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On the natural history of the Neotropical spider *Enoploctenus cyclothorax* (Araneae, Ctenidae)

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Summary

Enoploctenus cyclothorax (Bertkau, 1880) is a Neotropical spider which inhabits rainforests. We studied the relationship between the meteorological conditions and the use of retreats and their surroundings by males and females. We also report on feeding and defensive behaviour. Movement of individuals was studied by marking all the individuals seen in the study area. Two kinds of observations were carried out: (1) inter-night: during 11 consecutive nights in winter and 11 consecutive nights in spring we searched one hour per day between 20:00–23:00, and noted the exact location of each individual seen; (2) intra-night: on individual nights, we regularly monitored the marked individuals, at 30 min intervals. *Enoploctenus cyclothorax* used a variety of crevices as retreats during the day and occasionally left these places after dusk. The number of individuals seen out of the retreats at night was correlated with humidity and/or temperature in winter but not in spring. Adult males were the wandering sex, while females spent most of the time at rest. *Enoploctenus cyclothorax* preyed on a variety of arthropods, including conspecifics, but harvestmen (Arachnida, Opiliones) were rejected in three out of four attacks. The most common defensive behaviour observed was fleeing, although biting and the ejection of hindgut contents towards the observer were also seen.

Introduction

The family Ctenidae is well represented in the neotropics by medium to large sized spiders that typically inhabit rainforests. Among ctenids, the genus *Cupiennius* has received considerable attention on behavioural and ecological aspects (see references in Barth & Seyfarth, 1979; Schuster *et al.*, 1994). Ecological and behavioural data on some species of the genus *Ctenus* have recently been provided by Höfer *et al.* (1994), Vieira & Höfer (1998), Almeida *et al.* (2000), Gasnier & Höfer (2001), Salvestrini & Gasnier (2001) and Gasnier *et al.* (2002). Some behavioural aspects of the genus *Phoneutria* (armed spiders) have also been studied, mainly by Lucas (1988) and Folly-Ramos *et al.* (1998). The genus *Enoploctenus* is widely distributed in South America, from the Antilles to southern Brazil (Brescovit, 1999). These spiders inhabit moist forests and cave entrances in São Paulo and Paraná states (Pinto-da-Rocha, 1995). Only a few anecdotal accounts of the behaviour of these spiders have been provided in the literature (Bücherl, 1952; Gnaspini & Trajano, 1994; Sabino & Gnaspini, 1999; Machado *et al.*, 2000), despite their widespread distribution, abundance, presumed predatory impact, and the possibility of comparison with related genera that have already been studied.

Here, we report on an initial study of the natural history of *Enoploctenus cyclothorax* (Bertkau), a particularly interesting species with the widest distribution of the genus (Brescovit, 1999). We focused mainly on surface activity patterns, but discuss also the influence of meteorological conditions on the use of retreats and mobility of individuals, on consecutive nights ("inter-night") and during single nights ("intra-night"). Additionally, we provide descriptions of the retreat sites used by *E. cyclothorax*, and report on their defensive and feeding behaviour.

Material and methods

Study area

This study was carried out in a damp area of 5.0 × 4.5 m, near a stream, in 10 ha of well-developed secondary forest, at Reserva da Cidade Universitária Armando de Salles Oliveira (C.U.A.S.O.), São Paulo city (SP state), Brazil (23°33′S, 46°43′W). The vegetation is represented by four strata, one of them herbaceous, and palm trees are very abundant (see Rossi, 1994 for a detailed description). The climate is temperate warm and humid, with a drier period between May and September. The average annual rainfall is 1428 mm, with an annual average temperature of 17.6°C and relative humidity around 80% (Rossi, 1994). This area was chosen because of the large number of *E. cyclothorax* found there.

Marking technique

Specimens were found by visual inspection using headlamps. Each specimen of *E. cyclothorax* found was marked with acrylic paint on the abdomen, cephalothorax and legs using 4 different colours (blue, white, yellow and cream). To avoid handling stress, we simply touched the spider's body with the acrylic paint on a thin paintbrush. By recording the colour code, we could recognise each marked specimen individually.

