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NOTES

Florivory by the Crab *Armases angustipes* (Grapsidae) Influences Hummingbird Visits to *Aechmea pectinata* (Bromeliaceae)[1]

ABSTRACT

Armases angustipes (Grapsidae) crabs were recorded on 31.5 percent of *Aechmea pectinata* inflorescences, a common ornithofilous bromeliad in rain forests of southeastern Brazil. Crabs foraged mainly in the morning and used newly opened flowers, usually damaging the corolla, consuming the stamens and stigma, and interfering with hummingbird visits. This florivory may reduce the reproductive success of *A. pectinata*, both directly through consumption of flowers and indirectly by reducing pollinator visits.

Key words: Aechmea pectinata; *bromelicolous crab; florivory; hummingbirds; pollination success; southeastern Brazil; submontane rain forest.*

Herbivores that feed upon floral structures may reduce the reproductive success of plants either through the loss of gametes due to damage to anthers and ovaries or by hindering pollinator visits (Krupnick *et al.* 1999, Mothershead & Marquis 2000, Malo *et al.* 2001). Low visitation is caused either by changes in floral display or rewards (Zammit & Hood 1986, English-Loeb & Karban 1992, Karban & Strauss 1993, Cunningham 1995) that reduce the attractiveness of flowers to pollinators (Schemske 1980, Roubik & Buckmann 1984) or by the presence of herbivores inhibiting pollinators (Roubik 1982, Piratelli 1997).

Several crab species have been reported as herbivorous, feeding on leaves, stems, roots, seeds, and seedlings (Capitoli *et al.* 1977, Hagen 1977, Garcia-Franco *et al.* 1991, Kneib *et al.* 1999, Sherman 2002). Individuals of *Armases angustipes* Dana (1852; Grapsidae) are usually present in the water accumulated among the basal leaves of bromeliads in different habitats (Hagen 1977, Abele 1992), mainly in the marginal zones of mangrove swamps (Anger *et al.* 1990). Analyses of crabs' gastric contents have revealed chitinous parts of insects, detritus, plant material, and many stellate trichomes (Sattler & Sattler 1965), but no evidence of floral tissues. The first record of flowers as part of crab diets was provided by Fischer *et al.* (1997). These authors observed individuals of *Armases rubripes* Rathbun (1917; = *Metasesarma rubripes*; Grapsidae) eating flowers of bromeliads, among them *Aechmea pectinata* Baker (Bromeliaceae). Here, we describe florivory by *A. angustipes* and its effects on the pollination success of this bromeliad species.

Fieldwork was carried out in Parque Estadual da Serra do Mar-Núcleo Picinguaba in São Paulo (23°22′S, 44°50′W), a submontane rain forest in southeastern Brazil (details in Morellato *et al.* 2000). Individuals of *A. pectinata* are commonly found in mangrove and in restinga scrub, and on rocky shores in Picinguaba, either as epiphytic, terrestrial, or saxicolous plants. Plants occur mainly in assemblages of 10 to 15 individuals (76%), but isolated individuals are also common (24%). This bromeliad species blooms from October to February, exhibiting red leaf tips during this period. The inflorescences bear 150–250 densely packed flowers and last 20–25 days. The 1–15 flowers that open each day per inflorescence are greenish white and tubular. Anthesis begins at *ca* 0400 h and lasts for *ca* 13 hours. Nectar production is highest in the morning when the hummingbirds *Thalurania glaucopis* Gmelin, *Amazilia fimbriata* Elliot, and *Ramphodon naevius* Dumont (Trochilidae), its main pollinators, are most frequent (Canela & Sazima, pers. obs.). *Aechmea pectinata* is self-incompatible, and thus, pollinator-dependent (Canela & Sazima, pers. obs.).

