

Vertebrate florivory on the short-columnar cactus *Echinopsis rhodotricha* K. Schum. in the Brazilian Chaco

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Abstract Florivory can negatively affect the reproductive success of plants through its effects on fruit set. We report flower consumption of *Echinopsis rhodotricha* by *Mazama americana* and *Pecari tajacu* in the Brazilian Chaco. In order to evaluate the effects of florivory on the reproductive success of *E. rhodotricha*, we quantified and compared the fruit set between damaged and undamaged flowers in a natural population of this cactus. We recorded 21 damaged flowers in the year 2015 and 43 in 2016. Florivores consumed the whole flowers and therefore no fruits developed. The result of this study indicates that florivory decreases the fruit set in the studied population, both directly by damaging the reproductive organs and indirectly through the reduction of floral attractiveness and rewards for pollinators.

Keywords Cactaceae · Fruit set · Humid Chaco · Reproductive success

Introduction

Cactaceae is one of the most diverse families in the Neotropics (Anderson 2001), and Eastern Brazil is the third center of diversity (Taylor and Zappi 2004). Flowers typically have colored, thick and fleshy petals, and an elevated number of stamens and ovules (Anderson 2001). Bees, hummingbirds, butterflies, moths, and bats typically mediate pollination (Schlumpberger 2010).

In Brazil, Cactaceae are represented by 260 species, including *Echinopsis rhodotricha* K. Schum., a short-columnar cactus that occurs in Chaco vegetation (BFG—The Brazil Flora Group 2015). *Echinopsis rhodotricha* produces large, white-colored and funnel-shaped flowers, with prolonged anthesis (Gomes and Araujo 2015). These traits suggest pollination by sphingids, as recorded for other species in the genera (Schlumpberger and Badano 2005; Ortega-Baes et al. 2011).

In the Brazilian Chaco, *E. rhodotricha* produces many flowers but few fruits (data not published), a phenomenon also observed in other cacti species (Fleming et al. 2001; Piña et al. 2010; Gomes et al. 2013; Ortega-Baes and Gorostiague 2013). This fact is normally associated with low local abundance of

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pollinators, low visitation rates, and inefficient behavior of pollinators in transferring pollen, pollen limitation, inbreeding depression, and florivory (Fleming et al. 2001; Mandujano et al. 2013; Ortega-Baes and Gorostiague 2013; Gorostiague and Ortega-Baes 2015).

Florivory is the consumption of floral structures, commonly associated with several animal taxa (Johnson et al. 2015). Usually, invertebrate florivory causes little damage to flower tissues when compared with vertebrates, which often eliminate entire inflorescence or flowers (Fletcher et al. 2001; Riba-Hernandez and Stoner 2005). Florivores reduce the visual attractiveness of flowers, reduce the reward levels and negatively affect pollination, thereby compromising fruit set and reproductive success of plants (Krupnick et al. 1999; McCall and Irwin 2006). Florivores can act as selective forces reducing pollinator-mediated selection (Gómez 2003; Teixido et al. 2011; McCall et al. 2013). Selection on floral color by a pollinator may be countered by a florivore if both animals are attracted by the same colors (Strauss and Irwin 2004; McCall et al. 2013).

Florivory has already been reported for Cactaceae; however, the majority of records include mostly invertebrates (Piña et al. 2010; Martínez-Peralta and Mandujano 2011; Mandujano et al. 2013). In *Opuntia macrocentra*, florivory by lepidopteran larvae and inbreeding depression were the major factors decreasing fruit set (Mandujano et al. 2013). Similarly, severe attack of lepidopteran larvae reduced the fruit set in *Opuntia microdasys* (Piña et al. 2010), whereas high levels of florivory by Tenebrionid beetles limit *Ariocarpus fissuratus* reproduction (Martínez-Peralta and Mandujano 2011). However, in *Melocactus ernestii*, consumption of petals by lizards probably reduces flower attractiveness (Gomes et al. 2013), although it did not affect directly its reproductive success, and fruits were produced normally.

During the monitoring of the reproductive phenology of *E. rhodotricha* in the Brazilian Chaco, we observed that some individuals had damaged flowers, with petals, stamens, and pistils totally removed. We hypothesized that the recorded damage probably resulted from vertebrates' consumption, considering the signs left in the remaining floral parts and large flower size (Gomes and Araujo 2015). Therefore, to address this hypothesis, we monitored flowers using camera traps to record and identify the florivores

consuming the flowers. In order to evaluate the effects of florivory on the reproductive success of *E. rhodotricha*, we also compared the fruit set between damaged and undamaged flowers in a natural population of *E. rhodotricha*.