Use of retreats, mobility, and measurements of temperature and relative humidity

Inter-night monitoring: In order to detect changes of foraging site by *E. cyclothorax* on consecutive nights, we searched for one hour per night, always within the period of 20:00 to 23:00, both in winter (11–14 July and 16–22 July) and at the beginning of spring (13–23 September). As we were not to observe the individuals continuously, we did not use red filters on our headlamps.

The influence of meteorological conditions on the use of retreats and mobility of *E. cyclothorax* was inferred by comparison with topic temperature and relative humidity on all sampled days (except between 11–14 July), using a portable whirling hygrometer. Measures of meteorological conditions were always taken at the same place (within the study area) and within the one-hour period when we were in the study area.

Intra-night monitoring: In order to evaluate the mobility of *E. cyclothorax* during single nights, we monitored individuals at 30 min intervals, using headlamps covered with a red plastic filter, to reduce

	Males	Immature males	Females	Unknown sex	Total
Winter					
(11–22 July)	—	5	13	2	20
Spring					
(13–23 September)	11	0 (5)	9 (11)	3	23 (16)

Table 1: Number of individuals marked in winter and spring and, in parenthesis for September, the number of individuals recaptured from July; 11 days of observation in each period.

disturbance to the spiders. At each observation we recorded the position of each individual (relative to physical characteristics of the environment), and whether the individual was walking or not. The recordings were made only at night, since this species is known to be nocturnal (A. D. Brescovit, pers. comm.), during the following days and times in 2000: night 1: 22–23 July, 23.30–03.00; night 2: 1–2 August, 22.30–07.30; night 3: 22–23 August, 00.00–07.30; night 4: 4–5 October, 18.30–00.30; night 5: 14–15 November, 19.30–06.30. Information on movement patterns was deduced from changes in location among observations of the same individual.

Statistical analysis: Analyses were conducted with SIGMASTAT statistical software version 2.0. This software tests for homoscedasticity and normality before analysing the data with parametric tests. The tests used are indicated in the text. An $\alpha=0.05$ was used to detect significance.

Other behavioural observations

Detectable defensive behaviours and predation events involving *E. cyclothorax* were noted. All interactions involving individuals of *E. cyclothorax* were observed with headlamps covered with a red plastic filter. Prey items were collected and preserved in 70% alcohol, measured and identified in the laboratory. Whenever possible, we noted whether the prey was being consumed where caught or not.

Results

Retreats

Enoploctenus cyclothorax used a large variety of natural retreats for shelter, and apparently did not burrow or construct shelters protected with web sheets. Most of these natural retreats used were composed of dead vegetable matter, including: (1) fallen trees: crevices in the soil attached to tree roots, holes inside tree trunks or crevices under bark or dead leaves on stems; (2) dead palm sheaths: a folded edge on a hanging dead palm sheath, and the space underneath a dead palm sheath on the ground. Finally, some individuals used living palm trees, and were found in the space between the sheath and the stem. The retreats we were able to observe apparently did not follow specific patterns of distribution throughout the range between 0 and 2.5 m above the ground.

Inter-night monitoring

Mobility: The number of marked individuals is presented in Table 1. In July, all but two individuals moved less than 30 cm throughout the period (the exceptions, one male and one female, moved 60 and 150 cm, respectively).

In September, 12 out of the 16 spiders recaptured from July (Table 1) were approximately in the same places (<30 cm of displacement) in which they were found in July (and they remained in these places during September). Two immature males had moved 95 and 130 cm, while two females had moved 190 and 240 cm. Of the 23 newly marked individuals, 17 (eight adult males, six females and three specimens of which the sex could not be determined) did not move more than 60 cm away from their original position in September; three females were found at a maximum distance of 115 cm from their original position, and three adult males moved between 75 and 295 cm (two of them were found at the exact places where females had been seen on several days in winter and spring).

