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Original article

Factors affecting seed predation of *Eriotheca gracilipes* (Bombacaceae) by parakeets in a cerrado fragment

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ABSTRACT

Psittacids are important pre-dispersal seed predators. However, little is known about the parameters that may determine seed predation rates by these birds, such as plants' characteristics and microhabitat. *Eriotheca gracilipes* (Bombacaceae) is a semi-deciduous tree widely distributed in the Brazilian cerrado. The fruits are dehiscent pods and the seeds are wind-dispersed. Some individuals lose their leaves during the fruiting season, getting very conspicuous. Here we tested the hypothesis that the absence of leaves in *E. gracilipes* during the fruiting season may increase pre-dispersal seed predation by psittacids. We also tested the hypotheses that (1) seed predation intensity increases with increasing plant size and (2) number of fruits, (3) seed predation decreases with the increasing number of conspecific plants in a range of 15 m, and (4) seed predation intensity is lower in plants with higher vegetation cover over their crowns. The small parakeet *Brotogeris versicolurus* was the only species observed preying upon the seeds of *E. gracilipes*. The percentage of fruits damaged by the parakeets ranged from 0 to 100% ($66.98 \pm 43.11\%$, $n = 72$) among the different plants. Our data give weak support to the hypothesis that the absence of leaves may facilitate plants and/or fruits detection by the parakeets. However, seed predation intensity was significantly affected by crop size. The hypothesis that conspecific fruiting plants surrounding the studied individuals may reduce predation rate was not supported. Nevertheless, trees without higher vegetation cover over their crowns were significantly affected by increased seed predation. This suggests that seed predation by parakeets can be a potential selective factor influencing fruit crop sizes in *E. gracilipes*.

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1. Introduction

Seed predation is one of the major ecological and evolutionary forces affecting individual plants, populations and

communities all over the world (Schupp, 1988; Hulme, 1998; Hulme and Benkman, 2002). Some seeds are accessible to predators while still in the plants, i.e., the pre-dispersal stage, representing a concentrated source of protein and

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minerals that can be exploited by a wide range of organisms (Janzen, 1971; Fenner et al., 2002). The percentage of seed loss in this phase varies widely between species and populations, but is frequently above 90% (Mattson, 1980; Sheppard et al., 1994; Turner et al., 1996).

It has been demonstrated that pre-dispersal seed predation intensity can be correlated to several plant characteristics, such as floral display (Brody and Mitchell, 1997; Hemborg and Després, 1999; Fenner et al., 2002), flowering phenology (Biere and Honders, 1996; Ollerton and Lack, 1998), plant size and number of fruits (Brody, 1992; Greig, 1993; Sperens, 1997), representing a selective factor that can modify plant traits (Leimu et al., 2002). Moreover, it can be influenced by habitat parameters, such as vegetation density, canopy closure and distance from other conspecific plants (Molau et al., 1989; Brody, 1992; Sheppard et al., 1994; Notman et al., 1996; Leimu et al., 2002).

