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The dry season governs the reproduction of three pseudostigmatid zygopterans in Costa Rica (Odonata: Pseudostigmatidae)

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Abstract

The large Neotropical zygopterans *Megaloprepus caerulatus*, *Mecistogaster linearis* and *M. ornata* (Pesudostigmatidae) were surveyed during five years, and striking differences in their reproduction patterns were shown: (1) At two study sites in seasonal, tropical semi-dry forests in Pacific Costa Rica, adult *M. ornata* could be observed throughout the year, occasionally during the dry season up to 24 individuals at one time. Larvae were found from the middle to the end of the wet season suggesting a generation time of one year. (2) At two other study sites in aseasonal tropical wet forest in Caribbean Costa Rica, adults of *M. caerulatus* were observed year round, often in rather low numbers. Larvae of this species as well as *M. linearis* appeared throughout the year. While dry periods and rainfall certainly are key factors in governing the reproductive patterns of these species in relation to the climatic regimes of their preferred life zones, it is also concluded that competition from other container dwellers, including tadpoles of poison arrow frogs, may be additional factors in explaining their seasonal variation. It is also argued that all three species seem to have a high plasticity in their life cycles and hence are able to adapt to local conditions rather than displaying the same behaviour throughout their range.

Introduction

It is well known that in the tropics, many odonates have life cycles that are cued on climatic conditions. It is common that species have a larval development of three to five months and after hatching spend the dry season as pre- or nonreproductive adults, sometimes as eggs (compilation in Corbet 1999: 217-223). The life cycles of certain species are even more dependent on climatic conditions due to local conditions. Odonata confined to phytotelmata, for instance, are known only from tropical forests. These species are thus confined to these forests and are unable to leave that habitat if conditions become unfavourable. They are dependent on the presence of water for their larval development (Corbet 1999: 144-146). It is known that these

species have a facultative strategy for surviving the dry season as proposed by Fincke (1992b), working on Barro Colorado Island (BCI) in Panama. She showed that the three species *Mecistogaster linearis* (Fabricius), *M. ornata* Rambur and *Megaloprepus caerulatus* (Drury) all had slightly different strategies to survive dry conditions. While *M. ornata* oviposited during the wet season only, the latter two species continued to lay eggs also during the whole (*M. linearis*) or the first half (*M. caerulatus*) of the dry season. The adults of the first species thus spend the dry season in reproductive diapause, while this is not the case in the other two species, apart from a period of aestivation at the end of the dry season in *M. caerulatus* (Fincke 1992b). These different strategies enable the species to synchronise their larval cohorts. Fincke (1992b) noted that most cohorts emerged at the end of the wet season, but in *M. caerulatus* many adults emerged also in the middle of the dry season before the phytotelmata dried up as well as in the middle of the wet season.

Naturally, the observed life cycles of these odonates may be influenced also by other factors than climate alone. For instance, the phytotelmata (here: tree holes) in the seasonally moist forest of BCI was observed to have a more complex array of top predators than noted elsewhere (Fincke 1999), but on the other hand, the predators may also be dependent on the seasonality of the forests on BCI.

We were interested in the plasticity of the life cycles in these species. In this long-term study, we document differences in reproductive periods among *M. linearis*, *M. ornata* and *M. caerulatus* in four different forests in Costa Rica, Central America. These species are known to oviposit in water-filled cavities in trees and water-filled pans created when a large tree falls and irregularities on the trunk subsequently collect water (Fincke, 1984). On the Caribbean slope in Costa Rica, *M. linearis* and *M. caerulatus* are active year round in aseasonal, tropical wet lowland forest and tropical moist forest at mid-elevation (Hedström & Sahlén 2001). In contrast, *M. ornata* is missing entirely from aseasonal forest life zones in Costa Rica, but active in the Pacific Costa Rican seasonal, semi-dry tropical lowland forests (Hedström & Sahlén 2001). Collecting data on the life cycles of these species from localities across the country, we aim to shed further light on the different survival strategies employed by these species in different climates. We further aim to correlate the observed patterns to the climatic regime and thus also to food availability as well as competing predators.

