

Research Article

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Attracted to feed, not to be fed upon – on the biology of *Toxomerus basalis* (Walker, 1836), the kleptoparasitic ‘sundew flower fly’ (Diptera: Syrphidae)

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Abstract

The complete life history of the kleptoparasitic ‘sundew flower fly’, *Toxomerus basalis*, is presented and illustrated. Adults of this species are photographed alive for the first time, including video recordings of larval and adult behaviour. Adult flies of both sexes visit *Drosera* (sundews) and show territorial behaviour around the plants, avoiding the dangerous sticky traps and demonstrating recognition of their larval host plant. Females lay eggs directly on non-sticky parts of the *Drosera* host plants, such as on the lower surface of the leaves and flower stalks, but apparently also on other plants growing in close proximity with the sundews.

Introduction

Toxomerus Macquart, 1855 (Diptera, Syrphidae, Syrphinae), is a New World flower fly genus with most species occurring in the Neotropics (Thompson *et al.* 2010), although *Toxomerus floralis* (Fabricius, 1798) has been recently introduced in the Afrotropics (Jordaens *et al.* 2015). More than 140 described *Toxomerus* species are known (Thompson *et al.* 2010), and 39 species have been recorded from Brazil (Borges & Couri 2009; Morales & Marinoni 2021). While changes to its taxonomy and inferred evolutionary relationships have been recently accomplished (Metz & Thompson 2001; Thompson & Thompson 2006; Mengual *et al.* 2008, 2012; Borges & Couri 2009; Mengual 2011; Thompson 2016), the life history and larval biology of few species have been documented. In common with most tropical Syrphinae species, the larval stages of most *Toxomerus* species are unstudied, but the species with described larval life histories are either pollen-feeders (Reemer & Rotheray 2009; Nunes-Silva *et al.* 2010; Jordaens *et al.* 2015; Dumbardon-Martial 2016) or predaceous on a wide-range of soft-bodied arthropods including aphids, caterpillars, beetle larvae, planthoppers, gall midges, thrips, mealybugs, whiteflies, mites, or insect eggs (Sampson *et al.* 2002; Rojo *et al.* 2003; Hopper *et al.* 2011; Fok *et al.* 2014; Sturza *et al.* 2014; Torres *et al.* 2014; Campos *et al.* 2017; Jirón-Pablo *et al.* 2018; Soares *et al.* 2020).

Observations of *Toxomerus basalis* (Walker, 1836) larvae and their unusual kleptoparasitic larval behaviour on the sticky leaves of carnivorous sundew plants (*Drosera* L., Droseraceae) were first reported by Fleischmann *et al.* (2016). The entire larval development of *T. basalis*, including all instar stages (L₁ – L₃), occurs on sticky *Drosera* leaves, where the larvae freely and quickly move between sundew tentacles. They do not adhere to the sticky mucilage, probably because their body is also covered by a thin layer of slime (Fleischmann *et al.* 2016). They feed on captured, immobilized insect prey caught by the *Drosera* leaves, an interaction that can be considered true kleptoparasitism *sensu* Hamilton (2002), as the larvae do not return nutrients to the plant, not even through their excretions, as predatory syrphine larvae do not defecate until they pupate (Rotheray & Gilbert 2011).

Fleischmann *et al.* (2016) also gave a detailed morphological description of the last larval instar (L₃) of *T. basalis* based on alcohol-preserved material, but did not observe living larvae and adults *in situ*. In December 2018, additional field observations were made in Minas Gerais, Brazil, by AF and PMG, which revealed new data on the biology of *T. basalis*, including oviposition, presence of all larval instars, foraging and feeding behaviour of the larvae, and insight into the adult behaviour of both sexes. Presented here is the summary of new data on the biology, behaviour, and entire life history of the larvae and adults of *T. basalis*, a species endemic to Brazil, increasing knowledge of the kleptoparasitic ‘sundew flower fly’ more than 180 years after the species’ description.

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Materials and methods

Larval behaviour of *Toxomerus basalis* on *Drosera* leaves was observed by AF and PMG over several days during the 2018 rainy season (early December) at five sites in Minas Gerais, Brazil, both on *Drosera* species with erect, thread-like leaves (*D. spiralis* A.St.-Hill and *D. magnifica* Rivadavia & Gonella), and on flat-rosetted species with semi-erect leaves (*D. graomogolensis* T.R.S.Silva and *D. latifolia* (Eichler) Gonella & Rivadavia). Additional observations were made at site 1 by PMG in March 2021 (late rainy season); five adults were collected on that occasion by Danilo Pacheco Cordeiro and deposited at the zoological collection of the Instituto Nacional da Mata Atlântica/Museu de Biologia Professor Mello Leitão (MBML). In total, >50 individuals of *T. basalis* were studied (12 adults and ca. 40 larvae). All observations were made during clear, sunny weather conditions (with only short rain shower events at sites 1 and 4, during which no flying adults were observed and larvae stayed on the leaves of their host plant). At all sites, adults and larvae were observed from late morning to late afternoon (ca. 11:00 to 17:00). Eggs, larvae, pupae, and adults were documented *in situ* using a Lumix DMC-FZ50 digital camera (Panasonic, Japan) with macro-filters (achromat close-up lenses +3 to +8 dioptres, Kenko, Japan, and Raynox, Japan). Short video recordings were made with the same equipment. In addition, simple experiments with freshly captured, living mosquitoes were performed to study the feeding behaviour of *T. basalis* larvae on *Drosera* leaves.

