99%) is unusually high compared to other anole populations (between 70 and 90% annual mortality). Further, we did not detect any sign of sarcophagid infection in a nearby (within 50 km) swamp population in which sarcophagid flies are known to occur (G. Gentry, pers obs.).

Any discussion of why normally rare parasites become common must consider the ecological circumstances of both the parasite and the host (e.g., geographical ranges, susceptibility; Moore, 2002; Thomas et al., 2005). One possibility is that *L. blakeae* occurs at the Tulane site but not in other nearby areas, such as Good Hope Field. Little detailed range information is available for sarcophagid flies, but casual observations suggest that this is not the case, because we have observed *L. blakeae* in other nearby (e.g., swamps) outside of New Orleans (G. Gentry, pers. obs.), although we cannot refute the possibility that *L. blakeae* occurs at a much higher abundance in New Orleans. A second possibility is that some attribute of the environment at the Tulane site makes Green Anoles more susceptible to infection by *L. blakeae*.

A notable feature of the Tulane habitat is the general lack of normal mortality sources, such as predators and drought (Irschick et al., 2005), which begs the question for why this population suffers such high rates of sarcophagid parasitism, as well as high mortality (for adult males). Previous syntheses have stressed the influence of habitat structure on social structure and patterns of male competition (Shuster and Wade, 2003; Zamudio and Sinervo, 2003). The male-biased pattern of sarcophagid infection in Green Anoles, particularly

in the winter of 2003/2004, hints that agonistic interactions among males may be a key factor, as they will fight aggressively for access to territories, sometimes resulting in severe bite scars that could facilitate sarcophagid fly infection (McMann, 1993; Jenssen et al., 2000, 2001; Lailvaux et al., 2004). Indeed, the high densities (threefold higher at Tulane, N. Bloch and D. J. Irschick, in press) and the close proximity of territorial Green Anole males (males occur nearly exclusively in dense clumps of vegetation) on the Tulane site would seem to foster intense male competition. Intense male competition in an environment in which predation pressure is relaxed would be expected to result in a higher frequency of normally risky, and highly exhausting visual displays (Leal, 1999; Brandt, 2003, see also McMann, 1993). Accordingly, Tulane Green Anole adult males display about twice as often during the spring reproductive period (about 10% of the time) compared to Good Hope Field anoles (about 5% of the time; N. Bloch and D. J. Irschick, unpubl. data).

Another distinctive feature of the Tulane Green Anole population is their ability to survive normally fatal sarcophagid infections (Dial and Roughgarden, 1996). This form of parasite resistance, although not complete (see Fig. 2), suggests an extended period of coexistence with sarcophagid flies. Our study also raises other questions that would benefit from further research. For example, do males with particularly poor condition following the spring incur a greater risk of parasitism? If one experimentally induces poor male condition in anoles from populations with no incidence of parasitism (e.g., Good Hope Field), does this consequently result in sarcophagid infections? Finally, we suggest that other populations of reptiles and amphibians occurring in "atypical" habitats (i.e., urban environments) might also show high incidence of such normally rare parasites, especially if these environments strongly affect the social context of the populations. We note, for example, that we did not detect live infections of sarcophagid infections of green anoles until we sampled during the winter, a period when herpetologists are less likely to sample reptiles and amphibians.

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Gastrointestinal Fermentation in Greater Sirens (*Siren lacertina*)

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ABSTRACT.—The nutritional ecology and digestive physiology of salamanders in the Family Sirenidae remain poorly understood. Although the intestinal contents of these salamanders include herbivorous dietary items, the nutritional significance of such ingested matter is unknown. In this study, we examined gut contents, gastrointestinal structure, and microbial fermentation in wild-caught Greater Sirens (*Siren lacertina*). Ingested items included aquatic invertebrates, vascular plants, and algae. The guts of these amphibians were not as voluminous or morphologically specialized as in many herbivores, but the posterior intestine was enlarged and exhibited a distinct folding pattern and an ileocolonic valve that may help maintain a symbiotic microbial population. An active microbial fermentation was indicated by relatively high levels of short-chain fatty acids in the medial-posterior and posterior gut regions. This is the first account of gastrointestinal fermentation in the Family Sirenidae and only the second account in the Class Amphibia.

It has only recently been determined that some herbivorous amphibians (i.e., larval *Rana catesbeiana*) exhibit a microbial fermentation similar to that of other herbivorous vertebrates (Pryor and Bjorndal, 2005a,b). It remains unknown whether any other amphibians benefit from gastrointestinal fermentation of an herbivorous diet. Considering the diversity of feeding strategies employed among amphibians (Duellman and Trueb, 1994), it would be surprising if anuran larvae were the only herbivorous members of this class with an active gastrointestinal fermentation that contributes to their nutritional requirements.

One group of amphibians worth investigating in these regards is the Family Sirenidae, which includes the Greater Siren (*Siren lacertina*). The diet of *S. lacertina* includes vascular plants, plant-based detritus, filamentous algae, and phytoplankton (Dunn, 1924; Ultsch, 1973; Hanlin, 1978; Conant and Collins, 1991; Behler and King, 1997). Hanlin (1978) reported that plant debris and algae were the two most commonly ingested items in these aquatic salamanders, and Ultsch (1973) found that nonanimal material represented at least 75% of ingested biomass. Despite the predominance

of such plant- and algae-based dietary items in the gastrointestinal tracts of *S. lacertina*, some authors have reported that mollusks are an important component of the diet (Moler, 1994 and references therein), and others have questioned whether the ingestion of herbivorous dietary items is incidental to feeding on invertebrate and vertebrate prey (Scroggin and Davis, 1956; Conant and Collins, 1991). However, Ultsch (1973) and Hanlin (1978) provide anecdotal accounts that suggest *S. lacertina* feeds actively and deliberately upon some aquatic vascular plants.

Regardless of the mechanism or intent with which herbivorous food items are ingested, an investigation is warranted to determine whether *S. lacertina* have the gastrointestinal specializations and symbiotic gut communities that would allow them to digest such foods. In many herbivores, symbiotic microbes living in the gut ferment the structural carbohydrates that the host cannot digest enzymatically (e.g., cellulose), and release byproducts such as short-chain fatty acids (SCFA). These metabolic byproducts can be absorbed through the gut wall and used as an energy source by the herbivorous hosts (reviewed in Stevens and Hume, 1995). Accordingly, high levels of SCFA within the gut of an herbivorous host are indicators of microbial fermentation.

The objectives of this study were to investigate the gastrointestinal tract contents, gross gut morphology, and relative concentrations of SCFA within the gut of *S. lacertina*.

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