Materials and methods

To assess the abundance of *Mecistogaster* and *Megaloprepus* larvae, egg-laying traps made from plastic bottles (Hedström & Sahlén 2001) were used. The traps were secured to living or fallen trees at a height of between 1 and 2 m, which corresponded to the distribution of water-filled holes observed on fallen tree-trunks in the areas. In general, the traps were monitored two to three times per year, thus enabling egg laying and larval growth to go on almost uninterrupted throughout the seasons. Since the known larval development time of phytotelmata dwellers is normally three to five months (Corbet 1999: 220), we assume that no or just a few adults emerged between our samplings. At monitoring, the material was sieved and any larvae present determined to species. If any larvae could not be determined in the field, they were transported to the laboratory in San José for rearing and subsequent hatching. Apart from some larvae that were preserved for two other studies (Hedström & Sahlén 2002; Sahlén & Hedström 2005), most larvae were returned to the traps after identification. The presence of any other animals in the traps, including tadpoles and

other odonate larvae, was noted; as well as observations of adult pseudostigmatids present at the study sites.

Traps were set in four different areas from west to east in the country: Firstly, in Carara National Park in the Central Pacific area, nearly at sea level in seasonal primary, tropical semi-dry forest, with a prolonged nearly rainless dry season between January and April. Traps (n = 12) were installed in May 2000 along the Tárcoles River Trail, (09°46'N, 84°36'W), 0.5 km south of the large bridge over Río Grande de Tárcoles. See Hedström & Sahlén (2001) for a more detailed site description. Monitoring of larvae in traps was conducted during a 5-year period, from January 2000 to January 2006, with 4-6 samplings per year, except during the first year when only two samplings were conducted (August and November). Additional visits (2-8 times per year) were conducted to note the presence of adult individuals.

Secondly, in Atenas Municipal Forest (09°58'N, 84°26'W) on the Central Pacific slope. This area consists of relatively old secondary forest (9 ha, alt. 860 m) that has not been logged since the 1930s, initially established to preserve the area's watershed. As the nearby town of Atenas grew larger and other sources of water were used, the land was for the most part forgotten. Atenas MF appears to be a transition zone between tropical dry forest, characterized by semi-deciduous plant composition, and pre-montane moist forest. Traps (n = 12) were installed in March 2002 and they were monitored for larvae 3-5 times per year from May 2002 to December 2004. Additional visits (2-3 times per year) were conducted to note the presence of adults.

Thirdly, in Braulio Carrillo National Park, the Quebrada González section (10°09'N, 83°56'W), alt. 500 m. This park is located on the Caribbean slope of the Cordillera Central. The traps (n = 15) were installed in December 2000 and monitoring conducted from February 2001 to February 2005. At this location additional visits (5-6 times per year) were conducted to note presence of adult individuals.

Finally, within and near Rio Dantas Wildlife Refuge (10°00'N, 83°26'W) on the Caribbean slope, alt. 200-500 m, north of the border of Barbilla National Park, Limón Province; see Hedström (2004, 2006) for a detailed account of the area. The area has aseasonal primary wet forest and secondary growth. A total of 75 traps were installed in February 1999, and monitoring was conducted three times a year from January 2000 to January 2004. As before, the presence of adults was also noted.

In Carara NP and Atenas MF, during the dry season between the middle of December and end of April, fresh water was added to the traps once or twice a month; thus all traps in this study contained water all year round.

Average numbers of observed adult pseudostigmatids as well as larvae in traps per month at each site were calculated. Some sites were not visited during certain months, while other sites were visited up to five times in certain months during the study period. Hence, the average values are based on one to five visits each month at each site. The abundance was correlated with average precipitation. Precipitation data were obtained from the School for Field Studies (SFS) in Atenas: Alajuela Province, rainfall 1997-2002 and from Instituto Costarricense de Electricidad (ICE): Braulio Carrillo National Park (Quebrada González Station, Limón Province, 1996-2001), Rio Dantas Wildlife Refuge (Finca Mirador, 7 km north of Las Brisas de Pacuarito, Limón Province, 1992-2003). It was not possible to obtain rain data from Carara National Park so we used data (1986-2000) from Estación Lagunillas in Orotina, Puntarenas Province, a locality 20 km to the north of our sampling site but within the same zone of tropical dry forest.