Study sites:

1. Brazil: Minas Gerais, Conselheiro Pena municipality, summit of Pico do Padre Ângelo, 19° 19' 12" S 41° 34' 42" W, 1530 m a.s.l.
2. Minas Gerais, Diamantina municipality, Distrito de São João da Chapada, Rio das Lajes, 18° 02' 09" S 43° 47' 20" W, 1285 m a.s.l.
3. Minas Gerais, Buenópolis municipality, Parque Nacional das Sempre Vivas, 17° 55' 00" S 43° 47' 07" W, 1280 m a.s.l.
4. Minas Gerais, Grão Mogol municipality, Estrada Grão Mogol – Montes Claros (MG-307), km 48, 16° 35' 21" S 42° 54' 54" W, 730 m a.s.l.
5. Minas Gerais, Botumirim municipality, Rio do Peixe, 16° 55' 10" S 43° 00' 28" W, 780 m a.s.l.

Results and discussion

Adults of *Toxomerus basalis* were observed at study sites 1, 2, and 4, and larval instars 1–3 were recorded at all five study sites in Minas Gerais at upland elevations between 730–1530 m a.s.l. (Figures 1–5). Larvae were found only in larger *Drosera* populations and exclusively on the large-leaved *Drosera* species *D. graomogolensis*, the semi-erect-leaved species *D. latifolia*, and *D. magnifica* and *D. spiralis*, which both have thread-like leaves. Despite exhaustive searches, no *Toxomerus* larvae or adults were detected on the closely related and morphologically similar thread-leaved *D. graminifolia* A.St.-Hil., which grows at higher elevations in southern Minas Gerais; the several smaller, sympatric species that occurred at sites 3 and 5 (*D. communis* A.St.-Hil., *D. grantsau* Rivadavia, *D. hirtella* A.St.-Hil., *D. montana* A.St.-Hil., and *D. tomentosa* A.St.-Hil.); the larger-leaved *D. ascendens* A.St.-Hil., which grows in drier microhabitats than the other species (Gonella *et al.* 2014). The other sites (1, 2, and 4) each had a single *Drosera* species, which was inhabited by *T. basalis* larvae.

Notes on the biology and phenology of *Toxomerus basalis* adults

Males of many flower fly species guard small territories or lek on or near flowers, on sunlit vegetation, in flight, or close to oviposition

sites (Rotheray & Gilbert 2011). There are several studies that document syrphid territoriality (Fitzpatrick & Wellington 1983), including some species with predatory larvae (Heinrich & Pantle 1975). *Toxomerus basalis* adult behaviour was similar to other predatory species reported previously. Adult male *T. basalis* were observed on a suitable perch (taller plants, exposed twigs, grasses and herbs) close to their *Drosera* host plants (Figure 2i and j). We observed that males regularly stray from their lookout posts to feed at flowers and to observe *Drosera* plants (presumably searching for females). Females were observed patrolling suitable host plants (Video 1).

Adults of both sexes were regular floral visitors on *Drosera* flowers where they fed on pollen (Figure 4e). *Drosera* flowers are a theoretically rather poor food resource for *Toxomerus* adults. The ephemeral flowers of all Brazilian species lack nectar and open only for a few hours on a single day (AF pers. obs.; Gonella *et al.* 2014; Cross *et al.* 2018). Moreover, *T. basalis* adults rest on the *Drosera* plants, searching for shelter among or underneath the sticky leaves (not only ovipositing females, but also males, see Figure 4a–d and f). At site 4, a male adult fly was observed sheltering under a *Drosera graomogolensis* individual during a rain shower (Figure 4a). It approached the *Drosera* while AF was taking photographs of the plant and landed directly on an old, rain-washed and hence not-very-adhesive leaf (Figure 4d) before crawling underneath the rosettes, resting on the non-glandular abaxial side during the rain shower, where it groomed and cleaned itself (Figure 4b, c and f).

Toxomerus basalis adults seem to have some capacity to escape entrapment by the sticky *Drosera* leaves provided they do not come into contact with too many tentacles. When AF was trying to catch an adult male at Pico do Padre Ângelo for closer examination, the fly escaped but one wing briefly came into contact with the sticky tentacles of a *Drosera magnifica* leaf. It struggled but was able to free itself and move to the safety of the lower surface of the leaf where it cleaned its body, rested, and eventually flew back to its lek.

Interestingly, a female of *Toxomerus lacrymosus* (Bigot, 1884) was documented sitting on the lower leaf surface of *Drosera magnifica* at Pico do Padre Ângelo (Figure 6). That image additionally shows a freshly deposited syrphid egg on the leaf above the female. It was impossible to determine whether the egg was laid on the *Drosera* by this female or by a previous visitor. However, at least some predatory Syrphinae avoid potential oviposition sites where they detect intra- or interspecific competitors to reduce the effect of intraguild interactions (Benestad-Hågvar 1973; Branquart *et al.* 1997; Almohamad *et al.* 2009, 2010). Accordingly, the presence of an egg close to this *T. lacrymosus* female suggests either that it was laid by her or that she was not ovipositing. In support of the latter point, it does appear that the adult syrphid was caught by the plant as (exceptional) prey and then escaped to the lower leaf surface (note that its right wing and left abdomen margin are adhering to the mucilage of some *Drosera* tentacles; Figure 6). If this inference is true, then it is reasonable to infer that the egg and the puparium visible in the centre of that plant both belong to *T. basalis* (which has been documented from the same location by Fleischmann *et al.* 2016 and in this study).

Based on field observations (the present study and Fleischmann *et al.* 2016) and collection dates of museum specimens, *T. basalis* is apparently a multivoltine species with continuous development and multiple generations per year. Adults, eggs, larvae, and pupae were found at the same time in the same habitat, sometimes on the same individual plants. Records and reports of adults and larvae are known from both dry and rainy seasons (Fleischmann *et al.* 2016).