Surface activity and meteorological conditions: Table 2 presents the mean temperature, relative humidity and number of days when each individual was found outside retreats, in both seasons. In July, the number of individuals outside retreats was positively correlated with temperature (Fig. 1A) and relative humidity (Fig. 1B). As these two environmental variables were also correlated (Spearman correlation: $r_s=0.775$; $p=0.0251$; $n=7$ nights), we cannot be sure whether one or both together influenced the activity of the spiders. In September, the number of individuals outside retreats was not correlated with either temperature or relative humidity (although the number of individuals tended to decrease with higher temperatures) (Fig. 1A). Temperature and

	Days out of retreat			Meteorological conditions	
	Males	**Immature males**	**Females**	**Temperature (°C)**	**Humidity (%)**
Winter	—	4.60 ± 2.41	4.00 ± 2.74	11.10 ± 3.74	79.71 ± 7.43
(11–22 July)		(2–7) [5]	(1–9) [13]	(6.8–17.1) [7]	(71–90) [7]
Spring	3.80 ± 3.77	6.20 ± 3.70	6.75 ± 3.37	18.13 ± 1.96	92.73 ± 2.69
(13–23 September)	(1–11) [10]	(2–11) [5]	(2–11) [21]	(15.2–20.8) [11]	(89–95) [11]

Table 2: Mean number of days in winter and spring when each individual was found outside retreat, and meteorological conditions, with standard deviation, range (in parentheses), and number of observations (in square brackets), respectively; 11 days of spider observations in each period.

humidity were not correlated in September (Spearman correlation: $r_s=0.282$; $p=0.384$; $n=11$ nights).

There were significant differences between July and September in the number of spiders found outside retreats (Mann–Whitney: $T=28.00$; $p<0.001$), temperature (*t* test: $t=5.257$; d.f.$=16$; $p<0.001$) and relative humidity (*t*-test: $t=5.359$; d.f.$=16$; $p<0.001$).

Intra-night monitoring

Mobility and intra-specific interactions: Females spent more time stationary than moving on all observed nights, both in winter and spring (Fig. 2A and 2B). Little can be said about male activity owing to the small quantity of data obtained. When stationary, both males and females either did not move or cleaned their legs between the chelicerae. When they moved, displacements were less than 50 cm. Adult males were often seen wandering, tapping the substrate with the dorsal part of the cymbium. We observed one male apparently trying to approach a motionless female. He slowly approached the female from behind on three consecutive occasions, but was repelled (the female rapidly moved towards the approaching male, without biting).