Most researches on pre-dispersal seed predation have focused on specialized insects (Brody, 1992; Greig, 1993; Sheppard et al., 1994; Forget et al., 1999; Fenner et al., 2002; Leimu et al., 2002), and very few data are available about the interactions between plants and vertebrate pre-dispersal seed predators (Downhower and Racine, 1976; Benkman et al., 2001, 2003; Francisco et al., 2002; Parchman and Benkman, 2002; Siepielski and Benkman, 2004). Psittacids (parrots, parakeets and macaws) have been pointed out as important pre-dispersal seed predators in the Neotropics (Janzen, 1972, 1981; Higgins, 1979; Howe, 1980; Galetti and Rodrigues, 1992; Coates-Estrada et al., 1993; Francisco et al., 2002). In relatively undisturbed areas the intensity of seed predation by *Amazona farinosa* and *A. autumnalis* on *Tetragastris panamensis* (Burseraceae) was estimated to be 6.4% of the seed crop (Howe, 1980). *Pionus menstruus* consumed 8% of the seed crop of *Albizia* sp. (Leguminosae) (Galetti and Rodrigues, 1992). Janzen (1972) found that *Amazona ochrocephala* (and the squirrels *Sciurus variegatoides*) were responsible for 30% of the seed mortality of *Sterculia apetala* (Sterculiaceae), and the smaller parrots *Amazona albifrons*, *Brotogeris jugularis* and *Aratinga canicularis* were responsible for further 10%. Trivedi et al. (2004) reported that 10% of the crop of *Bertholletia excelsa* (Lecythidaceae) was lost to *Ara macao*, *A. ararauna* and *A. chloroptera*. In disturbed areas *Pionus maximiliani* destroyed approximately 20% of the fruit crop of *Inga* spp. (Leguminosae) (Galetti and Rodrigues, 1992) and *Brotogeris versicolurus* preyed upon 100% of the seeds of *Pseudobombax grandiflorum* (Bombacaceae) (Francisco et al., 2002). Despite the potential impact caused by the psittacids on plant recruitment, little is known about the parameters that may determine seed predation rates by these birds, such as plants' characteristics and microhabitat.

The Bombacaceae plants are common items in the diets of most Neotropical psittacids (Roth, 1984; Galetti, 1993, 1997; Barros, 1995; Martuscelli, 1995; Paranhos, 1995; Pizo et al., 1995). *Eriotheca gracilipes* (Bombacaceae) is a semi-deciduous tree distributed in the Brazilian cerrado in central and south-eastern Brazil. The fruits are dehiscent pods and the seeds, covered with cotton-like fibers, are wind-dispersed (Lorenzi, 1998). Like many other Bombacaceae species (specially those belonging to the genera *Chorisia*, *Pseudobombax* and *Eriotheca*), some individuals of *E. gracilipes* lose their leaves during the fruiting season (M.R. Francisco, personal observations).

During this phenophase these plants get very conspicuous among the species that maintain their leaves, creating a display that may be potentially attractive to visual predators. In this paper, we tested the hypothesis that the absence of leaves in *E. gracilipes* during the fruiting season may increase pre-dispersal seed predation by psittacids. We also tested the hypotheses that (1) seed predation intensity increases with increasing plant size and (2) number of fruits, (3) seed predation decreases with the increasing number of conspecific plants in a range of 15 m, and (4) seed predation intensity is lower in plants with higher vegetation cover over their crowns.

2. Materials and methods

Cerrado is the predominant vegetation of Central Brazil. Although it resembles a savanna in the broadest sense, its structural form ranges from open grasslands to forested areas, such as the gallery forests that grow alongside the water-courses (Eiten, 1972, 1984; Cavalcanti, 1988). This study was carried out in a 124.68 ha non-forested cerrado fragment localized within the non-urbanized area of the campus of São Carlos Federal University, in Southeastern Brazil (21°58' S, 47°52' W).

A total of 72 *Eriotheca* trees were individually marked and the number of fruits, as well as the presence or absence of leaves, were recorded weekly. Predation was considered when the fruits presented the walls damaged to the point that the seeds were exposed, and fruits that escaped predation were those that opened without being preyed upon. The observations in a target plant finished when all of the fruits were destroyed or opened naturally. During the visits, before approaching the plants, they were observed by distance (at least 30 m) using 8 × 40 binoculars in order to account for the presence of avian pre-dispersal seed predators and their behaviors. Plant heights and crown diameters were obtained using tape measurement. Individuals were considered to have higher vegetation cover over their crowns (overshadowed individuals) if they were totally covered by the crowns of taller trees of other species. Individuals without higher vegetation cover were those which crowns were visually totally exposed for a bird flying over it. Plants with intermediary cover status were not considered in the analyses.