From October 2000 to February 2001, 38 individuals of *A. pectinata* were sampled, 12 in mangroves (10 epiphytic and 2 terrestrial individuals), 13 in the restinga scrub (9 epiphytic and 4 terrestrial), and 13 saxicolous individuals on rocks near the shore. During 19 days, observations were made either directly or by using binoculars from early morning (0400 h) to late afternoon (1800 h), which totaled 112 hours (62 hours in the morning and 50 hours in the afternoon). We recorded plant habitat, habit, daily number

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of open flowers per inflorescence, presence or absence of crabs, time and duration of crab and hummingbird visits/inflorescence/day, and behavior of both the crabs and the birds. Crabs and hummingbirds were photographed and videotaped during their visits to the flowers. Crab specimens were collected for identification and deposited as vouchers at the Museu de Zoologia, Universidade de São Paulo, Brazil (MZUSP 13820).

Individuals of *A. angustipes* foraged on flowers of *A. pectinata* (Fig. 1a) mainly during the flowering peak (November to mid-January). At the beginning and end of the flowering season, when the number of *A. pectinata* individuals with flowers was low, crabs were rarely recorded. Although some individuals of other bromeliad species, namely *Aechmea distichantha* Lem., *Neoregelia johanis* (Car.) L. B. Sm., and *Aechmea nudicaulis* (L.) Griseb., flowered during the same period as *A. pectinata*, no crabs were seen foraging on their flowers. *Aechmea pectinata* is an important feeding resource due to the high quantity of both individuals and flowers, and apparently, the other bromeliad species are less important because their flowers are not in clusters (Fischer *et al.* 1997). During the remaining part of the year, the crab *A. angustipes* likely feeds on other bromeliads with dense clusters of flowers, such as *Quesnelia arvensis* (Vell.) Mez, *Nidularium inocentii* Lem., and *Bromelia antiacantha* Bertoloni (Fischer *et al.* 1997), which are also abundant at our study site. Many species of grapsid crabs are known to live and breed in several bromeliad species (McWilliams 1969, Hartnoll 1971, Abele 1972), and the use of different bromeliad species may indicate that Bromeliaceae plays an important ecological role for grapsid crabs at the population level.

Crab florivory was recorded on 12 of the 38 observed *A. pectinata* individuals (31.5%). Six of these were in mangroves (50%), 3 in the restinga scrub (25%), and 3 on the rocks near the shore (25%); 8 were epiphytic individuals (67%), 3 were saxicolous (25%), and only 1 was a terrestrial plant (8.3%). Typically, 1 or 2 (rarely 3) crabs were recorded per inflorescence at the same time, totaling 19 crabs during the study period. The frequency of *A. angustipes* on *A. pectinata* was 0.5 crabs/inflorescence, nearly an order of magnitude greater than the recorded frequency of *A. rubripes* on *A. pectinata* (0.06 crabs/ inflorescence) at the Ecological Station of Juréia in southeastern Brazil (Fischer *et al.* 1997). This difference may be explained by the higher number of other flowering bromeliad species and individuals at this latter site (Fischer *et al.* 1997).

Although crabs foraged from 0400 to 1800 h, 82 percent of the flower-feeding records ($N = 23$) were in the morning (Fig. 2). Crabs used 3–5 flowers on the same inflorescence per visit, spending 10–30 minutes foraging on a given flower before moving to another. A visit to a given inflorescence could last up to two hours, and crabs could visit the same inflorescence up to three times a day. Some inflorescences were visited by crabs on consecutive days. When visiting a flower, the crab separated the sepals and petals with its chelae (Fig. 1a), usually damaging these floral structures, and consumed only the stamens and stigma. The crabs preferred newly open flowers and rarely disturbed buds or old flowers. Our observations on *A. angustipes* of foraging primarily in the morning and favoring newly open flowers are consistent with those recorded for *A. rubripes* by Fischer *et al.* (1997) and may be related to the greater availability of pollen, a highly nutritional part of the flower (Stanley & Linskens 1974).

Of the 12 plants with crabs, 11 individuals occurred in clumps (92%) and 10 had inflorescences with more than 5 flowers/day (83%). These facts may indicate that crabs are attracted by high flower density (Fischer *et al.* 1997), analogous to pollinating insects that concentrate their visits to plant clusters with high rewards (Thomson 1981, Klinkhamer *et al.* 1989). Therefore, plants of *A. pectinata* blooming at the beginning or end of the season, as well as isolated individuals and those with few flowers, likely are less attractive and have a greater chance of escaping from crab florivory.