Figure 1. Oviposition of *Toxomerus basalis*. (a) female ovipositing on the tip of the abaxial (lower, non-carnivorous) surface of a developing leaf of *Drosera latifolia*. (b)–(d) Freshly deposited egg attached to the abaxial (lower) surface of an unfolding leaf of *Drosera magnifica*. (e)–(f) same female individual as pictured in (a) on plants growing in close proximity to *Drosera*. (e) Probing a leaf of *Ericaulon* sp. (Eriocaulaceae) – oviposition did not occur. (f) After oviposition on *Microlícia* sp. (Melastomataceae), with freshly laid egg visible (left arrow) – the same plant already held another *Toxomerus* egg (right arrow). (g) Overview of a colony of *Drosera latifolia* and associated plants, with oviposition sites documented under a, e, and f indicated. Image combined from two different photographs showing two different sides of that vegetation island that was patrolled by the *Toxomerus basalis* female. a, e–g: Diamantina, Distrito de São João da Chapada, Rio das Lajes, Minas Gerais, Brazil, 06 December 2018. b–d: summit of Pico do Padre Ângelo, Conselheiro Pena, Minas Gerais, Brazil, 04 December 2018. Photos by A. Fleischmann.



Figure 2. Life cycle stages of *Toxomerus basalidis* documented *in situ* in Minas Gerais, Brazil. (a) first-instar larva L_1 (b) L_2 larva (c) L_3 larva, figures 1a–c to the same scale. (d) L_3 larva attaching to pupate on a freshly enrolling *Drosera* leaf (arrow), note another puparium (arrow with *) on a developing leaf in bud on the same plant. (e) Puparium. (f) L_3 larva starting to pupate on a leaf base. (g) Puparium with emerging pharate adult – note the translucent puparium exoskeleton with opening fissures visible at the anterior end. (h) empty puparium exuvia on a developing *Drosera* leaf. a–c on *Drosera spiralis*, Parque Nacional das Sempre Vivas, Buenópolis, Minas Gerais, 06 December 2018. d–h on *Drosera magnifica*, Pico do Padre Ângelo, Minas Gerais, 04 December 2018. (i) + (j) adults resting on exposed perches near their *Drosera* hosts: (i) female, Rio das Lajes, 06 December 2018. (j) male, summit of Pico do Padre Ângelo, 04 December 2018. Photos by A. Fleischmann.



Figure 3. Biology and feeding habit of *Toxomerus basalis* larvae on *Drosera* leaves, documented *in situ* in Minas Gerais, Brazil (see also video material in the Electronic Appendix to this article). (a) L₃ larva hiding in the rosette centre of *Drosera* upon disturbance. (b) L₃ resting on the abaxial leaf tip. (c) L₂ larva approaching a captured, still-alive spider, not feeding on it as the prey is not yet fully immobilized. (d) L₃ feeding up a small, captured prey item, note where the tentacles have bent around the prey (arrow) but not commenced its digestion, as the tentacles heads have not yet darkened. (e) L₃ larva crawling to captured, immobilized nematoceran prey. (f)–(h) L₃ feeding on an immobilized but still living nematoceran that had been freshly placed on a leaf of *Drosera graomogolensis* (tentacles have not yet started bending over the prey), Botumirim, Rio do Peixe, Minas Gerais, 09 December 2018. * indicates anterior respiratory process visible during feeding. a on *Drosera latifolia*, Rio das Lajes, 06 December 2018. b, d, e on *Drosera spiralis*, Parque Nacional das Sempre Vivas, 06 December 2018. c on *Drosera magnifica*, summit of Pico do Padre Ângelo, 04 December 2018. Photos by A. Fleischmann.



Figure 4. Biology of *Toxomerus basalis* adult flies associated with *Drosera*, documented *in situ* in Minas Gerais, Brazil. (a)–(d) + (f) Adult male sheltering beneath a leaf of *Drosera graomogolensis* during rain shower, Grão Mogol, Minas Gerais, 08 December 2018: (a)–(c) resting and showing cleaning behaviour, (d) leaving its carnivorous refuge by crawling over the sticky (yet rain-washed) leaves. (e) adult female feeding on pollen from a flower of *Drosera latifolia*, Rio das Lajas, 06 December 2018. Photos by A. Fleischmann.

Oviposition and female host plant choice

Oviposition behaviour and host plant recognition of *T. basalis* was unknown to Fleischmann *et al.* (2016) and is reported here for the first time. Five individuals of females laying eggs were observed (two at site 2 in 2018, two at site 1 in 2018, and one at site 1 in 2021). Females oviposit directly on *Drosera* leaves (observed

multiple times at sites 1 and 2 in 2018 and 2021); the eggs are laid individually on the non-sticky adaxial (lower) surface of freshly unfolding juvenile leaves, or leaf buds (Figure 1a–d, Video 2), or occasionally (observed once at site 2) on other vegetation growing next to the *Drosera* (Figure 1f and g). Exposed leaves seem to be preferred as an oviposition site, as freshly laid eggs and oviposition were observed only on the uppermost, young leaves.