Results

Carara National Park

All 39 larvae found in the 12 traps at Carara NP were identified as *Mecistogaster ornata*. Larvae were found between July and December, most individuals during July (Fig. 1). Presence of larvae corresponded to the latter half of the rainy season at Carara, which started in April and continued until November (Fig. 1). Up to seven adults of *M. ornata* were observed at the same time all year round except in February, March, October and November. In addition, on 16 December 2000 and 15 January 2001, one female of *Megaloprepus caerulatus* was observed at around 10:30 - 10:45 h solar time. It is not known if this was one or two individuals.

Atenas Municipal Forest

Only 20 larvae were found in the 12 traps during the study, all identified as *M. ornata*. As in Carara NP, larvae were found between July and December. Presence of larvae corresponded to the latter half of the rainy season which started in April-May and continued until November-December (Fig. 1). Most adults were seen during the dry months February to April, but a few were seen in October and November, towards the end of the wet season. The highest numbers of adults observed in this study were noted in February and March of 2004 with 23 and 24 individuals simultaneously at the traps respectively (Fig. 1).

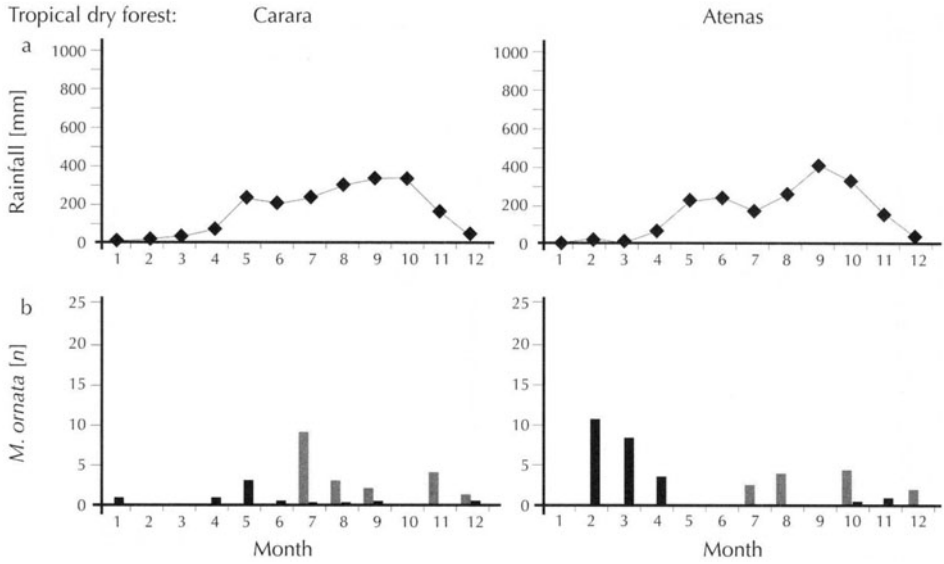

Figure 1: Rainfall and abundance of *Mecistogaster ornata* at two Costa Rican study sites in tropical dry forest — (a) average monthly precipitation [mm] in Carara National Park, represented by Lagunillas Orotina (Puntarenas Provinces, during 1986-2000), and Atenas Municipal Forest (Alajuela Province, during 1997-2002); — (b) grey bars: average number of larvae of *M. ornata* found in traps; in Carara between April 2000 and December 2004; and in Atenas between March 2002 and December 2004; black bars: average number of adults of *M. ornata* observed at trap emptying, during the same study periods as mentioned for larvae. No visit in October (Carara) and September (Atenas). Months numbered 1-12 (January to December).

Braulio Carrillo National Park

A total of 93 larvae of *M. caerulatus* were present in the 15 traps. Larvae were found year round with no pronounced peaks (Fig. 2). Precipitation in Braulio Carrillo NP was high throughout the year, with a small drop around March (Fig. 1). Adults were seen during March to July and October to December, at the most six individuals at one time.

