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SEASONALITY, ABUNDANCE AND INVERTEBRATE ASSOCIATES OF *LEPTAGRION SIQUEIRAI* SANTOS IN *AECHMEA* BROMELIADS IN VENEZUELAN RAIN FOREST (ZYGOPTERA: COENAGRIONIDAE)

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In lowland tropical rainforest in eastern Venezuela the aquatic invertebrate fauna of 160 *A. nudicaulis* and 157 *A. aquilega* of 50-100 ml fluid capacity was inventoried. Larvae of *L. siqueirai* occurred in 35.3% of *A. aquilega* which has a small central tank and many axils but in only 11.0% of *A. nudicaulis* which possesses a larger central tank but fewer axils. The incidence of larvae was significantly higher in the dry (29.4%) than in the wet (16.6%) season. Up to 7 *L. siqueirai* larvae were recorded from individual *A. aquilega*, and the frequency distribution of larvae in this bromeliad sp. fits a negative binomial. The most abundant invertebrates in *Aechmea* were Diptera (Culicidae, Thaumaleidae, Chironomidae, Ceratopogonidae, Psychodidae, Tipulidae), Coleoptera (Helodidae), and oligochaete worms. Reductions in abundance among any of these taxa due to predation by *L. siqueirai* could not be demonstrated. However, the predaceous mosquito *Toxorhynchites haemorrhoidalis* was negatively associated with and suffered reduced survivorship in the presence of *L. siqueirai*, probably due to predation by the latter.

INTRODUCTION

Phytotelmata, pools of water held by terrestrial or epiphytic plants, are significant habitats for tropical Zygoptera. CORBET (1983) recorded 36 species from ten genera of Zygoptera believed to be relatively specific for phytotelmata. These include eight species of the neotropical genus *Leptagrion* identified from terrestrial and epiphytic bromeliads in Brazil (SANTOS, 1966, 1968a, 1968b, 1978, 1979).

In the course of experiments on a predatory mosquito larva, *Toxorhynchites haemorrhoidalis* (Fabr.), in Venezuelan phytotelmata, we discovered the relatively common occurrence of damselfly larvae in epiphytic bromeliads. On the basis of one adult female and one adult male reared from these larvae, the species was identified by Professor A.B.M. Machado as *Leptagrion siqueirai* Santos. The remaining collected larvae were assumed to be *L. siqueirai* on the basis of a common phenotype, but positive identifications on adults were not made. Elsewhere in Venezuela *Leptagrion fernandezianum* Rácenis has been reported from *Aechmea* bromeliads (DE MARMELS, 1985); however larvae of this species do not bear a conspicuous yellow thoracic mark which we observed on all specimens assumed to be *L. siqueirai*. Prior to our collections, only males of *L. siqueirai* had been known, these being from Pernambuco state in Brazil (SANTOS, 1968b). Quantitative information from our collections is reported here as a contribution to the scanty information about the life history of *Leptagrion* in bromeliads.

STUDY SITE AND SAMPLING METHODS

Collections were made on a cacao plantation in lowland tropical rain forest near Panaquire, Venezuela (10° 13′ N, 66° 14′ W) in the wet season (July and August) of 1983 and dry season (March and April) of 1984. The mean annual rainfall at Panaquire is approximately 2,500 mm, and temperature rarely fluctuates more than a few degrees from the annual mean of 26.3° C (MACHADO-ALLISON et al., 1983). July is usually the rainiest and March the driest month of the year. Although records for 1983-84 were not available from Panaquire, at El Café, 15 km to the SW, 46% less rainfall was registered during July 1983 than the 1961-70 mean of 262.8 mm. In March 1984, only 15% of the ten-year average of 43.2 mm rainfall was recorded at El Café.

Shade and cacao trees at the plantation support five species of bromeliads which maintain phytotelmata (MACHADO-ALLISON et al 1985). For experiments reported in detail elsewhere (LOUNIBOS et al., in press), we selected four phytotelmata, including two species of *Aechmea* which differ in structure. *Aechmea nudicaulis* (L.) possesses a prominent central tank and relatively few axils and *Aechmea aquilega* (Salisb.) has a reduced tank and many axils (MACHADO-ALLISON et al., 1985). Bromeliads holding 50-100 ml of fluid were cut at levels 1 to 10 m above ground from trees and suspended in pairs in the shade on a rack 1.5 m above ground for one to three months to allow natural colonization after rainfall. Bromeliads were not washed before suspension on the rack.

Single first-instar larvae of *T. haemorrhoidalis* were released into the central tanks of 40 *A. aquilega* and 40 *A. nudicaulis* once during the wet and once during the dry season; paired controls received no introductions. One-half of the bromeliads were sampled 10 d after, and the remainder 20 d after the introduction. Bromeliads were removed from the rack, shaken vigorously in a bucket of water to dislodge inhabitant fauna, washed with a stream of water, and the contents of the bucket passed through a sieve of 160 micron mesh width. Specimens were later separated from detritus in ethanol and preserved in formalin. All aquatic invertebrates visible with the naked eye were counted and identified. Similar methods have been used to census the invertebrate fauna of *Tillandsia* bromeliads in Florida (FRANK, et al., 1976).

