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PRE-DISPERSAL SEED PREDATION BY BLUE-AND-YELLOW MACAW (*ARA ARARAUNA*, PSITTACIDAE), ON FRUIT CROPS OF THE PEQUI (*CARYOCAR BRASILIENSE*, CARYOCARIACEAE), IN THE BRAZILIAN CERRADO

José Ragusa-Netto

Departamento de Ciências Naturais, Campus Três Lagoas, Universidade Federal do
Mato Grosso do Sul, C.P. 210, 79620–080, Três Lagoas, MS, Brazil.
E-mail: jragusanetto@yahoo.com

Resumo. – Predação pré-dispersão de sementes de Pequi (*Caryocar brasiliense*, Caryocariaceae), pela Arara Canindé (*Ara ararauna*, Psittacidae) no cerrado brasileiro. – Avaliei durante dois episódios de frutificação os danos causados pela Arara Canindé (*Ara ararauna*), sobre as cargas de frutos de Pequi (*Caryocar brasiliense*), no cerrado brasileiro. Também, analisei as relações entre a taxa predação e tanto o tamanho da carga de frutos, quanto à distância do pequizeiro mais próximo predado. Os pequizeiros frutificaram massivamente no primeiro e moderadamente no segundo ano. No primeiro ano a taxa de predação sobre as cargas de frutos foi no mínimo duas vezes maior. As araras frequentemente se alimentaram em árvores mais produtivas e, raramente, visitaram aquelas com poucos frutos. Nesse sentido, a relação entre o tamanho das cargas de frutos e taxa de predação pelas araras foi significativa. Além disso, as araras causaram grandes danos às cargas de frutos de pequizeiros cujos vizinhos próximos também haviam sido predados. Presumivelmente, as araras procuravam por manchas de pequizeiros frutificando em lugar, apenas, de árvores com cargas maiores de frutos. As variações anuais da produção de frutos influenciaram substancialmente a dinâmica de predação, a qual mostrou ser dependente da densidade. Potencialmente, em razão das elevadas taxas de predação de sementes, as araras são importantes para manutenção da riqueza de espécies arbóreas no cerrado.

Abstract. – At a Brazilian savanna, I evaluated the proportional crop loss of Pequi (*Caryocar brasiliense*) to the Blue-and-Yellow Macaw (*Ara ararauna*) during two consecutive fruiting periods. Also, I analyzed the relationship between proportional crop loss to macaws and both fruit crop size and the distance from the nearest damaged conspecific. Trees fruited massively and subsequently moderately, so that crop damage was, at least, twice higher in the first fruiting episode. Moreover, macaws foraged more often on trees bearing larger fruit crop size, while seldom visiting less productive trees. As a result, the relationship between fruit crop size and proportional crop loss to macaws was significant. Also, macaws severely damaged the fruit crops of close neighboring trees. Hence, presumably, macaws searched for patches of fruiting *C. brasiliense* rather than for trees, only according to its fruit crop size. The annual variation of the fruiting pattern strongly influenced the dynamic of fruit loss caused by this macaw according to a density-dependent effect. Potentially, due to the increased damage on *C. brasiliense* fruit crops, macaws are important for the maintenance of tree species diversity in the Cerrado. *Accepted 11 May 2011.*

Key words: Brazil, Psittacidae, Cerrado, parrot, seed predation.

INTRODUCTION

Seed predation is among the major selective factors affecting plant demography patterns (Augspurger 1983, Schupp 1988a) and diversity in tropical areas (Janzen 1970, Dirzo & Miranda 1990). By damaging much of the fruit crops, seed predators may reduce the breeding success of abundant species, thus enhancing the recruiting chance of rare species (Janzen 1970).

Among seed predators, insects, mammals, and birds are well known by their impact on fruit production, since these groups include abundant species which rely extensively on seeds (Bodmer, 1991). With respect to vertebrates, mammals may be both pre- (Peres 1991) and post-dispersal seed predators (Peres *et al.* 1997) while birds are mainly pre-dispersal seed predators (Janzen 1981, Trivedi *et al.* 2004, Villaseñor-Sánchez *et al.* 2010). Among them, parrots are ubiquitous pre-dispersal seed predators, exhibiting large and mobile populations (Terborgh *et al.* 1990). They often damage around 10% of the fruit crops of Neotropical tree species (Janzen 1972, Howe 1980, Trivedi *et al.* 2004), although total crop loss may be higher for some tree species (Francisco *et al.* 2003, Haugaasen 2008, Villaseñor-Sanchez *et al.* 2010).