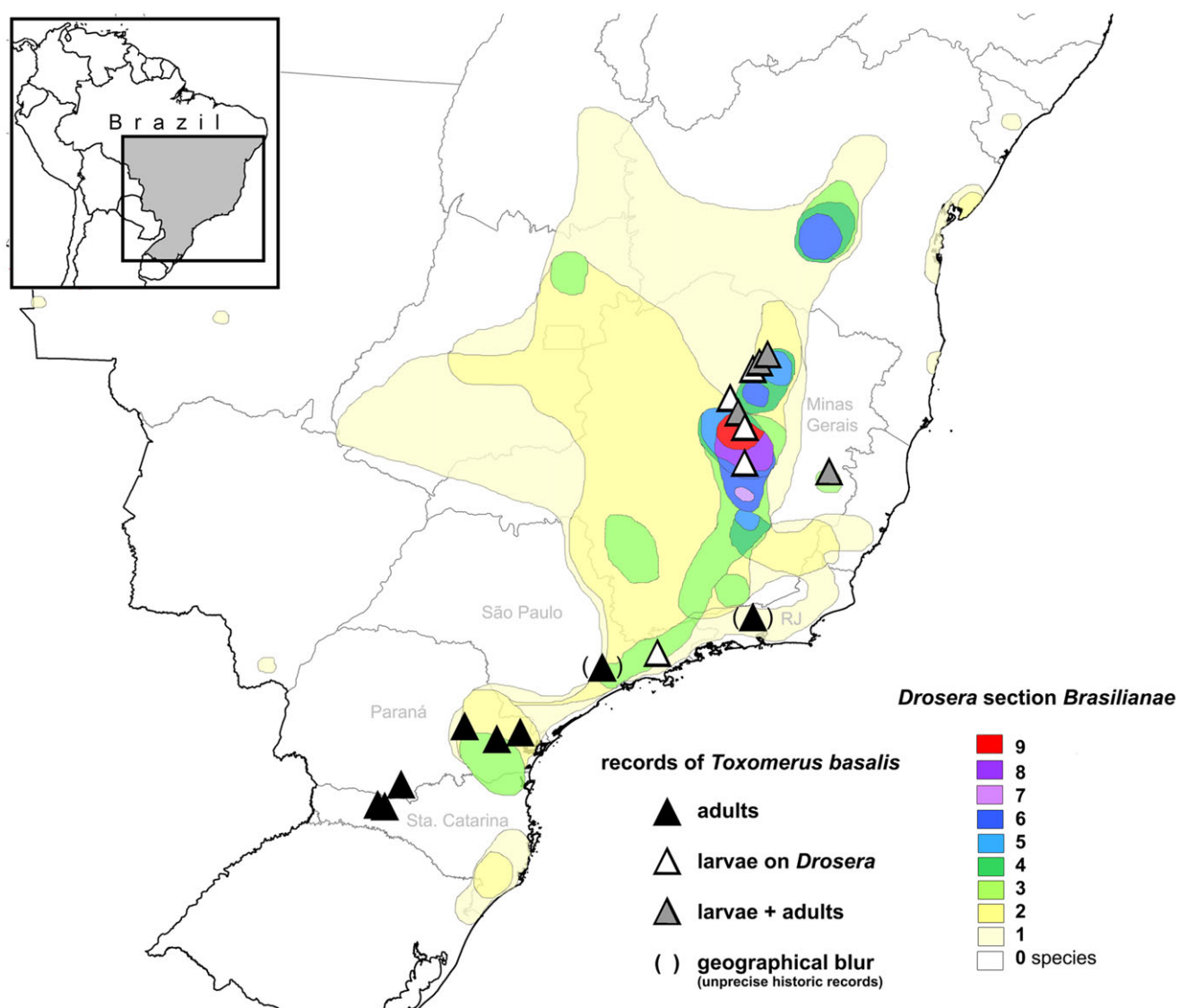


Figure 5. Known distribution of *Toxomerus basalis* based on museum specimens examined, field studies (AF and PMG), literature records (Borges & Couri 2009; Mengual 2011; Fleischmann *et al.* 2016), and database records (SpeciesLink: <http://www.splink.org.br/> [accessed 17 February 2021]). Distribution range and species numbers of the confirmed larval host plants from *Drosera* section *Brasilianae* indicated (based on Gonella *et al.* 2022). Map drawn by A. Fleischmann.

A female ovipositing on the lower leaf surfaces of *Drosera latifolia* at Rio das Lajes, Diamantina (Figure 1a), also probed the leaf of a nearby, glabrous Eriocaulaceae with her abdomen, but did not lay an egg (Figure 1e). She laid on another *Drosera* leaf and was also observed laying a single egg on a nearby *Microlizia* sp. (Melastomataceae) with eglandular hairy leaves, which, already had a fly egg identical to that on the nearby *Drosera* (both plants used for oviposition were in direct physical contact; Figure 1f). The female fly on the host plant was observed alternately extending and withdrawing its proboscis and moving its abdominal tip, presumably to test the suitability of the oviposition site guided by gustatory, visual, and chemical cues, as observed during oviposition in other syrphids (Dixon 1959; Rotheray & Gilbert 2011).

In Syrphidae, the choice of oviposition sites is the key parameter determining the future survival of offspring, which have a limited dispersal capacity compared with adults (Almohamad *et al.* 2009), but also to minimize interspecific competition (Almohamad *et al.* 2010). It is well-known that members of Syrphinae with predaceous larvae oviposit near their potential prey (e.g., aphid

colonies), but also on suitable host plants before any obvious prey colonies have established (Almohamad *et al.* 2009, and references therein). In predatory Syrphinae, volatiles emitted from the larval prey, but often also from the prey's preferred host plants, are used as semiochemicals for female oviposition choice and additionally represent effective infochemical sources for the hatched syrphid larvae (Almohamad *et al.* 2009). In the case of *Toxomerus*, adults of some species are attracted by methyl salicylate (Rodríguez-Saona *et al.* 2011; Salamanca *et al.* 2018; Legaspi *et al.* 2020), a herbivore-induced plant volatile (HIPV); however, *Drosera* does not emit it, unlike some other carnivorous plants (Jürgens *et al.* 2009). Thus, flower fly females are able to recognize and distinguish different plant species while looking for those which their larval prey inhabit. Host plant recognition in predaceous Syrphidae is often multifactorial (Almohamad *et al.* 2009; Amiri-Jami *et al.* 2016), but predominantly guided by visual and olfactory cues. Our observations indicate that male and female adults of *T. basalis* can recognize *Drosera* plants among surrounding vegetation. Colour vision has been documented for



Figure 6. A female of *Toxomerus lacrymosus* apparently captured by the sticky tentacles of *Drosera magnifica* on Pico do Padre Ângelo, but which escaped on lower leaf surface. Note a syrphid egg (probably from *T. basalis*) on the same leaf, right above the female. Photo by L. Medeiros.