RESULTS

SEASONALITY AND ABUNDANCE

Larvae were recovered from 16.6% of *Aechmea* sampled in the wet season of 1983 and from 29.4% of plants inventoried in the dry season of 1984 (Fig. 1). A G-test confirmed that the occurrence of *L. siqueirai* in *Aechmea* was not independent of season (G adj = 141.8, P << 0.001).

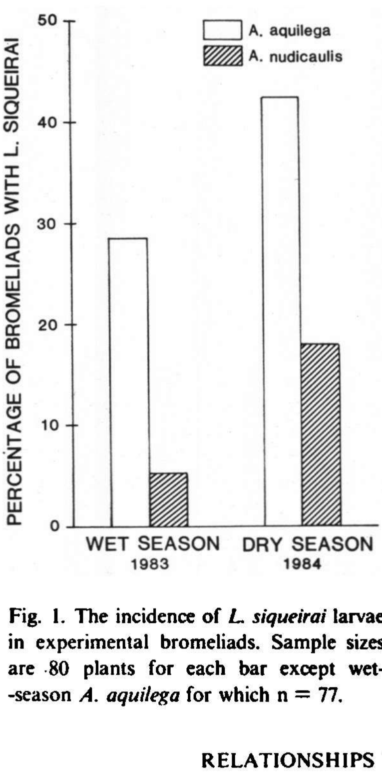

Fig. 1. The incidence of *L. siqueirai* larvae in experimental bromeliads. Sample sizes are 80 plants for each bar except wet-season *A. aquilega* for which n = 77.

These same data revealed the presence of *L. siqueirai* in 11.3% of all *A. nudicaulis* and 35.0% of *A. aquilega,* indicating a significant habitat preference for the latter bromeliad species (G adj = 160.5, P << 0.001).

Although *L. siqueirai* occurred most often as single individuals in plants, a maximum of five larvae was recorded from a single *A. nudicaulis* and a maximum of seven from a single *A. aquilega* (Fig. 2). The frequency distribution of numbers in *A. aquilega* deviated significantly from a random (Poisson) distribution (chi-squared = 18.49, P < 0.001, 2 df), but a negative binomial calculated by the iterative method of BLISS & FISHER (1953) provided an acceptable fit to the data (chi-squared = 5.73, P < 0.05, 2 df). The small value of K = 0.895 indicates aggregation of *L. siqueirai* in *A. aquilega.*

RELATIONSHIPS TO OTHER INVERTEBRATES

Most invertebrates were identified only to family. Eight taxa which include seven families of insects and one class of annelids accounted for 97.4% of 11,050 organisms identified from experimental *A. aquilega* and 95.0% of 5,656 specimens from experimental *A. nudicaulis.* A. complete listing of all identifications is presented elsewhere (LOUNIBOS et al., in press). *Leptagrion siqueirai* accounted for only 0.8% and 0.4% of invertebrates identified from *A. aquilega* and *A. nudicaulis,* respectively.

The median and maximum values of number of individuals of the eight

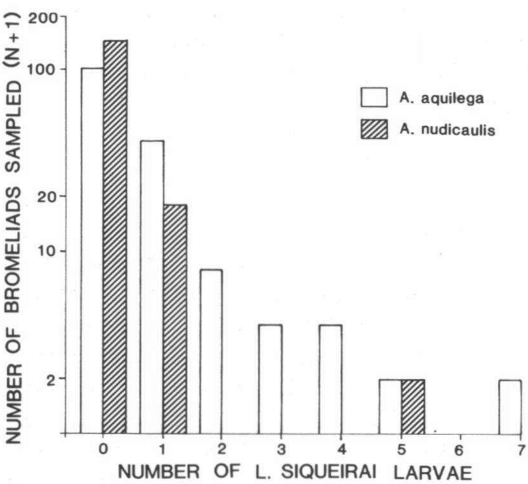

Fig. 2. The frequency distributions of numbers of *L. siqueirai* larvae per plant in 157 experimental *A. aquilega* and 160 *A. nudicaulis*.

commonest taxa are given in Table I for *Aechmea* with and without *L. siqueirai* which contained no *T. haemorrhoidalis*. In *A. nudicaulis*, no significant differences were detected within taxa in the presence versus absence of *L. siqueirai*. However, in *A. aquilega*, Culicidae, Thaumaleidae, Chironomidae, Tipulidae, and Helodidae were significantly more abundant in plants containing *L. siqueirai*.