Hummingbirds made 44 approaches to 12 *A. pectinata* plants bearing crabs, of which 25 were successful visits and 19 were interrupted (Fig. 3). Interrupted visits (Fig. 1b) occurred at eight inflorescences; four inflorescences with crabs were not approached by hummingbirds (Fig. 3). Hummingbird approaches to inflorescences with crabs were significantly reduced compared to approaches ($N = 423$)

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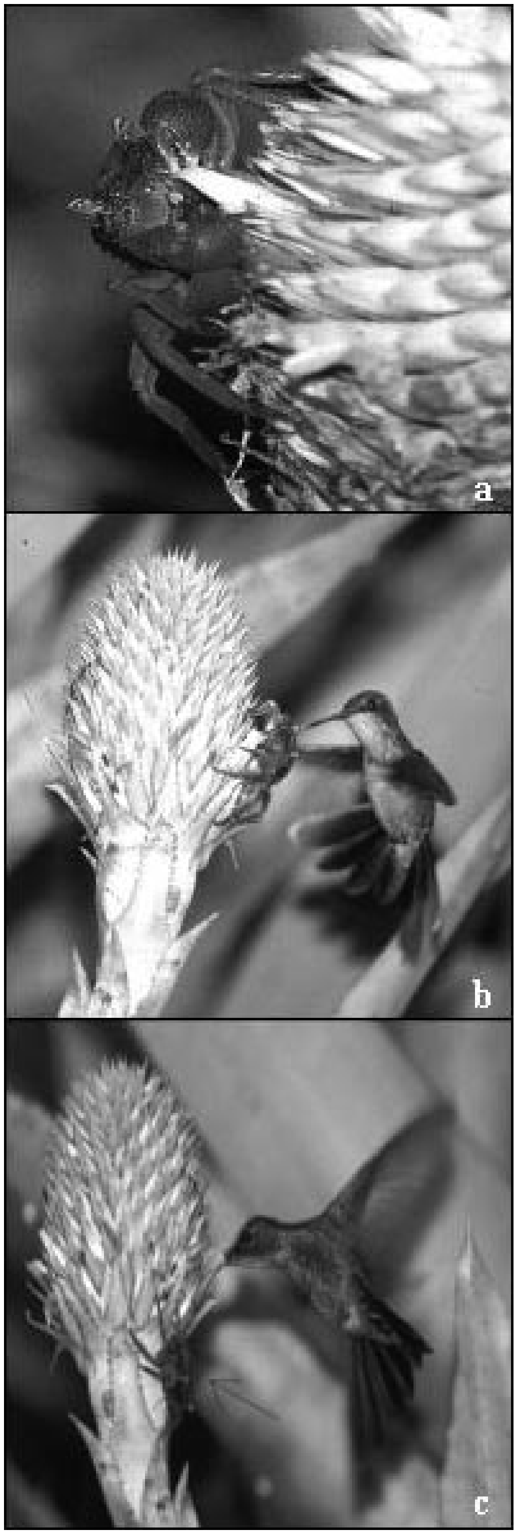
FIGURE 1. (a) The grapsid crab *Armases angustipes* handling a flower of the bromeliad *Aechmea pectinata*; (b) interruption of a visit by *Thalurania glaucopis* (female) to an inflorescence of *A. pectinata* with a crab, *A. angustipes*; (c) *Thalurania glaucopis* (male) visiting a flower of *A. pectinata* when crab (arrow) moves from the inflorescence.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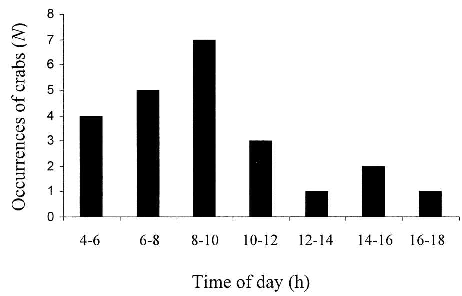