To test if there is any effect of crop size on fruit destruction ("density-dependence effects"), the data were fitted to the power-law function (see Harms et al., 2000). We used the log-log least square regression to fit the power-law, according to Harms et al. (2000):

$$\log(y + 1) = a + b \log(x + 1)$$

where x is the initial number of fruits at the tree and y is the number of fruits preyed upon by parakeets at the end of the observation, and b is the slope representing the rate in which the number of fruits predated increases in relation to crop size. If $b = 1$, fruit predation is density independent (i.e. proportional). If $b > 1$, the proportion of predated fruits increases with crop size and if $b < 1$, the proportion of predated fruits decreases with crop size. The slope was tested with a paired t-test to compare the observed number of surviving seeds

and the expected if $b = 1$ (Harms et al., 2000). The expected values were calculated by substituting b for 1. We used the residuals of the above log-log regression to investigate the effects of other plant features on seed predation after controlling for crop size.

3. Results

The fruiting season (ripening-dispersal period) occurred from September to October 2002. The number of fruits per plant varied from 1 to 96 (14.62 ± 16.66 , $n = 72$) (mean \pm SD). The fruits were 56.9 ± 11.40 mm in length, 35.7 ± 4.53 mm in width and presented from 4 to 27 seeds (10.91 ± 5.65) ($n = 23$). The seeds were 9.32 ± 0.58 mm in length and weighed 0.30 ± 0.05 g ($n = 30$). We also analyzed 30 fruits that were opened by the parakeets (*Brotogeris versicolurus*). The number of remaining seeds ranged from 0 to 24 (2.57 ± 4.90), and from the 77 seeds contained in these fruits 39 (50.65%) were decomposing, while in the fruits that escaped predation all of the seeds were undamaged ($n = 251$).

Plants were 0.98 to 10 m high (3.62 ± 1.77) and the crown diameter varied from 0.3 to 8.2 m (2.08 ± 1.21). The plant sizes (height multiplied by the crown diameter) ranged from 0.29 to 82 m (9.05 ± 11.04) ($n = 72$). Seventeen plants (23.61%) did not present leaves ($n = 72$), and their status did not change until the end of the fructification period. The same number of plants had their crowns covered by higher vegetation. The number of conspecific plants producing fruits in the range of 15 m surrounding the studied individuals varied from 0 to 25 (9.57 ± 6.40 , $n = 72$). Although several psittacid species occur in our study area (*Amazona aestiva*, *Pionus maximiliani*, *Aratinga leucophthalmus*, *Aratinga aurea* and *Forpus xanthopterigius*) only the small parakeet *Brotogeris versicolurus* was observed preying upon the seeds of *E. gracilipes*. They opened the fruits with their beaks, perching upside-down, and tearing away pieces of the wall until expose the seeds for consumption. One to three individuals were observed feeding on the plants (2.17 ± 0.58 , $n = 12$).

From the 72 plants analyzed, 54 (75%) presented at least one fruit destroyed by the end of the fruiting season, and the percentage of fruits damaged by the parakeets ranged from 0% to 100% ($66.98 \pm 43.11\%$) among the different individuals. Counting was possible because like in other Bombacaceae species (see Francisco et al., 2002) the walls of the damaged fruits remained attached to the plants, even when their entire contents are consumed. The birds probably adopted the strategy of consuming the seeds without removing the fruits because they would be too big to be handled by small birds. One potential bias of estimating the percentage of seeds preyed upon by psittacids is that, unlike most insects, birds consume the entire seeds. Then, censusing the original number of seeds contained in each fruit is intractable when fruits are found after being eaten. However, if birds consume all of the seeds of each destroyed fruit, the percentage of damaged fruits would be representative of the percentage of seed predation. Although it did not occur for all of the fruits that were destroyed, most of the remaining seeds were decomposing, and those that were not decomposing would be probably unviable because fruits were damaged while still unripe. Since

the parakeets were also indirectly responsible for this further loss, we assumed 100% of seed predation for all of the fruits damaged by the parakeets, and we considered that the percentage of destroyed fruits would be representative of the percentage of seed loss.

