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NOTES

Competition for Prey Between the Carnivorous Bromeliaceae *Brocchinia reducta* and Sarraceneacea *Heliamphora nutans*

The terrestrial bromeliad species *Brocchinia reducta* Baker is found south of the Orinoco River, either in the Gran Sabana (Estado Bolivar, Venezuela) or on the summit of table mountains called tepuis. Geologically, tepuis belong to the Roraima formation, dominated by bleached sandstone of Precambrian origin. Peat or sandy soils, extremely poor in nutrients and highly acidic, overlay the rotting sandstone (Givnish *et al.* 1984, Cuevas 1987). On tepuis, the species shares its general habitat with carnivorous plants of the genus *Heliamphora*. *B. reducta* has a cylindrical rosette, formed with leaves with a slippery waxed surface, that help capture prey (Givnish 1988). *Heliamphora* has pitcher-shaped leaves covered internally with downward pointing hairs that prevent captured prey from crawling out (Brewer-Carias 1973). The leaves of both plants act as pitfall traps (Givnish 1988).

Givnish *et al.* (1984) claim that *B. reducta* should be considered carnivorous, because it has the two traits which they use to define carnivory: the plant absorbs nutrients from dead animals through the leaves, and the plant has unequivocal adaptations for active attraction, capture, and/or digestion of prey. Juniper *et al.* (1989) suggest that this species does not fall within their definition of true carnivory; *i.e.*, plants need to possess all of the following traits: attraction of prey through special signals, trapping and killing of prey, digestion of prey through secreted enzymes, presence of commensals, and absorption of nutrients. Moreover, Juniper *et al.* (1989) are unwilling to consider species of *Heliamphora* truly carnivorous, but recent evidence shows that *Heliamphora* species are highly specialized carnivorous plants, fulfilling both definitions of carnivory (Jaffe *et al.* pers. obs.).

If both species are carnivorous, and are found sympatrically, they may have different strategies in order to reduce competition for prey. The species we studied, *H. nutans* (Bentham), and *B. reducta* occur sympatrically on the tepuis Kukenan and Roraima in South East Venezuela (Steyermark 1984). At the chosen site on Kukenan-tepuy (2200 m.a.s.l.), we examined the content of the "leaf-tanks" of 11 *B. reducta* plants, from a colony of 70; and 15 *H. nutans* pitchers, from a colony of 69. Plants were chosen by collecting one plant of each species every 30 cm in a dense patch containing both species, approximately 8 m^2 large. We found arthropods, either as inhabitants of the leaf-tanks or as prey (dead and semidecomposed adults). Our data are summarized in Table 1.

Live individuals (larvae) of the midge *Metriocnemus* sp. (Chironomidae) were found living in the liquid of both plant species. Larger plants of *B. reducta* had fewer midge larvae than smaller plants. Water in the tank may possibly become contaminated by bacteria and microorganisms as the plant grows older. This contamination could diminish the percentage of oxygen in the water, making the tank less tolerable for the midge (Cameron *et al.* 1977). The midge larvae may accelerate breakdown of captured prey, thus increasing the rate of nitrogen release (Bradshaw 1983). A similar role may be played by the *Wyeomyia* sp. (Culicidae) larvae which were found living in pitchers of *H. nutans*.

Spider webs were common at the entrance of the plant's leaf-tank. They were encountered on over half of the *B. reducta* sampled, while on *H. nutans* they were less abundant. The presence of a spider web at the entrance of *B. reducta* leaf-tanks reduces the probability of prey dropping into the tank. Thus, spiders might be considered parasitic on the carnivorous habit. In Table 1, we represent as Aranea the specimens collected inside the tank, which might be the ones which accidentally dropped into the tank or which died and then dropped.

If the data on dead prey collected from the "tanks" are analyzed (Table 1), it appears that small plants of *B. reducta* collect a greater diversity of prey than pitchers of *H. nutans*. The parasitic Chalcidoidea wasps, a curious group of prey, were found only in small plants of *B. reducta*. The most common prey for both species were ants (*Solenopsis* sp.). We collected large numbers of this ant (the only species found on the tepuy) in the "tanks" of both plant species. Both plant species are competing for ants and Diptera, as they are trapping the same prey species, but *B. reducta* (small plants) appears to be more of a generalist, trapping a greater variety of prey.