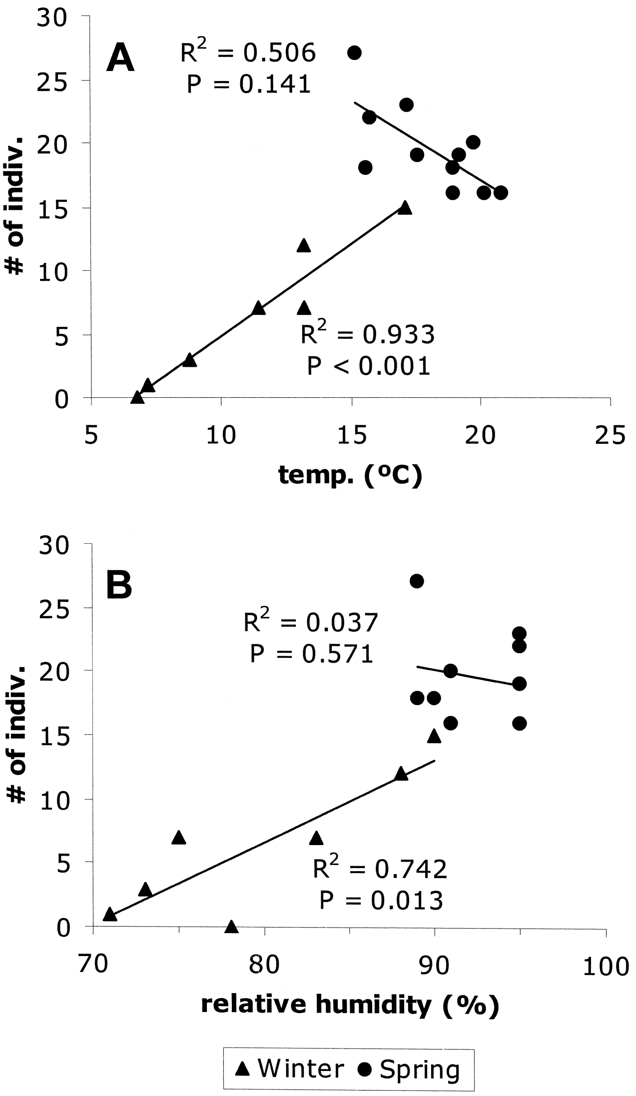

Fig. 1: Relationship between (**A**) temperature and (**B**) relative humidity and the number of individuals of *Enoploctenus cyclothorax* seen outside retreats.

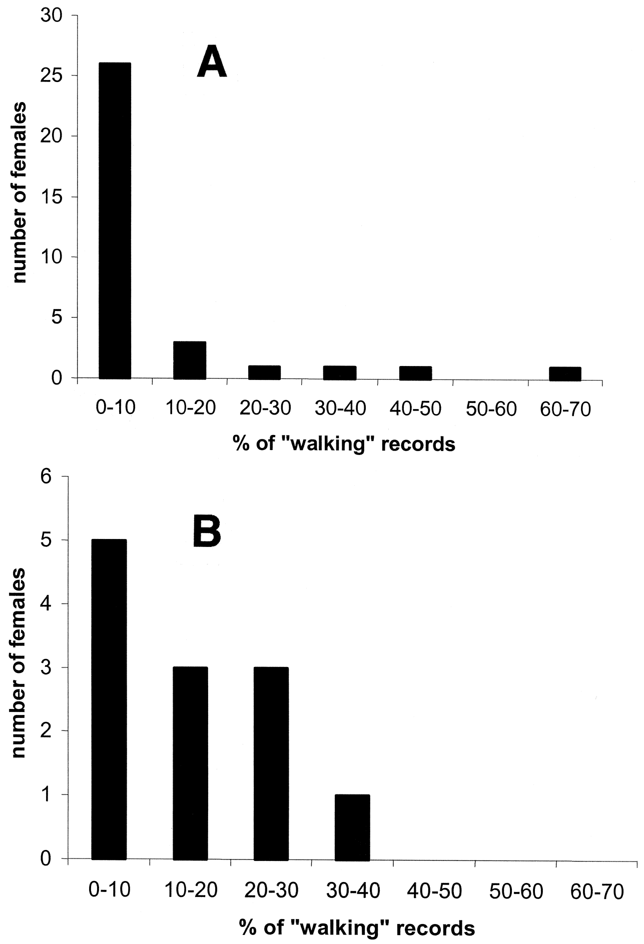

Fig. 2: Mobility of *Enoploctenus cyclothorax* females on (**A**) three winter nights and (**B**) on two spring nights (see text for further information.

Feeding

The spiders were seen feeding on a variety of arthropods, both small and large. Some of the prey items could not be measured because they were fragmented when observed: we recorded three cockroaches (Blattaria), of which only two were measured (length including wings 41.3 mm and 14.8 mm), one fly (Diptera, Nematocera), one cricket (*Neomorpha* sp., Podoscirtidae: length including wings 25.0 mm), one corinnid spider (*Ianduba varia* (Keyserling): length 5.90 mm), one conspecific, one sparassid spider (*Olios* sp: length 10.50 mm) and one isopod (Crustacea, Isopoda). The two cockroaches that were measured, the cricket, *Olios* sp. and the isopod were consumed where caught. *Enoploctenus cyclothorax* (total length/cephalothorax length: adult female ~20.0/9.0 mm, adult male ~15.0/7.0 mm) held its prey between the chelicerae, raising the anterior portion of the cephalothorax, thus preventing contact between the prey and the substrate.

The prey items captured by *E. cyclothorax* were commonly seen wandering in the study area. Although conspecifics and *Olios* sp. were not typically seen wandering, they were often seen close to *E. cyclothorax*, so the probability of encounters appeared to be high.