At the population or community level, fruit production is variable in time and space, which may influence the intensity of fruit use by seed predators, such as parrots (van Schaik *et al.* 1993). These mobile birds are well known by tracking the erratic pattern of fruit availability (Renton 2001, Moeremburgh & Levey 2003, Ragusa-Netto 2006, 2007, 2008); consequently, the proportional crop loss to them may vary from year to year according to fruit production (Schupp 1988a, 1990, Peres 1991). In fact, seed predation may be either positively or negatively density-dependent, and the pattern can be expected to vary with the relative abundance of seeds and their predators. When food resources are scarce for a particular seed predator population, predation is likely to be positively density-dependent. However, when the resources are abundant, seed predators become satiated and a negatively density-dependent response is expected to occur (Janzen 1970, Clark & Clark 1994, Manson *et al.* 1998). Studies focusing on crop damage by parrots have evaluated only one fruiting season. Thus, the relationship between the inter-annual variation in fruit production and crop loss to these birds remains unclear.

Macaws, the largest Neotropical parrots, are potential important seed predators (Trivedi *et al.* 2004, Ragusa-Netto 2006, Haugaasen 2008), which also may affect the structure and maintenance of forests (e.g., Terborgh 1992, Silman *et al.* 2003). Nevertheless, only two recent studies, performed during one fruiting period, assessed the intensity of pre-dispersal seed predation by these parrots on Lecythidaceae from Amazonia. In one case, macaws were observed to damage a moderate proportion (around 10%) of *Bertholletia excelsa* fruit crops (Trivedi *et al.* 2004), while in the other case they destroyed 99% of the fruits of *Couratari guianensis* trees (Haugaasen 2008).

The "Pequi" (*Caryocar brasiliense*, Caryocariaceae) is an abundant tree species in the Cerrado, which every year produces large globular fruits with one or two (exceptionally four) large and highly nutritive seeds (Ribeiro & Walter 1998, Silva *et al.* 2001). In cerrado areas, these seeds are among the major food resources of the Blue-and-Yellow Macaw (*Ara ararauna*; Ragusa-Netto unpubl.), a locally abundant seed predator in this habitat (del Hoyo *et al.* 1997, Sick 1997). Fruit crop size in Pequi trees varies between years, so that massive fruit production alternates with a moderate one (pers. observ.). These variations, as well as other factors, such as fruit crop size and distance between fruiting trees (Janzen 1970, Coates-Estrada *et al.* 1993), may have implications on the dynamics of pre-dispersal seed predation by parrots. In this study, I assessed the proportional crop loss of Pequi trees to macaws during two consecutive fruiting episodes. Also, I analyzed the relationships between proportional crop loss to macaws and both fruit crop size and the distance from the nearest damaged conspecific tree.

METHODS

Study area. This study was carried out in the Emas National Park (hereafter ENP), which is in the cerrado core region with an area of 133,000 ha, located in the Brazilian Central Plateau, southwestern Goiás State (17°19'–18°28'S and 52°39'–53°10'W, altitude 900–1100 m a.s.l.). Data were collected in the southern part of ENP (18°15'S and 52°53'W, altitude 900 m a.s.l.). The climate is markedly seasonal, with a wet (October–March) and a pronounced dry season (April–September). Annual rainfall is approximately 1500 mm (70% in the wet season), and the mean annual temperature lies around 24.6 °C.

The vegetation in the area is a mosaic of gallery forest, palm (*Mauritia flexuosa*) stands, and the dominant cerrado (93% of the area), which exhibit a gradient in vegetation cover from open fields to dense wood vegetation. However, 70% of the cerrado is a savanna-like habitat, in which trees (2–6 m in height) are interspersed with open grassy areas. During the dry season, mainly in the late phase during August and September, tree species shed their leaves. The most diverse plant families are Asteraceae, Fabaceae, Poaceae, and Myrtaceae (for details see Batalha & Martins 2002).

Field procedures. For sampling trees in order to evaluate fruit production and crop damage by macaws, I used six 4 km-long permanent access trails, in which I marked with aluminum numbered tags all individuals of *Caryocar brasiliense* located within a 3.0 m margin on either sides of the trails, and with a diameter at the base ≥ 10 cm. This random sample included 115 individuals (12–28 per trail), which I monitored for fruit production and crop damage from early November to early February (2004–2005 and 2005–2006). Every two weeks, I checked fruit crop size by counting fruits present in every crown and assessed crop damage by inspecting the ground under the trees to count both fallen damaged and undamaged fruits (the rigid endocarp lasts 4–6 months until complete decay). The inspection of a given tree finished when all of the fruits were destroyed or matured to the point they dropped the seeds. Then, I looked for the nearest damaged conspecific tree, whether or not marked, and measured the distance (m) between them (Coates-Estrada *et al.* 1993). Previous observations suggested macaws as the putative seed predators as they widely pierce the fruits leaving evident beak marks on the damaged fruits when accessing the seeds. However, from early November to early February I sampled by direct observations (monthly 6 h, from 06:00 to 09:00 h EST, along the permanent access trails mentioned above), during both fruiting periods, parrots feeding on Pequi trees. Whenever at least one parrot individual was detected feeding on Pequi fruits, I recorded the species, the number of individuals, and time and date. From 15 trees, I collected fruits with different numbers of seeds to measure both fruit and seed size.