The observed slope of the log-log regression between the initial fruit crop size and the number of fruits destroyed by the parakeets was $b = 1.21$, being significantly different from $b = 0$ ($F = 120.02$, $r^2 = 0.63$, $n = 72$, $P < 0.0001$) and significantly above $b = 1$ ($t = 5.07$, $n = 72$, $P < 0.001$, Fig. 1), indicating that the intensity of seed predation increases with crop size.

The proportion of plants containing leaves that suffered any predation by *B. versicolurus* was similar (70.9%) to those without leaves (88.3%, $P = 0.13$, randomization test, 10,000 randomizations). We also investigated if the presence of leaves affected the amount of seed predation. The average percentages of fruit predation in plants with, and without leaves, are presented in Fig. 2. As we showed above, seed predation increases with crop size in a non-linear way. Thus, to control for the effects of variation in crop size, we used the residual fruit destruction of the previous log-log analysis to test if the quantity of seed predation is related to presence of leaves, independently of the potential variation in attractiveness due to variable fruit crop. We calculated the average residual fruit predation for both trees with leaves (-0.77 ± 0.85) and those without leaves (0.22 ± 0.63), and we tested the observed difference between the means ($D = -0.29$) using randomization tests (Manly, 1997). Difference was in the predicted direction, but was not significant ($D_{\text{rand}} = 0.002$, $P = 0.09$, 10,000 randomizations).

The trees without higher vegetation cover over their crowns were affected by increased seed predation (Fig. 2). The proportion of plants with any predation was significantly lower for those with overshadowed crowns (52.9%) than for trees with their crowns exposed (81.8%, $P = 0.02$, randomization test, 10,000 randomizations). We also calculated the average residual fruit predation for both trees in which crowns were covered by higher vegetation (-0.49 ± 0.85) and those

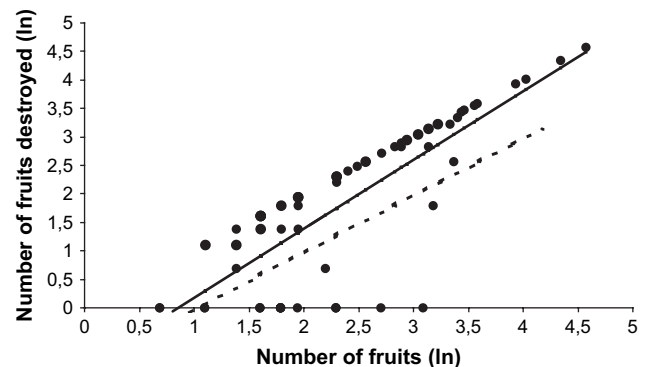


Fig. 1 – Relationship between number of fruits and number of fruits of *E. gracilipes* plants destroyed by parakeets. Continuous line describes the log-log regression indicating positive density-dependence (see text for further details). Dashed line describes the expected relationship in the absence of density-dependence.

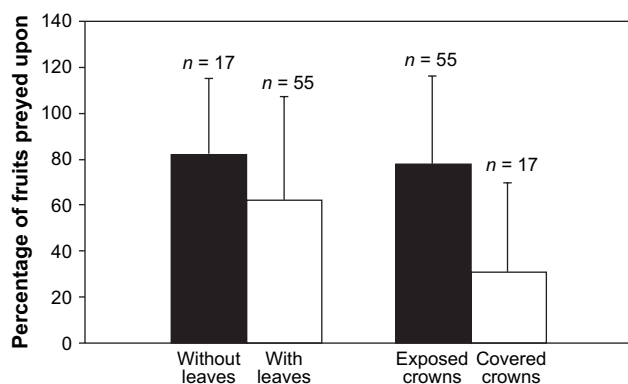


Fig. 2 – Comparative average percentages of fruit predation in plants with, and without leaves, as well as in plants with overshadowed and exposed crowns. Vertical bars represent SD.