Rio Dantas Wildlife Refuge

A total of 201 larvae of *M. caerulatus* and 72 larvae of *M. linearis* were found in the 75 traps. Larvae were found throughout the year, the highest numbers in May and December (*M. caerulatus*) and August (*M. linearis*) respectively (Fig. 2). Rain fell throughout the year, with peaks in May and December, corresponding to the peak

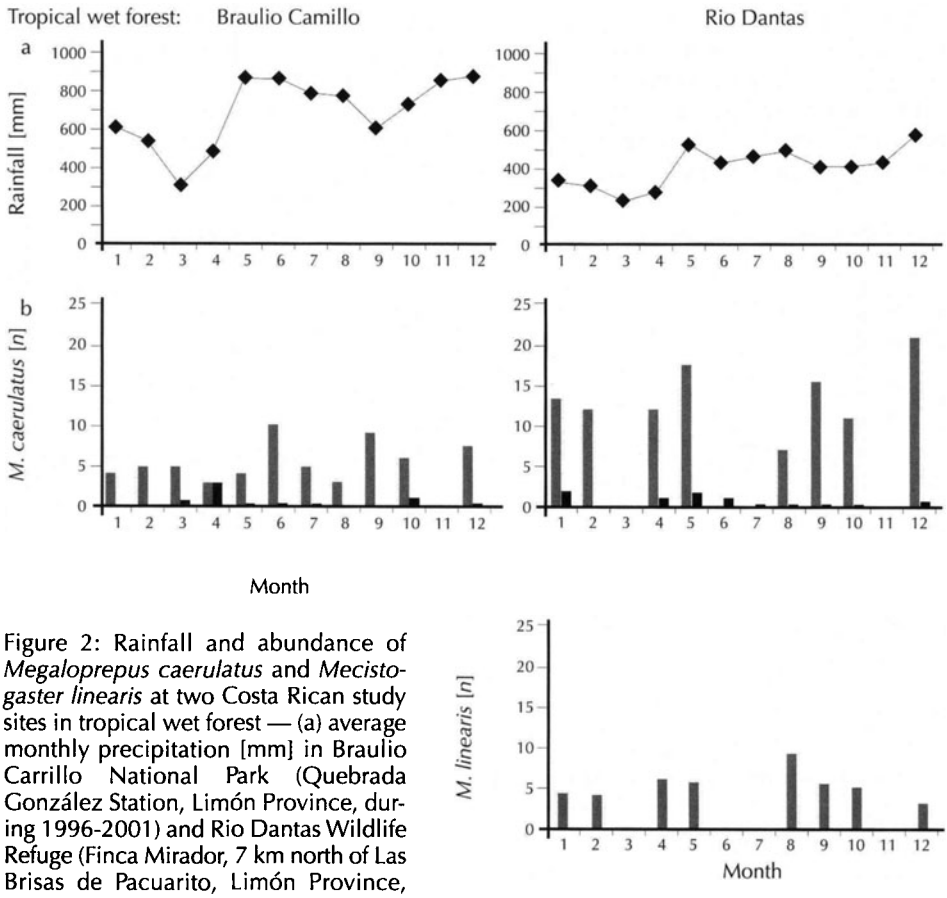

Figure 2: Rainfall and abundance of *Megaloprepus caerulatus* and *Mecistogaster linearis* at two Costa Rican study sites in tropical wet forest — (a) average monthly precipitation [mm] in Braulio Carrillo National Park (Quebrada González Station, Limón Province, during 1996-2001) and Rio Dantas Wildlife Refuge (Finca Mirador, 7 km north of Las Brisas de Pacuarito, Limón Province, during 1992-2003); — (b) grey bars: average number of larvae of *M. caerulatus* and *M. linearis* found in traps at Braulio Carrillo NP, between February 2001 and February 2005, and Rio Dantas WR, between January 2000 and January 2004; traps not emptied in August and November (Braulio Carrillo) or March, June, July and November (Rio Dantas); black bars: average number of adults of the same species; observations at trap emptying but also in November (Braulio Carrillo) and June and July (Barbilla). Months numbered 1-12 (January to December).

occurrences of *M. caerulatus* larvae (Fig. 2). Adults of *M. caerulatus* were seen year round except in February, March and November. The highest number of adults observed at one time was four. Only one visit to the site was made in February and none at all in March and November. No adults of *M. linearis* were seen during the visits, but prior to this investigation adults had been observed in the area during January, always between 09:30 h and 10:30 h solar time (data in Hedström & Sahlén 2001).