Analyses. To compare the fruit production between fruiting periods I used the Wilcoxon match test, in which I took as a replicate the fruit crop size of each Pequi tree. To test the relationship between fruit crop size and the chance of crop damage by macaws I used a logistic regression, in which the individual fruit crop size was coded as 0 (undamaged) or 1 (damaged by macaws). To analyze the relationship between fruit crop size and either tree size (diameter at the base) or the proportional crop loss to macaws, as well as the relationship between this parameter and the distance to the nearest depredated conspecific tree, I used the non-parametric Spearman correlation. To best fit a linear model, the distances between depredated conspecifics were Log_{10} transformed.

RESULTS

Trees bore fruits from early November to the end of February. From the end of November to early December, ripening fruits exhibited a globular shape including one to exceptionally four seeds. Fruits with one seed had on average 5.6 ± 0.5 cm in diameter (n = 24), with two seeds 8.1 ± 0.8 cm (n = 10), with three 8.4 ± 0.6 cm (n = 10), and with four 9.3 ± 0.9 cm (n = 10). Seeds measured 3.9 ± 0.3 cm in length and 2.6 ± 0.2 cm in diameter (n = 30). In the first fruiting period, 30 trees bore no fruit, while in the second 40 remained fruitless (n = 115 in both fruiting periods). In 2004/2005, the fruiting trees produced from 1 to 159 fruits (22.2 ± 15.7 fruits, total = 1865 fruits), and in 2005/2006 they bore from 1 to 150 fruits (16.5 ± 12.3, total = 1238). Overall, trees produced more fruits in 2004/2005 than in 2005/2006 (Wilcoxon match test, $H = 2.6$, $P = 0.03$). Tree size (diameter at the base) ranged from 11– 62 cm (25.4 ± 10.7 cm). However, this parameter was weak, as a significant correlation with fruit crop size could be found in 2004/2005 ($rs = 0.37$, $P < 0.01$, n = 85 trees) but none in 2005/2006 ($rs = 0.19$, $P = 0.10$, n = 75).

In 2004/2005, macaws foraged on most of the fruiting Pequis (68%, n = 85 fruiting trees), while in 2005/2006 only 39% (n = 75) of them lost fruits to macaws. As a result, they depredated a total of 1000 (54%, n = 1865 fruits) and 301 fruits (24%, n = 1238 fruits), respectively. In 2004/2005, macaws damaged on average 42.6 ± 33.3% of fruit crop but only 18.0 ± 15.1% in 2005/2006. Furthermore, in 2004/2005 41% of trees lost more than 50% of fruit crop to macaws, while only 17% suffered the same in 2005/2006. Nevertheless, in both fruiting periods macaws foraged more often on those trees bearing larger fruit crops (logistic regression, $\chi^2 = 18.8$, $P < 0.0001$, for 2004/2005, and $\chi^2 = 78.3$, $P < 0.0001$, for 2005/2006, Fig. 1). Following this trend, the relationship between proportional crop loss and individual crop size was positive and significant ($rs = 0.65$, $P < 0.0001$, n = 85, 2004/2005; $rs = 0.52$, $P < 0.001$, n = 75, 2005/2006). Also, the proportional crop loss to macaws was inversely related to the distance to the nearest damaged conspecific tree ($rs = –0.83$, $P < 0.0001$, n = 58, and $rs = –0.68$, $P < 0.0001$, n = 29, 2004/2005, and 2005/2006, respectively; Fig. 2). During 40 h of observations, I detected 21 (2004/2005: 13 pairs, 2 trios, 4 quartets, and 2 groups of six), and 13 (2005/2006: 8 pairs, 2 trios, and 3 quartets) groups of the Blue-and-Yellow Macaw feeding on Pequi fruits. No other parrot species was observed to forage on these fruits.