One species of harvestman, *Discocyrtus* sp. (Laniatores, Gonyleptidae) (body length 5.5–6.0 mm), was commonly seen wandering at the study site during the night. When *Discocyrtus* sp. approached *E. cyclothorax*, the spider moved towards the harvestman but usually retreated after touching it with legs I ($n=3$ females). However, on one occasion, a female preyed on a harvestman. In all the events described above, the harvestmen neither exuded defensive chemical compounds, nor displayed any aggressive behaviour. After the spiders attacked, the harvestmen continued to wander, one passing underneath the body of an *E. cyclothorax*.

Defence

Fleeing was the most common defensive behaviour observed when a spider was touched by a conspecific, or when we touched the spider with a paintbrush, but dropping suspended by a silk line followed by hiding under a leaf was once observed.

In four females we observed the ejection of black and white droplets from the anus, towards the aggressor. These were probably the contents of the hindgut, in view of their consistence and colour. They were typical of spider droppings, described by Savory (1928) as a milky fluid with some black particles. This behaviour was observed when we approached spiders without touching them but using headlamps without red filters. Two distinct types of ejection were observed. Twice, the females directed their abdomen forwards/laterally and ejected the droplets upwards, above their cephalothorax (Fig. 3A). On one occasion, a female in a vertical position, facing the ground, was illuminated from underneath. She rotated her body 180°, stopped, and discharged the droplets downwards (Fig. 3B). In the fourth case (when the droplets reached the maximum distance observed, ~20 cm) the position of the spider when ejecting the droplets was not observed. In all four observations, the spiders succeeded in hitting the observer, in the chest ($n=3$) or in the face ($n=1$).

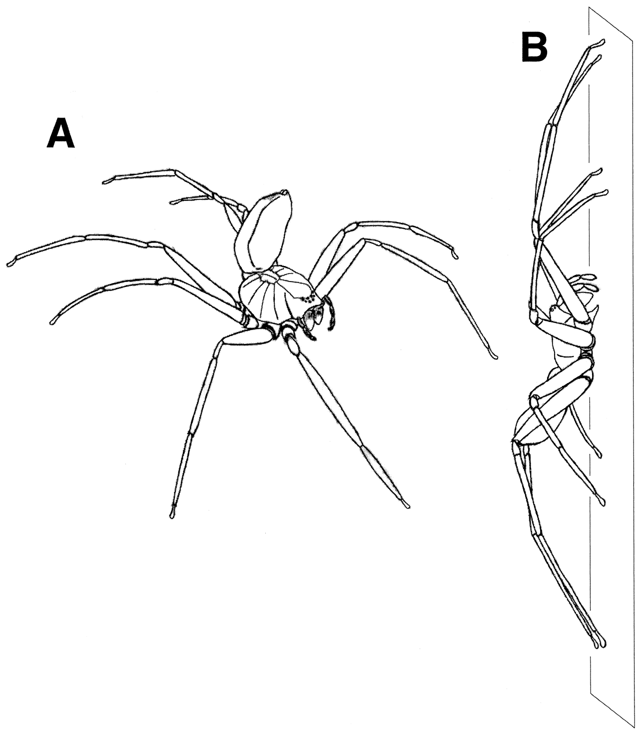

Fig. 3: The two observed positions adopted by females of *Enoploctenus cyclothorax* when ejecting hindgut contents towards an observer. **A** Directing abdomen forwards from horizontal position; **B** Discharging downwards from vertical position.

Discussion

Retreats

The use of natural retreats for hiding during the day is common in ctenid spiders (Bücherl, 1972; Barth & Seyfarth, 1979; Barth *et al.*, 1988; Lucas, 1988; Höfer *et al.*, 1994; Schuster *et al.*, 1994), and may be related to protection from predators and from desiccation (Barth *et al.*, 1988) and/or to avoid parasitism (e.g. by diurnal wasps) (Crouch & Lubin, 2000). Salvestrini & Gasnier (2001) reported that *Ctenus crulsi* Mello-Leitão and *C. amphora* Mello-Leitão do not have fixed retreats. In contrast, our observations suggest site fidelity, at least during the period of the study: some individuals may have used the same retreat for up to 70 days, as they were seen leaving and returning to the same retreat site on different occasions and were never seen far from it during winter and spring monitoring.