Other predators in traps

In all four areas, tadpoles of the poison arrow frog *Dendrobates auratus* (Dendrobatidae) frequently appeared. In Carara NP the number of frog tadpoles gradually increased during the four years of sampling. At the same time the number of *M. ornata* larvae decreased (Fig. 3). Also other unidentified tadpoles were sometimes encountered in all four areas. Again in Carara NP, the frog *Phrynohyas venulosa* (Hylidae) was observed during the start of the rainy season (April). On several occasions *Ptychophallus barbillaensis*, a small brachyuran crab species (see Rodríguez & Hedström 2000), appeared in traps in Rio Dantas WR. When any of these predators were present, no zygopteran larvae were present in the same traps. However, within Rio Dantas WR, large-sized larvae of *Libellula herculea* Karsch, an anisopteran, were on several occasions present in the same trap as a large individual of *M. caerulatus*. Other species observed in traps at Rio Dantas WR were tadpoles of *Smilisca phaeota* (Hylidae; found in January) and *Leptodeira septentrionalis*, a colubrid snake known to feed on eggs and adults of tree frogs (also found in January).

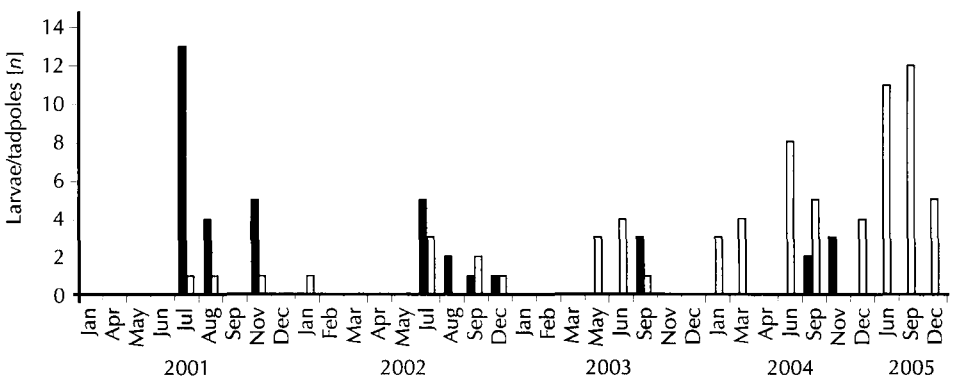

Figure 3: Pseudostigmatid larvae and poison arrow frog tadpoles found in traps — actual numbers of *Mecistogaster ornata* (black bars) and of *Dendrobates auratus* (white bars) in Carara NP 2001-2005. Note irregular scale on x-axis which indicates actual sampling occasions by month.

Discussion

There is a pronounced difference in how well defined the rainy season is in a gradient across Costa Rica. On the Pacific slope, rain falls from April to December, while on the Caribbean slope rain falls all year round. This is clearly mirrored in the occurrence of *Mecistogaster* and *Megaloprepus* larvae in our four areas (Figs 1, 2).

Seasonality is more pronounced the farther to the west one goes (in our case Carara NP), but there are no marked differences in the occurrences of *M. ornata* larvae between Carara NP and Atenas MF (Fig. 1). During the dry season, traps in Carara NP and Atenas MF would have lacked water and food for pseudostigmatid larvae if water had not been added. However, it is apparent that the presence of water in a small number of localities does not affect the general pattern of occurrence of *M. ornata*, nor did it attract breeding adults of the other two species, but note the occurrence of the frog *Dendrobates auratus* (below). On the Pacific slope of Volcán Orosi in northwestern Costa Rica, De la Rosa & Ramírez (1995) collected larvae of *M. ornata* in water-filled tree-holes. Adult *M. ornata* appeared all year round at that site, but they were more abundant during the second half of the rainy season (from July through October), which is not in agreement with our findings, since the highest numbers of adults in both our semi dry forests appeared in the dry season (Fig. 1). The tree-holes at Volcán Orosi were dry from December through April (De la Rosa & Ramírez 1995), and this is probably the normal conditions also in Carara NP and Atenas MF. We believe that the high number of adults we observed during the dry season may be explained by the areas being devoid of open water containers, and our water-filled traps thus work as veritable magnets to adults in the area.