Syrphidae, with food-foraging individuals being especially attracted towards yellowish colours (Peschken 1964; An *et al.* 2018), while ovipositioning aphidophagous species show site recognition for aphid-infested plants which often display chlorotic colouration (Sutherland *et al.* 2001; Almohamad *et al.* 2009). Coincidentally, the colour pattern of the leaves of *Drosera* species (and other carnivorous plants) is quite similar, with bright yellowish-green or reddish tones prevailing in most species, often in sharp contrast with the duller green of the surrounding vegetation. The bright colour pattern of *Drosera* leaves and those of other carnivorous plants is presumably connected to prey attraction (Darwin 1875; Lloyd 1942; Zamora 1995; Schaefer & Ruxton 2008; Fleischmann 2016), and this might also be perceivable among *Toxomerus* adults (Tagawa *et al.* 2018 even argue that some Syrphidae are able to distinguish *Drosera* leaves from flowers and other vegetation, apparently avoiding the former). Many carnivorous plants have reddish or pale yellowish-green colour schemes that are surprisingly similar to those of damaged, unhealthy, or stressed plants, and some of these plants may even use that coloration to attract their prey (Lloyd 1942; Zamora 1995; Schaefer & Ruxton 2008). This is especially true of reddish trap colours, which were found to enhance the overall trapping success of carnivorous plants, with particular regard to dipteran prey (Schaefer & Ruxton 2008), while the pale yellowish-green leaves of other carnivorous plants have been shown to effectively attract fungus gnats (Diptera, Mycetophilidae; Zamora 1995). From an evolutionary perspective, the bright yellowish-green or reddish colour of the carnivorous plant leaves, similar to the coloration of some herbivore-infested plants, might have played a role in the switch of a predatory syrphid to a kleptoparasitic habit on a carnivorous plant – by providing a similar stimulus to female oviposition site choice.

Flower flies, including *Toxomerus* species, are floral visitors of *Drosera* plants in the Neotropics (Freitas & Szazima 2006; AF and PMG, pers. obs.). Smaller syrphids like *Toxomerus basalis* (with an adult body length of 5.5–6.5 mm; Borges & Couri 2009; Mengual

2011) would easily fall in the prey size spectrum of large-leaved *Drosera* species (Gibson 1991), yet they are only rarely captured as prey (pers. obs., Murza *et al.* 2006; Tagawa *et al.* 2018). An avoidance/hesitation strategy of the flower fly with respect to the sticky leaves has been theorized to explain the low number of captured adults of the *Drosera* pollinating syrphid *Sphaerophoria* sp. in Japan (Tagawa *et al.* 2018, identified as '*Sphaerophoria menthastri* Linnaeus, 1758', but corresponding to *Sphaerophoria indiana* Bigot 1884; K. Ichige, pers. comm.). Of course, in the case of the kleptoparasitic *Toxomerus basalis*, the adults do not avoid *Drosera*, rather, both sexes actively approach even the sticky leaves of sundew plants. Apparently, there is some type of recognition of the sundew plant by those syrphid species studied which show minor pollinator-prey conflict (Murza *et al.* 2006; El-Sayed *et al.* 2016; Tagawa *et al.* 2018; Ojeda *et al.* 2021), or simply divergent attractants to leaves and flowers (Cross *et al.* 2018).

Remarkably, we observed larvae of *T. basalis* exclusively on *Drosera* species from *Drosera* section *Brasilianae* Rivadavia, Gonella & A. Fleischm., in accordance with the larval host species list by Fleischmann *et al.* (2016). This is a monophyletic group of tetraploid *Drosera* species (Fleischmann *et al.* 2018) with slightly divergent morphology from the sympatric diploid species of *Drosera* section *Drosera*. Fleischmann *et al.* (2016) and this study did not find a single *Toxomerus* larva on species from *D.* section *Drosera*. No other *Drosera* species have been identified as larval hosts of *T. basalis* beyond those listed by Fleischmann *et al.* (2016).

Drosera species have a specific chemical composition of secondary plant metabolites, especially among acetogenic naphthoquinones (Culham & Gornall 1994; Schlauer & Fleischmann 2016, 2022; Schlauer *et al.* 2019), but also other volatile compounds, some of which might even be involved in prey attraction in certain species (Fleischmann 2016). Nevertheless, the semiochemicals responsible for oviposition site recognition by *T. basalis* females are indisputably not the characteristic naphthoquinones, as their

distribution pattern and presence differ greatly between those species of *D.* section *Brasilianae* that have been documented as larval hosts by Fleischmann *et al.* (2016) and in this study: *Drosera latifolia* and *D. villosa* A.St. Hil. contain both naphthoquinone regioisomers 7-methyljuglone and plumbagin, while *D. spiralis*, *D. magnifica*, and *D. × fontinalis* Rivadavia contain only the former (while sympatric diploid *Drosera* species of *D.* section *Drosera* contain only the latter), and *D. chrysolepis* Taub., *D. camporupestris* Rivadavia and *D. graomogolensis* are devoid of any acetogenic naphthoquinones (Schlauer *et al.* 2019; Schlauer & Fleischmann 2022). Hence, the naphthoquinone patterns are too variable in the documented host species to serve in host recognition, but other characteristic *Drosera* volatiles might be perceived by gravid *Toxomerus* females, allowing them to recognize their larval host plants.