Surface activity

Winter vs. spring: The fact that more individuals were seen in spring than in winter may be related to four main factors: (1) meteorological conditions: temperature and relative humidity were higher in September than in July; (2) reproductive factors: in winter, we did not find adult males of *E. cyclothorax* and fewer females were seen, while in spring adult males were frequently seen and more females were observed (see also Bücherl, 1972); (3) seasonal variation in the population size, known to occur among several taxa (Begon & Mortimer, 1986); and (4) prey availability, which may vary throughout the year.

Meteorological features: In winter, more spiders were found when environmental temperatures were higher, but in spring fewer spiders were found when temperatures were higher (although not significantly in spring — Fig. 1A). This suggests that there may be an optimal foraging range of temperatures. This relationship between meteorological conditions and the behaviour of the spiders was to be expected since it has been demonstrated that various spiders thermoregulate through the use of burrows (Humphreys, 1974, 1975, 1978, 1987 (lycosids); Crouch & Lubin, 2000 (eresid)). Analogously, retreats might be used to thermoregulate. Meteorological features are therefore probably important factors to be considered when assessing what causes *E. cyclothorax* to leave its retreat.

Male vs. female activity: Both in winter and spring, the number of times adult females and immature males were seen outside retreats was approximately the same, regardless of the meteorological conditions. In contrast, in spring the number of times adult males were seen outside retreats was approximately half of the numbers obtained for adult females and immature males (Table 2), and none was found in winter. Therefore, either the adult males did not leave their retreats as often as adult females and immature males did, or they moved around more, and may have left the study plot. Although we do not know whether the first hypothesis is correct, we do know that (1) adult males can move much more than adult females and immature males, as shown by the males that were found relatively far from their original locations, and (2) that marked males were seen wandering on several occasions.

If we assume that adult males wander in search of females in order to mate, we may expect that immature males would move around less frequently, which is in accordance with our data. Moreover, adult males of *E. cyclothorax* have longer legs than immature individuals (relative to body size). This has also been observed in other ctenid spiders, and may be related to higher mobility (Gasnier *et al.*, 2002). Also important is our observation of a wandering adult male meeting a female and apparently attempting to approach her repeatedly, and that we found two males at the exact places where two females had been seen on several days in winter and spring. This could have been related to the release of pheromones by the females (see Foelix, 1996). Moreover, behaviours such as the search for mates, antipredatory responses, search for retreat sites, and search for prey have also been considered as factors that might affect the locomotor activity of spiders (Schmitt *et al.*, 1990). As the last three types of behaviour would affect both males and females equally, they would not account for the apparent greater locomotor activity of adult males of *E. cyclothorax* (see also Schmitt *et al.*, 1990). Hence, *E. cyclothorax* is most probably another example of a spider species in which adult males search actively for females (Vlijm *et al.*, 1970; Schmitt *et al.*, 1990; Salvestrini & Gasnier, 2001).

Feeding

General features: The feeding behaviour of *E. cyclothorax* is compatible with what is reported in the literature for hunting spiders: they do not usually allow captured prey to touch the substrate, thus reducing the ability of the prey to escape (Foelix, 1996), and they consume prey where caught, just as *Cupiennius salei* (Keyserling) does (Barth & Seyfarth, 1979). This is also known to occur in several other spider taxa (e.g. Morse, 1979; Jackson & van Olphen, 1991; Henschel, 1994). *Enoploctenus cyclothorax* captured large prey, which is an expected adaptation to periods of food deprivation in sit-and-wait predators (Riechert, 1992).