On BCI, *M. ornata* adults emerged in late wet or early dry season and foraged throughout the dry season (Fincke 1984, 1992b). None of the *M. ornata* females collected before April by Fincke (1992b) contained developing eggs or sperm loads. Fincke (1998) found that *M. ornata* females on BCI were reproductively active for 3-4 months and produced one generation per year. They remained in reproductive diapause from the time they emerged until the late dry season, shortly before the first wet-season rains (May-early June), when they quickly matured a mass of eggs and deposited them in tree holes. We assume that *M. ornata* in Carara NP and Atenas MF displays the same pattern of occurrence, with one generation per year.

M. ornata females in Panama (Fincke 1984, 1992b) amassed yellow fat bodies in the abdominal cavity while they were in reproductive diapause and turned these resources into eggs shortly before the first rains of the wet season. Fincke (1984) observed that the onset of *M. ornata* reproduction period was indicated by dimorphic changes in wing pigmentation; the ventral side of the yellow wing tips of the male turns black, whereas those of the females remain yellow. This colour change was also observed in Costa Rica (Hedström & Sahlén 2001).

At least one, probably two *M. caerulatus* females were also observed at Carara NP. To our knowledge, this species has not previously been reported from the Central Pacific lowlands north of the Osa Peninsula in south-western Costa Rica. However, adults of both *M. linearis* and *M. caerulatus* regularly occur in the same climatic zone as Carara NP (Hedström & Sahlén 2001), so theoretically they might breed under these conditions. If not, one might suspect that all occurrences of these two species in this climate zone in Central America are the results of migration from areas with year-round rain.

Traps on the Caribbean slope, with no defined dry period, contained plenty of water, and hence food, year round (Fig. 2). This was probably the main reason why in Braulio Carrillo NP and Rio Dantas WR, larvae and adults of *M. caerulatus* and *M. linearis* were distributed throughout the year. Both these species followed a year-round reproduction pattern in these areas. Looking at abundance, we note the high number of traps in Rio Dantas WR (75) against 12 or 15 at the other locations. Both species found in Rio Dantas WR are thus more uncommon than is apparent by looking at Figure 2. A division of the number of larvae by 5 will show comparable figures to Braulio Carrillo NP, Atenas MF and Carara NP. *M. caerulatus* is thus more common in Braulio Carrillo NP than further east on the Caribbean slope. More rain seems to generate more larvae, not unexpected since also shallower tree holes and phytotelmata containers would be filled with more rain, thus increasing the number of possible breeding sites.

While *M. linearis* larvae in Rio Dantas WR co-occurred with *M. caerulatus* larvae all year round (cf. also Sahlén & Hedström 2001; O. Fincke, I. Hedström unpubl.) indicating egg laying throughout the year, this was not so in Panama. There Fincke (1984, 1992b) found that the population numbers in adults of *M. linearis* peaked in the drier season (January-April) and declined in the late wet season (September-October). *M. linearis* in Panama mated from mid December and laid diapause eggs until the following wet season; the females even laid eggs in tree holes that dried out completely by late March (Fincke 1992b, 1998). Hence, *M. linearis* has a plastic life cycle and can colonise different climatic zones. It would be interesting to compare populations from these two zones for genetic diversity and isolation.

For *M. caerulatus* we see the same pattern. Long-term research conducted by Fincke (1984, 1992a, 1992b, 1998) in the lowland moist forest at Barro Colorado Island in Panama shows that although seasonality was less pronounced in Panama compared to the Costa Rican Pacific, *M. caerulatus* larvae appeared year round and mating was observed by Fincke (1992b) throughout the year, except in late dry and early wet season. Hence, this species too appears to be able to adjust its life cycle and breed in several climatic zones.

Populations of phytotelmata- and container-dwellers can be very dense. An example is *Leptagrion perlongum* Calvert, which was found to occupy 19% of all bromeliads of the right size near Santa Lucia Biological Station in Brazil (De Marco & Furieri 2000). Melnychuk & Srivastava (2002) found that the larval density of *Mecistogaster modesta* Selys in tropical wet forest at Estación Biologica Pitilla, Guanacaste, Costa Rica was on average 171 individuals per hectare. It is clear that under the right conditions this ecological group of zygopterans is capable of colonising a big portion of all waters large enough and available to them in the forest. With the high rainfall at Braulio Carrillo NP, the numbers in this study might be the highest density of *M. caerulatus* recorded in Costa Rica.