Life history of *Toxomerus basalis*

As already reported by Fleischmann *et al.* (2016), the larvae spend their entire development as commensals on the sticky leaves of the plant (Figure 2a–c), but they finally pupate attached to the non-sticky lower surface of the carnivorous leaves (Figure 2d–h). Before pupation begins, the larvae settle and empty their gut contents, changing their body colour to a dark brown (Figure 2f), while the puparia themselves are homogeneously bright green (Figure 2d and e; Fleischmann *et al.* 2016). This has been interpreted in other *Toxomerus* species as a form of camouflage (Reemer & Rotheray 2009). As in other Syrphinae, the puparium of *T. basalis* becomes translucent during preimaginal development and, consequently, the overall appearance is dark blackish-brownish (Figure 2e–f and h; Fleischmann *et al.* 2016). The translucent puparium reveals the adult head just before emergence (Figure 2g).

The duration of the pupal stage of *T. basalis* is short, between three and five days at most. This was evidenced by puparia observed on *Drosera magnifica* at Pico do Padre Ângelo in 2018 (temperatures on the summit of Pico do Padre Ângelo during the survey period in early December 2018: min. 12–16°C, max. 22–26°C; PMG pers. obs. and estimated from weather recordings for the region (CPTEC/INPE 2019)). Some of the puparia were attached to the abaxial (lower) surface at the outer part of an enfolding leaf, pointing outwards, with the adult flies inside close to emergence (Figure 2g). The leaves of *D. magnifica* are circinate in bud (Gonella *et al.* 2015), that is, enrolled like a mainspring (crozier), and a leaf of that *Drosera* species takes about one week to unfold from bud based on observations of the first author from cultivated material. Thus, the position where the puparium was attached was accessible to the pupating larva no more than about 3–5 days prior to the observation. Note a mature *Toxomerus* larva ready-to-pupate on an enfolding *Drosera* leaf and a puparium at a similar position on another leaf in Figure 2d.

Short pupal stages of 3–5 days agree with those reported from another tropical *Toxomerus* species (Jordaens *et al.* 2015), although they seem to be on the short range for the genus. Based on captive rearing of the likewise tropical *Toxomerus dispar* (Fabricius, 1794) under lab conditions, the duration of the pupal stage ranged from three to eight days (average = 5.12 days) (M.N. Morales & S.R., pers. obs.).

Biology and feeding behaviour of the larvae

Fleischmann *et al.* (2016) noted that the larvae of *Toxomerus basalis* usually occurred solitarily on their host plants, but this

observation was not corroborated during the most recent field studies, where up to five (1–2 on average) larvae were found, in addition to eggs and puparia on larger host plants (such as large individuals of *D. magnifica*). The larvae were usually found resting without movement on the leaves, where they are perfectly camouflaged, at least on *Drosera* species with green laminas (Figures 2a–c and 3b–e; Fleischmann *et al.* 2016). On host plants with red leaves, the greenish larvae are more conspicuous, at least to the human eye (Figure 3a and f). The larvae moved quickly on the leaves when disturbed, escaping towards the rosette centre of their host plant wherein they hide, firmly squeezing themselves into the narrow spaces created by enfolding *Drosera* leaves (Figure 3a). After some time (30 minutes to several hours), the larvae started to crawl back onto the sticky lamina again. The larvae approached freshly captured prey from their resting position (possibly attracted by the vibrations caused by struggling prey on the leaves). Most larvae were observed feeding on larger prey items (similar in size to the larvae or larger) and, more rarely, also on some of the numerous, smaller captured prey (Figure 3d, note that the bent tentacles indicate the position where the almost fully consumed prey was situated). Some larvae were also found foraging across the leaves of their host plant and moving between different sundew individuals in dense populations of their host plants, notably in (most likely clonal) patches of *D. graomogolensis* at Rio do Peixe, Botumirim (Video 3). This is in line with the normal hunting behaviour observed in starved predatory larvae of other syrphines (Rojo *et al.* 1996; Vosteen *et al.* 2018).

Fleischmann *et al.* (2016) reported that larvae of *T. basalis* fed on prey captured by the adhesive traps of *Drosera* and hypothesized that this might happen apparently only after the trapped insects were dead (presumed saprophagy). This assumption was found to be false based on these new, detailed field observations. The larvae appeared to ignore old prey and seemed to feed only on relatively freshly caught insect prey that was not dead, just immobilized (Figure 3c–h). All feeding larvae observed (based on five observations at sites 1, 3, and 5) were eating freshly caught, living prey, rather than dead insects or prey that was already pre-digested by the plant. Moreover, the larvae did not approach moving or struggling prey but waited at some distance on the leaves (a similar behaviour was observed in kleptoparasitic/mutualistic capsid bugs (Hemiptera, Miridae) living on *Drosera* and *Roridula* (Roridulaceae); AF pers. obs.). Prey was first probed by *Toxomerus* larvae with their mouthparts (Figure 3c) but not touched further if it still showed some movement. Only fully immobilized prey items were consumed by the larvae (Figure 3f–h; Video 4).