Methods

We collected data at São Fernando Ranch (21°37'51.0" S, 57°49'29.4" W), located in the municipality of Porto Murinho, Mato Grosso do Sul, Brazil. The area is a Chaco remnant, characterized by the presence of a discontinuous canopy, containing thorny and microphyllous species (UNESCO 1973). *Echinopsis rhodotricha* is distributed in northern Argentina, Paraguay, Uruguay, and Brazil (Eggl 2002). In Brazil, it is restricted to Chaco vegetation (BFG—The Brazil Flora Group 2015). Flowering and fruiting period occur between October and March. Flowers present 15 cm in length, with an average of 600 stamens and 2500 ovules, offering pollen and nectar as floral rewards (Gomes and Araujo 2015).

We carried out monthly phenological monitoring from October 2014 to March 2015 and then from October 2015 to March 2016. We concentrated the sampling of florivory in reproductive individuals in the months of flowering peak (January 2015 and January 2016). Buds and flowers produced by each individual were counted, and the flowers were classified as follows: undamaged (intact flowers), partially damaged (reproductive organs still present), and damaged (reproductive organs totally consumed). Florivory was scored shortly before the end of anthesis, usually by the end of the morning. The percentage of consumed flowers was calculated per plant to estimate the intensity of florivory. Consumed flowers were bagged ($N = 39$), and after 15 days, we evaluated the fruit production in order to assess the effects of florivory on the reproductive success. In order to compare the effects of florivory on fruit set against natural conditions, we tagged 18 intact flowers distributed in six different individuals to follow fruit production. These flowers were exposed to natural pollinators, and after 15 days we evaluated the fruit set.

Observations on the activity of florivores were carried out on three nonconsecutive sessions, comprising the whole period of anthesis (8:00 PM–11:00 AM), in January 2016. For monitoring the visits of florivores,

we used two camera traps (Reconyx Hyperfire HC500), totaling 96 h of sampling time. In each sample session, cameras were installed in front of six individuals of *E. rhodotricha*. Our records were then sent to specialists to confirm species identification.

Results

We recorded 60 flowers with florivory signs during the 2 years of study. In January 2015, among the 59 flowers produced, 21 (36 %) were totally consumed,

Table 1 Number of monitored individuals, flowers, and percentage of florivory on *Echinopsis rhodotricha* in the Brazilian Chaco

Years sampled	2015	2016
Total number of individuals	30	52
Total number of flowers	59	103
Number of undamaged flowers	38 (64 %)	64 (62 %)
Number of damaged flowers	21 (36 %)	39 (38 %)

whereas in January 2016, 39 (38 %) of the 103 produced flowers were eaten (Table 1). The mean number of open flowers per cactus was 1.95 ± 1.85 (ranging 1–9), and in the same individual, we reported both intact and consumed flowers. The flowers opened at 8:00 PM, when pollen is available and stigma is receptive, and remains functional until the next morning. Florivores were recorded exclusively at night, between 10:00 PM and 5:00 AM, and no florivory was recorded between the early morning and the end of anthesis (*ca.* 11:00 AM).

Camera traps recorded the red brocket deer *Mazama americana* Erxleben 1777 and the white-lipped peccary *Pecari tajacu* Linnaeus 1758 feeding on flowers in multiple occasions (Fig. 1). In most events, both animals consumed the whole flowers, including calyx, corolla, and the reproductive organs (Fig. 1). However, we also recorded four partially consumed flowers, in which stigma remained intact and still attached. Although some of the monitored individuals also presented buds and immature fruits, these structures were not consumed.