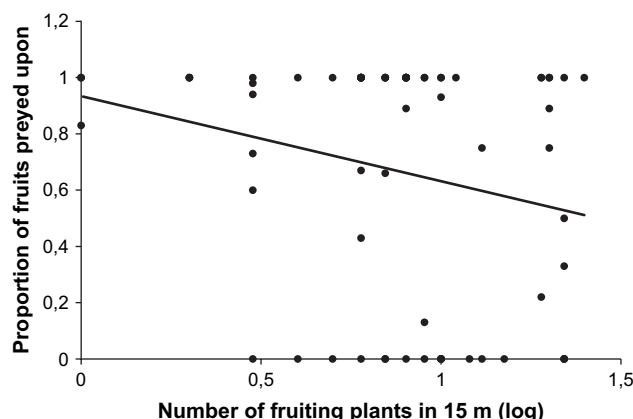


Fig. 4 – Linear regression between log-transformed numbers of *E. gracilipes* producing fruits in a range of 15 m versus proportion of fruits preyed upon.

in which crowns are not covered (0.15 ± 0.74). There is a significant trend for fruit predation to be higher in plants with exposed crowns ($D = -0.645$, $D_{\text{rand}} = -0.001$, $P = 0.003$, 10,000 randomizations).

After controlling for crop size effects, residual fruit destruction did not increase with plant size (slope = 0.01, $P = 0.085$, 10,000 randomizations), suggesting that larger plants are not likely to experience more seed predation, independently of the number of fruits produced (Fig. 3). In fact, plant size and crop size are not related (slope = 0.10, $P = 0.21$, 10,000 randomizations). The proportion of predation did not decrease significantly with the increasing number of conspecific fruiting plants in the range of 15 m (slope = -0.009 , $P = 0.27$, 10,000 randomizations) (Fig. 4).

4. Discussion

The high average percentage of damaged fruits presented here is characteristic of fragmented areas. An overwhelming destruction of cerrado vegetation occurred in central Brazil in the last decades, with the incentives of the government to

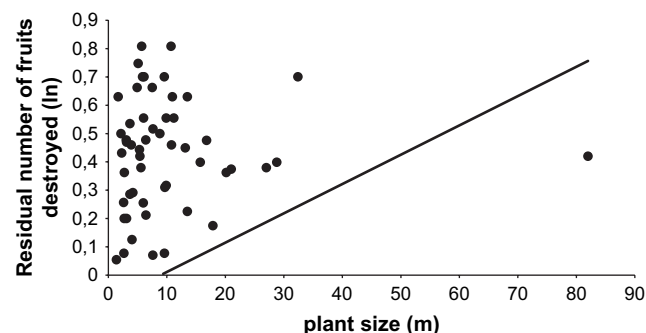


Fig. 3 – Linear regression of the relationship between plant size of *E. gracilipes* and fruit destruction by parakeets after controlling for differences in number of fruits (residual fruit production).

expand the agricultural frontiers to the flat areas of the cerrado domain. Today, locations that preserve the integrity of the natural conditions are increasingly rare, since only 20% of the primary vegetation remains (Myers et al., 2000), and even the largest conservation units are surrounded by agricultural areas. The higher seed predation rates by psittacids found in disturbed locations probably occur because these birds, especially some small species (such as *Aratinga* or *Broto-goris*), are positively affected by deforestation, increasing their densities in agricultural areas (Galetti, 1993; Francisco et al., 2002). On the other hand, the larger parrots and macaws, which need large tracts of undisturbed forests to survive, are vanishing (Collar and Juniper, 1992; Sick, 1997). Here we assumed that the potentially increased predation rate caused by habitat fragmentation is not limiting the effects of plant traits on differential seed predation.