Our new photographic evidence demonstrates that only freshly captured prey were eaten by the *Toxomerus* larvae, while those prey on which digestion by the plant had commenced were avoided. The colour of the gland head and stalk of the *Drosera* tentacle darkens through aggregative activity in the cell vacuoles during prey digestion, and this colour change is noticeable even to the naked eye (Darwin 1875; Gardiner 1886; Huie 1897; Lloyd 1942). This colour change is appreciable in the macro-photographs of *Drosera* leaves taken *in situ* in Brazil, where tentacles were bent over captured prey in a state of digestion (pers. obs.), but there is no colour variation in tentacles enclosing arthropod prey fed upon by *Toxomerus* larvae (Figure 3d–f). The consumed prey, therefore, had to have been freshly captured by the plant. The feeding behaviour of *T. basalis* larvae on *Drosera* is documented in Video 4 and does not differ from the feeding behaviour of other predaceous Syrphinae larvae, that is, the head skeleton pierces the prey and the mandibles then

macerate the internal tissues, completely sucking out the body fluids (Rotheray & Gilbert 2011).

Why is there no tentacle reaction induced by the movement of the *T. basalis* larvae on the *Drosera* leaves?

Drosera tentacles are thigmonastic (responding to touch or physical contact) and chemonastic + chemotropic (responding to and towards the presence of certain organic compounds), normally reacting quite quickly to the movements (mechanical stimuli) and/or presence (chemical stimuli) of prey on the lamina (Darwin 1875; Pfeffer 1885; Lloyd 1942; Williams & Pickard 1972).

In a small experimental setup, AF placed small, freshly captured, living mosquitoes on the leaves of *Drosera graomogolensis* plants at Rio do Peixe to observe the foraging and feeding behaviour of the larvae of *Toxomerus basalis*. The *Drosera* tentacles bent around the prey after some minutes (naturally captured prey as well as artificially placed mosquitoes), but not around *Toxomerus* larvae resting or moving on and among the leaves, directly touching the tentacle stalks and heads. Note mucilage threads between the tentacles, indicating the movement of the *Toxomerus* larva (Figure 2c). So interestingly, the larval movements on the leaves do not cause the *Drosera* tentacles to bend.

It is possible that the larvae's salivary secretions (slime) not only protect them from adhering to the *Drosera* mucilage (as postulated by Fleischmann *et al.* 2016) but also 'camouflage' the larvae from being recognized chemically as prey. A combination of electrical signalling and phytohormone signals is responsible for recognition of living prey by mechanical and chemical stimuli on the leaves of *Drosera* (Krausko *et al.* 2017). Once prey is sensed by electrophysiological signals, tentacle movement in *Drosera* is induced by endogenous plant signals from phytohormones like jasmonates (Nakamura *et al.* 2013), that is, substances normally involved in plant herbivore defence (Pavlovič & Mithöfer 2019). Numerous insects including dipteran larvae have found ways to overcome the defensive strategies of plants, for instance by producing antagonists for chemical defence (e.g., Alba *et al.* 2011; War *et al.* 2018). Thus, it is theoretically possible that certain chemical compounds present in larval exudates are capable of blocking the transmission of electrical signals in the tentacles or that they inhibit the jasmonate signalling cascade.

However, the absence of a tentacle response to the presence of the flower fly larvae may have a simpler explanation: in his benchmark experiments on carnivorous plants, Darwin (1875) found that drops of water do not cause any *Drosera* tentacle movement. It is possible that the fluid larval exudates acts similarly, provided it does not contain significant quantities of organic or inorganic particles. Thus, the salivary exudate used as lubricant for motion (Fleischmann *et al.* 2016) potentially has the additional side-effect of pushing the tentacles into a state of insensitivity (A. Pavlovič, pers. comm.); a film of water surrounding the tentacles can cause membrane hyperpolarization, which makes it more difficult to trigger action potentials (Williams & Pickard 1972). Based on the observation that the tentacles do not respond to the presence of *Toxomerus* larvae resting or moving on the *Drosera* leaves, whereby they touch both the tentacle stalks and the sensitive tentacle heads (Figures 2c and 3d–f; Video 3), it is indeed more likely that upstream signalling events from jasmonates are affected, that is, the initial electrical signals (A. Pavlovič, pers. comm.). It should be noted that the tentacle bending clearly visible around a *Toxomerus* larva pictured in Figure 1b and c of Fleischmann *et al.*

(2016) was caused by the photographer accidentally touching the leaf during photography (A. Peres, pers. comm.).

To date, the reported function of the oral secretions of syrphid larvae is to increase velocity as a lubricant during motion of the apodal larvae (Hindayana *et al.* 2001; Fleischmann *et al.* 2016) and also as a chemical defence against predators (Eisner 1972; Blum 1981; Hindayana *et al.* 2001; Betz & Kölsch 2004). Unfortunately, the chemistry of these secretions has not been studied since their early mention by Eisner (1972), but it has been assumed to be proteinaceous (Blum 1981). If this were true for all syrphid larvae, including *Toxomerus basalis*, then the salivary secretion would be ill-suited for 'chemical camouflage' on *Drosera*, whose tentacles are able to respond chemonastically and chemotropically to even small concentrations of proteins (Darwin 1875; Lloyd 1942). These observations suggest that the physical properties of the thin layer of slime covering the larvae could also protect them from causing leaf reactions that initiate the digestion process, as *Drosera* tentacles are insensitive to the presence of fluid (Darwin 1875; Pfeffer 1885).