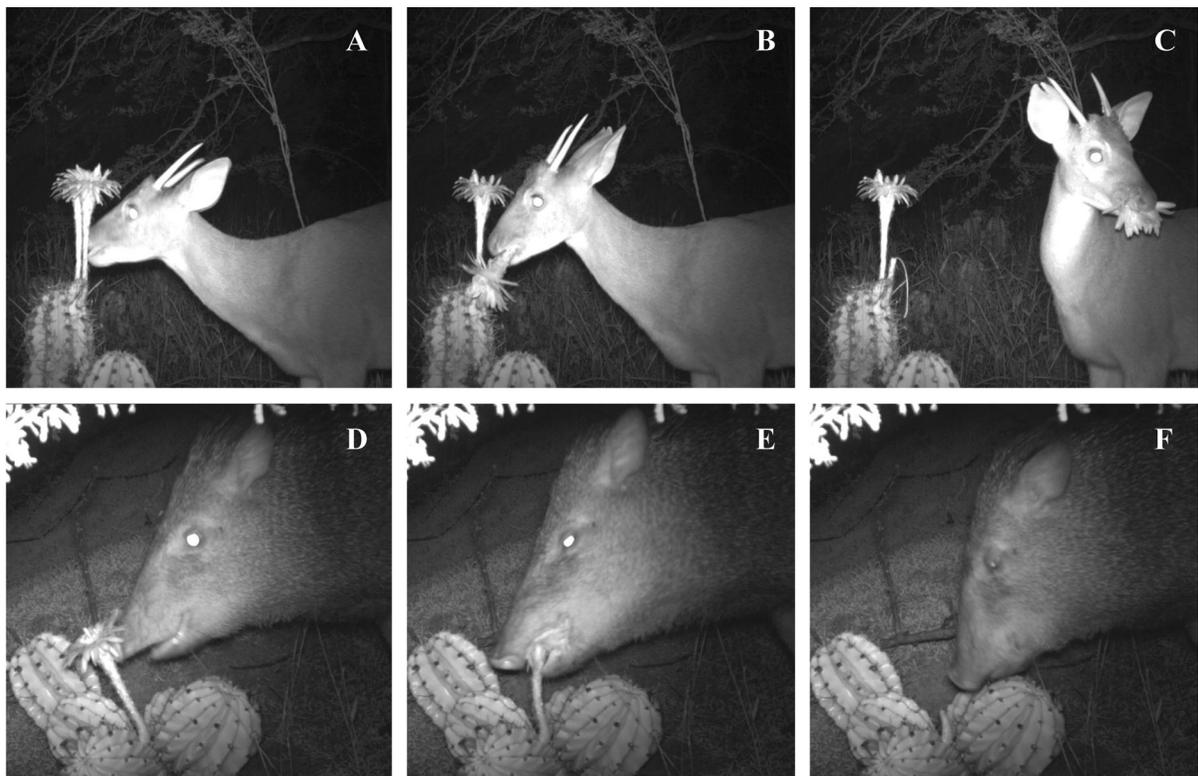


Fig. 1 Vertebrate florivory by *Mazama americana* (a–c) and *Pecari tajacu* (d–f) on *Echinopsis rhodotricha* in the Brazilian Chaco

It was not possible to say exactly what proportion of monitored flowers was destroyed by each species of florivores as they consumed the flower in a similar way. Both *M. americana* and *P. tajacu* bite the flowers at the base of the floral tube. Although the ovaries remain intact in the flower base, protected by thorns, no fruits developed in these damaged flowers ($N = 39$ flowers; fruit set = 0). Likewise, no fruits were produced in the partially damaged flowers ($N = 4$ flowers; fruit set = 0). Fruit set in natural conditions was 33 % ($N = 18$ flowers; fruit set = 6).

Discussion

Florivory on *E. rhodotricha* was promoted by vertebrates, based on the signs left on consumed flowers, as well as fleshy and large flowers located close to the ground, which make them attractive to florivores, which easily identify and access this resource. Deer and peccary consumed the whole flowers in the majority of the records, reducing *E. rhodotricha* fitness by destroying the reproductive parts of the flowers. Also, while consuming flowers, florivores reduce attractiveness and rewards for pollinators, discouraging pollinator visitation (McCall and Irwin 2006), which can decrease the fruit set.

Large and long-lasting flowers, as recorded for *E. rhodotricha*, have been related to higher pollinator attraction (Arista and Ortiz 2007), resulting in an increase in plant reproductive success, because they involve a greater pollen removal and higher amount of pollen deposition (Ashman and Schoen 1996). Nevertheless, florivores could also benefit from this great attractiveness, easily locating and attacking these flowers. In *Cistus ladanifer*, both large and long-lasting flowers undergo higher incidence of florivory, reducing fruit and seed set as a consequence of flower damage (Teixido et al. 2011). Thus, a trade-off involving flower size and longevity could be expected in order to enhance pollinator attraction and reduce florivory. Trade-offs between mutualistic and antagonistic organisms can occur when florivores have a preference pattern similar to that of pollinators (Ehrlén 1997; Galen and Cuba 2001; Lara and Ornelas 2001).

Extended anthesis favors participation of diurnal and nocturnal pollinators (Walter 2010; Ortega-Baes et al. 2011; Alonso-Pedano and Ortega-Baes 2012), being a strategy that ensures sexual reproduction in the

presence of unpredictable pollinators (Fleming et al. 2001). Extended anthesis in *E. rhodotricha* could offset negative effects caused by florivores since all records of florivory occurred in the night period. In this way, flowers not damaged at night still have chances of being pollinated by diurnal visitors. Studies on different species of *Echinopsis* report that nocturnal and diurnal floral visitors are important for reproductive assurance in these plants (Walter 2010; Ortega-Baes et al. 2011; Alonso-Pedano and Ortega-Baes 2012). However, it is still necessary to evaluate the effectiveness of both groups on pollination of *E. rhodotricha*.