Harvestmen: Harvestmen can emit secretions from their scent glands when handled (see Gnaspini & Cavalheiro, 1998 for references) or when disturbed by other harvestmen (Willemart, 2001). The secretions exuded by some species repel ants (Blum & Edgar, 1971; Eisner *et al.*, 1971; Duffield *et al.*, 1981), but their effects against spiders have never been tested. Gnaspini (1996) and Machado *et al.* (2000) observed *Ctenus fasciatus* Mello-Leitão preying on *Goniosoma*, even though species of this harvestman genus are known to exude chemicals when disturbed (Gnaspini & Cavalheiro, 1998; Machado *et al.*, 2000). *Cupiennius salei* is also known to prey both on harvestmen and on poisonous or distasteful insects such as species of Chrysomelidae (Coleoptera) and Pentatomidae (Heteroptera) (Nentwig, 1986). As some individuals of *E. cyclothorax* rejected *Discocyrtus* sp. after touching it, and the harvestmen did not exude any visible secretion, those spiders might have recognised it as distasteful and/or noxious. The level of hunger (Riechert & Łuczak, 1982), and previous experience of attacking *Discocyrtus* sp. may also play a role when *E. cyclothorax* meets an individual of this species of harvestman.

Foraging strategy: Both behavioural and dietary data should be considered when classifying an animal as an ambush predator or as an active searcher (Riechert & Łuczak, 1982). The latter may feed on less active prey (Riechert & Łuczak, 1982), which is not the case for sit-and-wait predators. The *Ctenus* spiders studied all prey on mobile arthropods (Barth & Seyfarth, 1979; Höfer *et al.*, 1994; Gasnier, 1996), and these spiders have been considered as sit-and-wait predators by Barth & Seyfarth (1979) and Höfer *et al.* (1994). Hunting spiders considered to be sit-and-wait predators may change their foraging sites occasionally during a single foraging event (Ford, 1978; Sabelis, 1992), which was also the case for *E. cyclothorax*. Thus, based on our dietary and behavioural data, we suggest that *E. cyclothorax* should also be regarded as a sit-and-wait predator. Females remain stationary, not only waiting for prey, but also monitoring potential mates (Schoener, 1969).

Defence

Fleeing: Running away from a stimulus was the defensive behaviour most frequently observed. However, *E. cyclothorax* may also jump up to about 10 cm to escape from a potential predator (R. H. Willemart & M. C. C. da Inês, unpublished data), as observed in a cave population at Gruta da Quarta Divisão, São Paulo state. Rapidly moving away from a stimulus is the most typical active secondary defensive mechanism (displayed after the detection of a potential predator, *sensu* Edmunds, 1974) in animals, being a way of avoiding predation without physical confrontation.

Ejection of hindgut contents: Ejecting the contents of the hindgut towards the disturber was the most unusual behaviour observed in our study. This has also been observed in the cave mentioned above, but only once (M. C. C. da Inês, unpublished data). We found only two references in the literature to similar behaviour. Mello-Leitão informed Bristowe (1941) that, when disturbed, *Ctenus rufibarbis* (= *Phoneutria rufibarbis* Perty — see Platnick, 2002) ejects, from its anus, droplets of a milky fluid that smells of ammonia, to a distance of more than 50 cm. Preston-Mafham & Preston-Mafham (1984) reported mygalomorph spiders turning their rear end towards the disturber and ejecting a clear liquid from the anus (see Cloudsley-Thompson, 1995). In all cases observed in our study, the females of *E. cyclothorax* had been illuminated with a headlamp without a red filter. Nevertheless, we cannot be sure that light was the stimulus that caused these females to eject their hindgut contents, since several others, when illuminated, showed no reaction. In the four observed cases, the females directed the anus towards the observer. Thus, we believe that these females attempted to hit the observer, although it is not known why only four out of several individuals of *E. cyclothorax* showed this behaviour. This might be analogous to deimatic behaviour (Edmunds, 1974) which frightens the aggressor. Furthermore, the droplets might be repugnant to some predators. In any case, the ejection of hindgut contents towards an aggressor deserves further study. Questions regarding the exact composition of the droplets, their efficiency, the occasions when used, and in which conditions, have yet to be answered.

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