Our data give weak support to the hypothesis that the absence of leaves may facilitate plants and/or fruits detection by the parakeets. It seems that, independently of other tree traits, keeping the leaves does not reduce pre-dispersal seed predation by the parakeets in the cerrado. One possible explanation is that the birds themselves would be more exposed to predators on plants without leaves, restricting their visits to these plants, even if they are easier to detect. Since in forested ecosystems target plants could be less visible than in cerrado areas, further analyses should be performed with the Bombacaceae species that are distributed in rainforests, in order to better elucidate the relationship between seed predation by psittacids and the absence of leaves during the fruiting season.

Seed predation intensity was significantly affected by crop size. Larger crop sizes of *Eriotheca gracilipes* lost a higher proportion of their fruits as a result of psittacid damage. Although an inverse relationship has been found between fecundity and the proportion of seeds lost to predation, both within (Molau et al., 1989; Brody, 1992; Sperens, 1997; Leimu et al., 2002; Trivedi et al., 2004) and between species (Janzen, 1969; Greig, 1993), in other plants pre-dispersal seed predators were demonstrated to represent a selective pressure constraining crop

size (Molau et al., 1989). These apparently controversial results seem to be related to the different plant reproductive systems, habitat characteristics (Forget et al., 1999; Greig, 1993; Leimu et al., 2002), as well as to wide predator strategies (i.e., generalist vs. specialist seed predators). Here, we propose two possible, non-exclusive hypotheses to explain the positive crop size dependence observed in *E. gracilipes* pre-dispersal seed predation by parakeets. First, the birds should stay longer on plants presenting a higher nutritional reward. Second, large crop sizes may be more conspicuous, facilitating their visual detection. In both cases, the relatively small fruit crop sizes would not be satiating the small flocks of the parakeets, resulting in a large fraction of the fruits preyed upon. The birds caused an additional negative impact by causing increased seed loss to pathogens for the seeds surviving in partially-consumed fruits.

Although distance from other conspecific plants and canopy closure are not inheritable traits, they can have ecologically important significances, like determining the mechanisms by which predators locate the plants (Brody, 1992). Canopy closure has been previously demonstrated to affect flowers and seed production, as well as pre-dispersal seed predation intensity (Leimu et al., 2002). Our significant results suggest that it may weaken the selective pressure imposed by the predators on genetically inherited traits of *E. gracilipes*, such as fruit production, since it makes the predation intensity variable in complex landscapes (see also Leimu et al., 2002).

Plant aggregation is also predicted to reduce the proportional seed loss to predators because of the higher local seed densities and the potential satiation effects (Molau et al., 1989; Forget et al., 1999). However, the absence of correlation between the number of conspecific fruiting plants in the scale we analyzed and the percentage of predation suggest that like in many other studies (Brody, 1992; Sheppard et al., 1994; Forget et al., 1999) this hypothesis was not supported. On the other hand, the resource concentration hypothesis (Root, 1973) predicts that herbivores are more likely to find hosts in dense stands and predators should concentrate their activities in areas where foraging success is expected (Schupp, 1988).

A co-evolutionary relationship between psittacids and fruiting plants has been suggested for the palms (*Attalea phalerata*, *Acrocomia aculeata* and *Syagrus coronata*), which evolved very hard nuts, and the predatory macaws of the genus *Anodorhynchus* (*A. hyacinthinus* and *A. leari*), with their powerful beaks (Munn et al., 1990; Yamashita and Valle, 1993). However, effects of psittacids on the evolution of other plant traits have not been previously demonstrated. Seed predators potentially affect plant evolution whenever they depress seed production among plants in relation to variation in some heritable plant traits (Hulme and Benkman, 2002). The results presented here indicate that seed predation by *B. versicolor* can be a potential selective factor constraining fruit crop size in *E. gracilipes* by causing disproportionately high seed loss. This suggests that in the Neotropics, scientists should pay more attention in the role of avian seed predators as selective agents of plant reproductive traits, chiefly psittacids, that are diverse and abundant, and have been increasingly pointed out as a limiting factor to seed survival in many plant families.

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