When small and large plants of the bromeliad were compared, we found that the former had a larger amount and a greater diversity of prey ($P < 0.01$, if prey numbers for each arthropod group in both

TABLE 1. *Percentage of plants containing arthropods in a patch of* Brocchinia reducta *and* Heliamphora nutans *in Kukenan-tepuy. Individuals per leaf-tank (mean diameter) is given in parentheses.*[a]

	Brocchinia reducta		
Diameter of leaf-tank:	Large plants >40 cm ($N = 5$)	Small plants <25 cm ($N = 6$)	*Heliamphora nutans* ($\bar{x}$ = 12 cm; $N = 15$)
Inhabitants			
Diptera (larvae)			
Culicidae			
Wyeomyia sp.	0 (0)	0 (0)	47 (1.9)[b]
Chironomidae			
Metriocnemus sp.	80 (14.2)	100 (33.2)[b]	67 (23.5)
Prey			
Aranea	80 (1.8)	67 (1.2)	13 (0.2)
Diplopoda	0 (0)	0 (0)	7 (0.1)
Acarina	20 (0.2)	50 (4.0)	0 (0)
Collembola	0 (0)	100 (36.2)[b]	0 (0)[b]
Homoptera	60 (0.6)	83 (2.3)[b]	0 (0)[b]
Lepidoptera	0 (0)	17 (2.3)	0 (0)
Coleoptera	80 (1.2)	0 (0)[b]	0 (0)
Diptera			
Ceratopogonidae			
Culicoides spp. (adults)	0 (0)	83 (11.2)[b]	27 (3.6)
Sciaridae	0 (0)	100 (7.3)[b]	13 (0.5)
Others	40 (1.2)	50 (0.8)	33 (0.4)
Hymenoptera			
Formicidae			
Solenopsis sp.	100 (28.8)	100 (144.7)[b]	100 (159.0)
Chalcidoidea	0 (0)	100 (2.8)[b]	0 (0)[b]

[a] Voucher specimens were deposited at: Herbario Nacional, Instituto Botanico, INPARQUES, Caracas (plants); and Museo de Ciencias Naturales, Universidad Simon Bolivar, Caracas (arthropods).
[b] Indicates statistically different samples (Mann-Whitney *U*-test) $P < 0.05$; between small and large *B. reducta* (in 2nd column) or between *H. nutans* and all *B. reducta* (in 3rd column).

categories are compared with a 12 × 2 chi-squared test). Also, small plants of *B. reducta* contained a larger number of ants than large plants (see Table 1).

Small plants of *B. reducta* have a very distinctive odor in the field. This has been previously reported by Givnish *et al.* (1984). This characteristic odor was not noticed in large plants. This suggests that chemicals, secreted at early stages of the plant's development, might be attracting insects and other arthropods. *Heliamphora* spp. secrete sarracenin as an efficient general attractant (Jaffé *et al.* pers. obs.).

Large plants of *B. reducta* have considerable amounts of frass and organic material of plant origin, which may explain their exceptional Coleoptera capture (Table 1), as many species of Coleoptera are attracted to decomposing plant materials. The ant *Solenopsis* sp., which build its nests among the leaves of large plants, as well as the spiders commonly encountered on large plants, both appear to use the leaf-tanks as middens, throwing their debris into the tanks.

Therefore, we propose that early stages of *B. reducta* are carnivorous and compete with *H. nutans* for prey. Large specimens of the bromeliad could be considered arthropod-fed rather than carnivorous.

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Jorge M. Gonzalez and **Klaus Jaffe**[1]

Universidad Simón Bolivar
Departamento de Biologia de Organismos
Apartado 89000, Caracas 1080, Venezuela

Fundación Terramar
Apartado 89000, Caracas 1080, Venezuela

Fabian Michelangeli

Instituto Venezolano de Investigaciones Cientificas
Centro de Biofisica y Bioquimica
Carretera Panamericana. Pipe, Edo. Miranda, Venezuela

Fundación Terramar
Apartado 89000, Caracas 1080, Venezuela

[1] To whom correspondence should be addressed.

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Dispersal of the Orchid *Dendrobium insigne* by the Ant *Iridomyrmex cordatus* in Papua New Guinea

Many species of plants native to a variety of habitats, including the canopies of tropical forests, are myrmecochorous (Beattie 1985). A small group of specialized epiphytes is noteworthy for additional ant dependence, specifically, for near or complete restriction to arboreal ant-nest gardens (Ule 1902, Kleinfeldt 1978, Madison 1979, Davidson 1988). These exceptional myrmecochores, like their terrestrial counterparts, attract seed carriers with eliaosomes or less conspicuous ant foods that are often accompanied by fragrances (Davidson 1988). A number of ant-house and other epiphytes feature similar rewards (Janzen 1974, Huxley 1980) and may also benefit from ant-constructed substrata (Longino 1986). In fact, propagules with edible parts characterize most of the heavily epiphytic families (Madison 1977) although how many species rely on ants for dispersal or rooting media is not known.

The recognized epiphytic myrmecochores are unevenly apportioned among taxa, and Orchidaceae is especially underrepresented. Yet this family dominates the arboreal flora (>60% of the species; Kress 1986), indicating that a buoyant, tiny seed with a delicate testa, like zoochory, is compatible with epiphytism. Only occasional species (*e.g., Coryanthes* spp. and *Epidendrum imatophyllum*) suggest ant carriage by consistently rooting in carton (Dressler 1981). We report another case of dependence of an orchid on ants in Papua New Guinea (PNG) that reveals new dimensions to myrmecochory.