Looking at adults, we see that the numbers observed at any site were normally lower than the number of larvae encountered, the exception being adult *M. ornata* during the dry season, especially the case mentioned for February and March 2004 when over 20 adults were observed in Atenas MF. As there is a certain mortality during the transition from larva to adult, the differences in numbers are not at all surprising. The very high number observed in Atenas MF, however, might be explained by the water in the traps attracting adults from a large area, should there be no other sources of open water (cf. above).

The predators found in the traps – tadpoles of mainly *Dendrobates auratus*, the crab *Ptychophallus barbillaensis* and *Libellula herculea* – were either competitors with (the first two) or coexisted with the pseudostigmatid larvae. Most tadpoles are believed to be herbivorous and should not compete with the pseudostigmatid larvae. In this study, however, when crabs, *Dendrobates* or other unidentified species of tadpoles were present in the traps, pseudostigmatid larvae were always absent. In Carara NP we observed that the number of *Dendrobates* tadpoles increased towards the end of the sampling period while *M. ornata* larvae became rarer (Fig. 3). We interpret this pattern as a resource competition for the water containers or, simply, a predator-prey relationship. While *M. ornata* is able to quickly colonise phytotelmata, it is not able to benefit from this ability in the long run, as the seasonal environment does not allow it to reproduce other than during the rainy season. In contrast, *D. auratus* seems to be able to breed also in drier conditions, as larvae are found also outside the rainy season (Fig. 3). Hence, while taking longer to colonise the traps, it outcompetes *Mecistogaster* larvae in the long run, as omnivorous frog larvae are present already when the first pseudostigmatid appears for egg laying. We thus believe *D. auratus* to have access to other sources of breeding waters during the dry season in Carara NP, as its larvae and hence breeding adults can be found year around (Fig. 3). This was also suggested by Fincke (1999) stating that *Dendrobates* tadpoles are less dependent on seasonal drying, as they breed in microhabitats other than tree holes. But Fincke also suggested that the survival of *Dendrobates* tadpoles in tree holes requires early colonisation, and on BCI most tree holes lack tadpoles after October, when odonate larvae outcompete them. *Dendrobates* adults depositing tadpoles are said to avoid tree holes containing odonate larvae on BCI (Fincke 1999), but our results point another way. In the dry forest of Carara NP tadpoles were observed in traps all year around with the exception of February, April and October. The competitive interaction between *M. ornata* and *Dendrobates* clearly is not the same in Costa Rica as on BCI, Panama.

Other predators are also known to eat pseudostigmatid larvae. De la Rosa & Ramírez (1995) found that the content of water-filled tree holes on the slope of Volcán Orosi were often disturbed by terrestrial predators such as coatimundis (*Nasua narica*), monkeys, ants and large spiders, presumably looking for food within traps. No such animals were observed disturbing any traps at our sites.

Looking at the species assemblage in the traps, we see another difference from the seasonal forests of Panama, as described in Fincke (1999). In Costa Rica, independent of climatic conditions, the number of (top) predators inhabiting traps (i.e. phytotelmata and tree holes) includes fewer species than in the area surveyed by Fincke. Thus, the seasonality of the forests changes distribution and flight season patterns of the pseudostigmatids studied, but it may not affect local conditions for species richness. Another question is whether all three species of pseudostigmatids included in this paper can be treated as top predators in tree holes or phytotelmata. O. Fincke and I. Hedström (unpubl.) state that a top tree-hole predator can affect the distribution of not only tree-hole mosquito larvae but also amphibians, including *Dendrobates* tadpoles. In this study we demonstrated that *M. ornata* is a weaker competitor compared to the tadpoles, and hence not a typical top predator, at least within the climatic zone of seasonal tropical semi-dry forest at Carara NP.

We conclude that the three species in this study are all able to adjust their life cycle to accommodate to local climatic conditions, ranging from seasonal to non-seasonal regimes. The range they can span varies, though, due to local conditions. Amount of rainfall and length of dry periods seem to be the most important factors, but competition from other container dwellers as well as predation may, combined with a flexibility to adapt their life cycles, also be important key factors in explaining the variation in seasonality of these species throughout their area of distribution.

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