In natural conditions, *E. rhodotricha* presents low fruit productivity (33 %), and this could be associated with frequent activity of florivores. We recorded a high proportion of damaged flowers in the studied population, and this percentage was similar in both years of study. Florivory caused by vertebrates on *E. rhodotricha* flowers meant a substantial decrease in reproductive success, as approximately 36 % and 38 % of their costly reproductive structures were destroyed in 2015 and 2016, respectively. However, other factors such as low frequency of visits and ineffective pollinators can also attend for these results.

In *M. ernestii*, florivory by lizards reduced flower attractiveness but did not affect directly its reproductive success, and the fruits were produced normally (Gomes et al. 2013). *Melocactus* spp. have flowers that develop inside the cephalium, a modified portion of the stem, containing bristles and wool, which serves to protect the developing flower buds and unripe fruits (Machado 2009). In *Echinopsis*, reproductive structures of flowers are completely exposed and only the ovary is partially protected by thorns, which provide some mechanical defense. Therefore, these differences in morphological traits between *Melocactus* and *Echinopsis* could explain differences regarding fruit production in damaged flowers in both species. Moreover, *M. ernestii* produces fruits with spontaneous self-pollination (Gomes et al. 2013), unlike *Echinopsis* spp.

Even partially damaged flowers were less attractive to pollinators, having fruit set negatively affected. However, the number of flowers in this treatment was low ($N = 4$), since partially damaged flowers were much less common in the studied population. This lower frequency of partially damaged flowers can be explained by the fact that vertebrate floral browsing is

often severe and eliminates entire inflorescences and flowers (Herrera 2000; Mellink and Riojas-López 2002).

The number of flowers that open simultaneously on an individual plant can affect the number and composition of pollen grains that are deposited on stigma (Ruane et al. 2014), also increasing geitonogamy (Barrett et al. 1994; Harder and Barrett 1995, 1996). In self-incompatible species, geitonogamy can reduce reproductive success, as self-pollen causes stigma clogging interfering with outcross pollen germination or tube growth (Waser and Price 1991; Sage et al. 2006). In *Echinopsis thelegona*, the reduced sexual reproduction is probably associated with ineffective foraging behaviors of pollinators, which deposit self-pollen on the flowers, thus negatively affecting fruit and seed production (Ortega-Baes and Gorostiague 2013). In this sense, consumption of only part of the flowers present in a given individual by florivores could be advantageous in promoting cross pollination, because pollinators are forced to move between different individuals in order to achieve their nutrient requirements. It could be even more important for self-incompatible species, such as several *Echinopsis*, that require pollinators for fruit and seed set.

Herbivory on leaves, fruits, and seeds by *M. americana* and *P. tajacu* is well documented in the literature (Altrichter et al. 2000; López et al. 2006; Mellink and Riojas-López 2002). However, records quantifying florivory effects are registered only for deers, mostly in the Northern Hemisphere, with detrimental effects on abundance and reproductive success of many plant species (Herrera 2000; Fletcher et al. 2001; Knight 2004; Geddes and Mopper 2006). Vertebrates probably consume flowers in the search of additional resources for supplying their diets, as nectar and proteins (Mellink and Riojas-López 2002), being the latter very abundant in *E. rhodotricha*, given its great number of anthers (Gomes and Araujo 2015).

Mellink and Riojas-López (2002) present an overview of consumption of different cacti species of the genus *Opuntia* by wild vertebrates in North America and Galápagos Islands, including reptiles, birds, and mammals. Among the mammals, *P. tajacu* and deer species *Odocoileus hemionus* Rafinesque, 1817 and *Odocoileus virginianus* Zimmermann, 1780, are reported consuming different parts of these plant species. Based on fecal analysis, those authors highlighted that pads and fruits are the parts most often

reported as consumed. However, in that review, there is a report about consumption of petals by *P. tajacu*, but no effect was evaluated.

Prado (2013) presents a list of plant species, detailing different structures consumed by five neotropical ungulates. *Mazama americana* and *P. tajacu* are among the ungulates included in that review. Consumption of fruits, seeds, pads, and roots of cactus species is recorded only for *P. tajacu*, but no records of flower consumption is reported. Our results add information of both *P. tajacu* and *M. americana* as consumers of cactus flowers and quantify the direct impacts caused by these animals on the reproductive success of *E. rhodotricha*.

We highlight that these records expand our knowledge about florivory for Cactaceae which included mostly invertebrates (Piña et al. 2010; Martínez-Peralta and Mandujano 2011; Mandujano et al. 2013). Vertebrate florivory, in reducing fruit set, could have negative impacts on the reproductive success of *E. rhodotricha*. However, it could enhance cross pollination by forcing pollinators to visit flowers of different individuals. We suggest that further studies evaluating the balance between these two effects, combining observations of pollination and florivory, should be addressed in order to better understand the impacts of these interactions on the reproductive performance of this species.

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