Elsewhere, we demonstrated that survival of introduced *T. haemorrhoidalis* was significantly (P = 0.06) less in experimental bromeliads which contained *L. siqueirai* than in plants which had no *L. siqueirai* larvae. Evidence of predation was also supported by a 2 X 2 contingency table analysis of pooled data from *A. aquilega* and *A. nudicaulis*, which indicated

Table I

Median numbers and ranges (parentheses)[1] of the most abundant invertebrates in the presence and absence of *L. siqueirai* in *Aechmea* bromeliads which contained no *Toxorhynchites*

	No. plants	Oligochaeta[2]	Helodidae	Culicidae	Thaumaleidae	Chironomidae	Ceratopogonidae	Psychodidae	Tipulidae
A. nudicaulis:									
Leptagrion present	14	7 (46)	1 (23)	3 (12)	1 (22)	1.5 (14)	0 (13)	3.5 (77)	1 (5)
		ns[3]	ns	ns	ns	ns	ns	ns	ns
Leptagrion absent	83	2 (62)	1 (49)	2 (41)	0 (19)	1 (15)	0 (22)	9 (74)	1 (17)
A. aquilega:									
Leptagrion present	45	0 (13)	0 (65)	10 (74)	0 (66)	9 (76)	1 (122)	28 (198)	2 (40)
		ns	*	***	**	*	ns	ns	*
Leptagrion absent	82	0 (33)	0 (27)	2 (96)	0 (22)	3.5 (41)	0 (35)	15.5 (129)	0.5 (21)

[1] All ranges begin at zero.
[2] Oligochaetes were only recognized in dry-season samples, therefore the number of plant samples for this taxon (only) is, top to bottom: 11, 38, 25, 40.
[3] Levels of significance tested by Mann-Whitney U (2-tailed): * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant.

a significant ($P < 0.05$) negative association between *L. siqueirai* and *T. haemorrhoidalis* (LOUNIBOS et al., in press). We have separated the presence-absence data by plant species, under which conditions the negative associations are no longer significant for *A. nudicaulis* (chi-squared = 1.42, 1 df) or *A. aquilega* (chi-squared = 0.24, 1 df).

DISCUSSION

SANTOS (1966) described *L. siqueirai* from a terrestrial bromeliad, *Canistrum*. At our plantation study site, only epiphytic bromeliads provide phytotelmata (MACHADO-ALLISON et al., 1985). In keeping with the valency suggested by CORBET (1983), we would expect *L. siqueirai* to occur in three other locally abundant bromeliads not sampled: *Guzmania monostachia* (L.), *Tillandsia elongata* H.B.K., and *Vriesia procera* (Schult.), but not in phytotelmata provided by other families of plants. Because of their longevity (FRANK, 1983), bromeliads are among the most suitable container habitats for odonate larvae with protracted developmental periods, such as some species occurring in phytotelmata (CORBET, 1983).

The habitat preference of *L. siqueirai* for *A. aquilega* over equal-sized *A. nudicaulis* is related to the contrasting structure of the two species. Each axil of *A. aquilega* serves as an isolated compartment for *L. siqueirai* which, unlike most other aquatic inhabitants, has the capacity to migrate to neighboring axils when prey are locally exhausted. The greater number of axils in *A. aquilega* provides more niches and, further, this species of bromeliad contains approximately twice as many invertebrates as the related *A. nudicaulis* (Tab. I).

Bromeliad habitat suitability for the predatory mosquito larva *T. haemorrhoidalis* is the converse of that for *L. siqueirai*. In *A. aquilega, T. haemorrhoidalis* suffered reduced survivorship compared to its survival in *A. nudicaulis*, and its predatory effect was detectable only in the latter species of bromeliad (LOUNIBOS et al., in press).

Reasons for the dry-season increase in abundance of *L. siqueirai* larvae (Fig. 1) are not clear. Non-predatory invertebrates were also more common in dry-season bromeliad samples, especially *A. aquilega* (LOUNIBOS et al., in press). The significantly greater abundance of certain taxa in the presence of *L. siqueirai* in *A. aquilega* (Tab. I), is probably the consequence of seasonal aggregations of fauna, perhaps in those bromeliads most resistant to desiccation. It is unknown whether gravid *L. siqueirai* are capable of detecting aquatic invertebrates in bromeliads and selecting for oviposition those habitats rich in potential prey.

The non-random distribution of *L. siqueirai* in *A. aquilega* is primarily due to over-dispersion, i.e. multiple occurrences in individual plants (Fig. 2). We noted that co-occurring larvae were usually of the same size class, thereby impeding cannibalism, which is usually by older conspecifics (POLIS, 1981). Possibly, co-occurring individuals represent cohorts derived from contemporaneous oviposition by damselfly adults.

LAESSLE (1961) recorded as many as eight larvae of the zygopteran *Diceratobasis macrogaster* (Selys) in a single leaf axil of an unspecified Jamaican bromeliad. He did not comment on the sizes of these larvae, nor did SANTOS (1966) who recovered 15 *Leptagrion andromache* Selys and *Leptagrion elongatum* Selys in a single *Vriesia regina* (Vell.) bromeliad. The bromeliads examined by both authors were apparently much larger in capacity than the specimens used in our experimental study. *Aechmea aquilega* holding as much as one liter of fluid occur at our study site (MACHADO-ALLISON et al., 1985) and these probably harbor more individual *L. siqueirai* than did our 50-100 ml plants.

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