Another way to prevent tentacle reactions in the *Drosera* host would be to employ an avoidance strategy, for example through careful movements such as those performed by some other arthropods living on adhesive plants (Voigt & Gorb 2010). Pfeffer (1885) established that mere contact with the gland head of a *Drosera* tentacle does not provoke a response, but that even minute friction on its surface does. Hence, living/moving prey causes much stronger tentacle movement than dead insect bodies placed onto the leaves (Darwin 1875). However, such special avoidance behaviour or careful, adapted motion was not observed in the *Toxomerus* larvae studied on *Drosera* leaves, which freely touch both tentacle stalks and touch-sensitive gland heads without effect during their movement (Videos 3, 4; also notice the larval cuticle touching the mucilage-laden tentacle head in Figure 2c).

Generally, the adhesive leaves of *Drosera* do not seem to be a suitable habitat for other dipteran larvae. Thus, it is apparently not the much-reduced apodal and acephalous dipteran larval habit which protects them. In cultivation experiments, larvae of *Drosophila melanogaster* Meigen, 1830, which were manually placed on the sticky laminae of *Drosera* species, were able to move for some time but did cause tentacle reactions, with most of them being immobilized and then digested by the leaves after some time (AF pers. obs.).

Geographic record and possible regionally divergent larval biologies of *T. basalis*

Toxomerus basalis seems to be limited to southeastern Brazil (Figure 5). Borges & Couri (2009) reported the species from Rio de Janeiro, São Paulo, and Santa Catarina states in Brazil based on adult specimens studied in natural history collections. Fleischmann *et al.* (2016) provided records of *Toxomerus basalis* for Minas Gerais and São Paulo states based on larvae observed *in situ* on *Drosera*. Additional records of *T. basalis* from the state of Paraná are presented here from museum specimens housed at the Universidade Federal do Paraná, Curitiba (UFPR) (Figure 5). Based on the occurrence of suitable habitat and *Drosera* host plants, future records of *Toxomerus basalis* in the Chapada Diamantina of Bahia state are likely. This area is strongly biogeographically connected to the Espinhaço Mountain Range of Minas Gerais, where most of the larval records of this species have been made so far (Figure 5) and where *T. basalis* is frequent

and common in wet, *Drosera*-rich *campos rupestres* habitats (AF and PMG pers. obs., Fleischmann *et al.* 2016). Most records of *T. basalis* overlap with the distributional range of *Drosera* section *Brasilianae* (Figure 5), especially with the upland centres (between 600–1500 m a.s.l.) of the section's species diversity and occurrences of large-leaved species from that lineage (Gonella *et al.* 2022).

However, the south Brazilian records of *T. basalis* adults from Nova Teutônia (Santa Catarina state) and adjacent south-central Paraná [based on several museum specimens housed at the National Museum of Natural History (Washington DC, USA), the Canadian National Collections (Ottawa, Canada) and the UPRF] are somewhat puzzling because that area is lowland (ca. 350 m a.s.l.) and far from any known *Drosera* populations. The closest known record of a *Drosera* is ca. 200 km away (Gonella *et al.* 2022) and belongs to a small species, namely *D. communis* (*Drosera* section *Drosera*), not falling within the host range of *T. basalis* larvae. Additionally, the specimens from Nova Teutônia were collected by the renowned entomologist Fritz Plaumann around his residence in the Upper Uruguay river region far away from any suitable *Drosera* habitat. Therefore, *T. basalis* in that region either utilizes a different sticky (non-carnivorous) plant as host for its kleptoparasitic larval habit or has a completely different larval biology. Alternatively, the taxa represent two cryptic flower fly species with different life histories. Interestingly, the records from Nova Teutônia were originally identified by F. C. Thompson as *Toxomerus rhea* (Hull, 1949), originally described as *Mesogramma rhea* Hull, 1949. Recently, Borges & Couri (2009) synonymized *T. rhea* under *T. basalis* based on the comparison of type material in a taxonomic revision of the Brazilian species of *Toxomerus*. They studied three male and one female co-types of *Mesogramma rhea* and compared male genitalia with the holotype of *Syrphus basalis* Walker, 1837. Mengual (2011) examined several specimens from Nova Teutônia and male genitalia compared favourably to the drawings from Borges & Couri (2009). It seems rather unlikely that adult *T. basalis* migrate over long distances to find new habitats, such as from *Drosera*-rich larval habitats several hundred kilometres distant, given the territorial behaviour of both sexes. The most likely explanation of *T. basalis* adults in *Drosera*-free habitats in southern Brazil is either a dietary strategy shift of the larvae [such as the one known from *Toxomerus floralis* with predaceous larvae in the Neotropics, but larvae that are pollinivorous in Africa (Jordaens *et al.* 2015), or as the well-known pollinivorous larvae of *T. politus* (Say, 1823) that are also capable of feeding on moth eggs (Jirón-Pablo *et al.* 2018)], or – probably more plausibly – the use of a different sticky, insect-trapping plant as larval habitat. This must constitute a glandular non-carnivorous species, as there are no other sticky carnivorous plants in the region (PMG, pers. obs.). More than 100 sticky, non-carnivorous plant genera casually trap insects ('defensive killing') and many of them are visited by opportunistic or adapted predatory/saprophagous arthropods (LoPresti *et al.* 2015). A single observation of a syrphid larva similar to those of *T. basalis* was cited by Fleischmann *et al.* (2016) from an adhesive species of the non-carnivorous legume *Chamaecrista* (L.) Moench, but the species identity of that larva could not be determined. Despite intensive searching in habitats of *T. basalis* and *Drosera* during our detailed field studies in Minas Gerais in December 2018, no syrphid larvae were found on other co-occurring plants with adhesive leaves or on inflorescences, including *Chamaecrista* and *Vellozia* Vand., which have resinous glands compared to the physically and chemically different polysaccharide

mucilage of *Drosera*. Therefore, based on current knowledge, it is not possible to ascertain whether *T. basalis* is able to use other glandular plants as larval host.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S0266467422000128>

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