FIGURE 2. Number of occurrences of crabs foraging at *Aechmea pectinata* inflorescences throughout the day, during 19 study day in Picinguaba/SP, Brazil.

to inflorescences without crabs ($N = 26$) during the same period ($\chi^2 = 17.49$, 1 df, $P < 0.001$). The number of interrupted visits ($N = 19$, 43%) to inflorescences with crabs was significantly greater when compared to the number of interrupted visits ($N = 9$, 2.1%) to inflorescences without crabs ($\chi^2 = 81.20$, 1 df, $P < 0.001$). During successful visits, the number of flowers visited per inflorescence with crabs was reduced by *ca* 70 percent and the visits were up to five times shorter compared to visits to inflorescences without crabs. In inflorescences with only one crab foraging during a short period, hummingbirds sometimes resumed their visits after the crab left the inflorescence (Fig. 1c). This occurred more frequently in the afternoon. Hummingbird species behaved differently at inflorescences with crabs. After first encountering such a situation, individuals of *R. naevius* usually discontinued visits to that inflorescence for the day. On the other hand, individuals of *A. fimbriata* and *T. glaucopis* (males) visited inflorescences with crabs at least a few times before giving up. This difference is probably linked to the territorial behavior of these latter hummingbird species; *R. naevius* is a typical high-reward trapliner (Feinsinger & Colwell 1978; Canela & Sazima, pers. obs.). It should also be noted that hummingbirds sometimes seemed to reject inflorescences with crab-damaged flowers; birds were observed approaching these inflorescences but not visiting any flowers.

As a probable result of interference by crabs in pollination, 5 of the 12 inflorescences of *A. pectinata* foraged by *A. angustipes* (42%) set no fruit versus 3 of the 26 crab-free inflorescences (11.5%; $\chi^2 = 2.70$, 1 df, $0.05 < P < 0.10$). Consumption of stamens and stigma by the crabs directly affects the export and receipt of pollen, respectively, and the damage caused to sepals and petals by florivory may

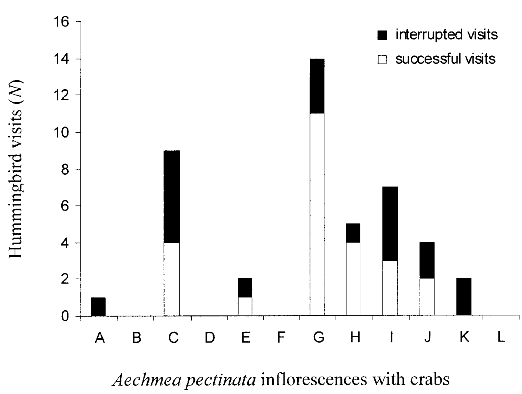

FIGURE 3. Number of successful ($N = 25$) and interrupted ($N = 19$) visits by the hummingbirds at 12 *Aechmea pectinata* (A– L) bearing crabs in Picinguaba/SP, Brazil. Total number of approaches = 44.

interfere in flower attractiveness and result in diminished pollinator visitation rates to the damaged plants (Lehtilã & Strauss 1997, Kudoh & Whigham 1998, Mothershead & Marquis 2000). Thus, it is possible that florivory by crabs also reduces the reproductive success of flowers not directly impacted. Gametes of these flowers may be wasted if hummingbirds carrying pollen fail to deposit it on stigmas when their attempts to visit flowers are interrupted by reduced floral display (Armbruster 1988, Krupnick *et al.* 1999) or by the presence of crabs (Roubik 1982, Piratelli 1997). These aspects may reduce fruit set (Gross & Werner 1983, Bertness *et al.* 1987, Cunningham 1995), and such an effect is expected to be greatest in self-incompatible species such as *A. pectinata*.

This study presents the first description of crab florivory in relation to pollinators, and suggests, based on consumption of floral structures and reduction of hummingbird visits, that *A. angustipes* interferes directly, as well as indirectly, with the reproductive success of *A. pectinata*. Crab florivory may play an important role in the population dynamics of this bromeliad and act as a selective force in the evolution of some of its ecological and reproductive features, such as spatial distribution, flowering phenology or vegetative reproduction.

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