DISCUSSION

Despite of a wide distribution and local abundance, at a variety of habitat types, the major food plants of the Blue-and-Yellow Macaw continues to be poorly known (Collar 1997, Sick 1997). Particularly in the Cerrado, few studies focused on feeding habits of the Blue-and-Yellow Macaw, which apparently often forages on tree species bearing fruits with large and nutritive seeds (Ragusa-Netto 2006, Tubellis 2009). At the ENP cerrado, the Blue-and-Yellow Macaw also exploits species (mainly *Pouteria torta*, *Anacardium humile*, *Geonoma geraensis*, and *Dimorphandra mollis*) with large and nutritive seeds, within which the Pequi seeds are among their major food resource (JRN unpubl.). These seeds include a very high content of lipids and proteins (Silva *et al.* 2001), similarly to the Brazil nut (*Bertholletia exelsa*) that is depredated by macaws (*Ara* spp.) in Amazonia (Trivedi *et al.* 2004). However, in the ENP I observed no

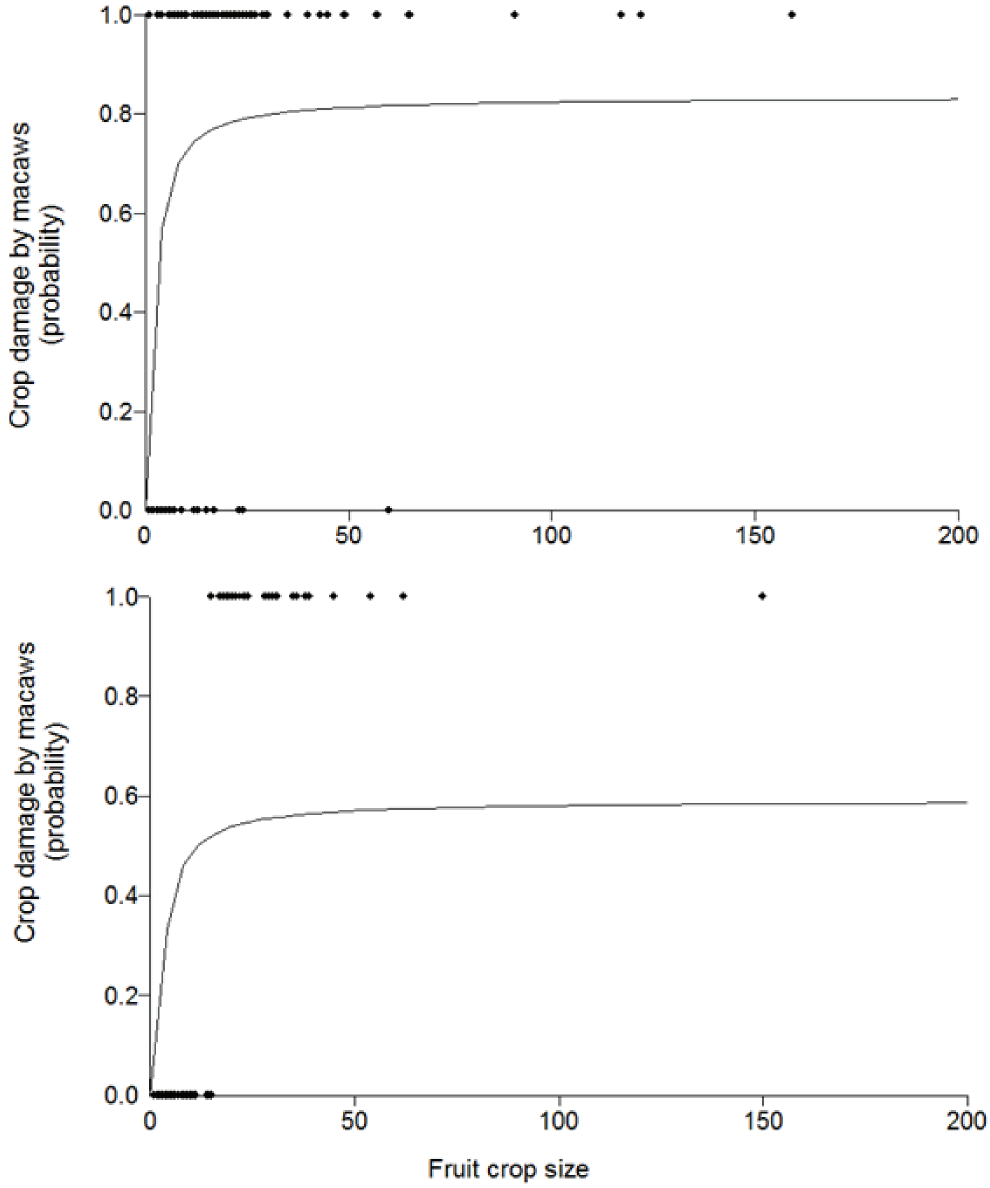

FIG. 1. Chance of crop damage by macaws as a function of *Caryocar brasiliense* fruit crop size (fruiting periods: 2004/2005, 2005/2006 below; Emas National Park, State of Goiás, Brazil).

other parrot species feeding on Pequi fruits either during this or another two-years study on parrot feeding ecology (JRN unpubl.). Apparently, the large and strong bills of macaws easily cut both the thick mesocarp and the rigid thorny endocarp. However, such a mechanical defense principally may prevent abundant and generalist parrot species (*Ama-*

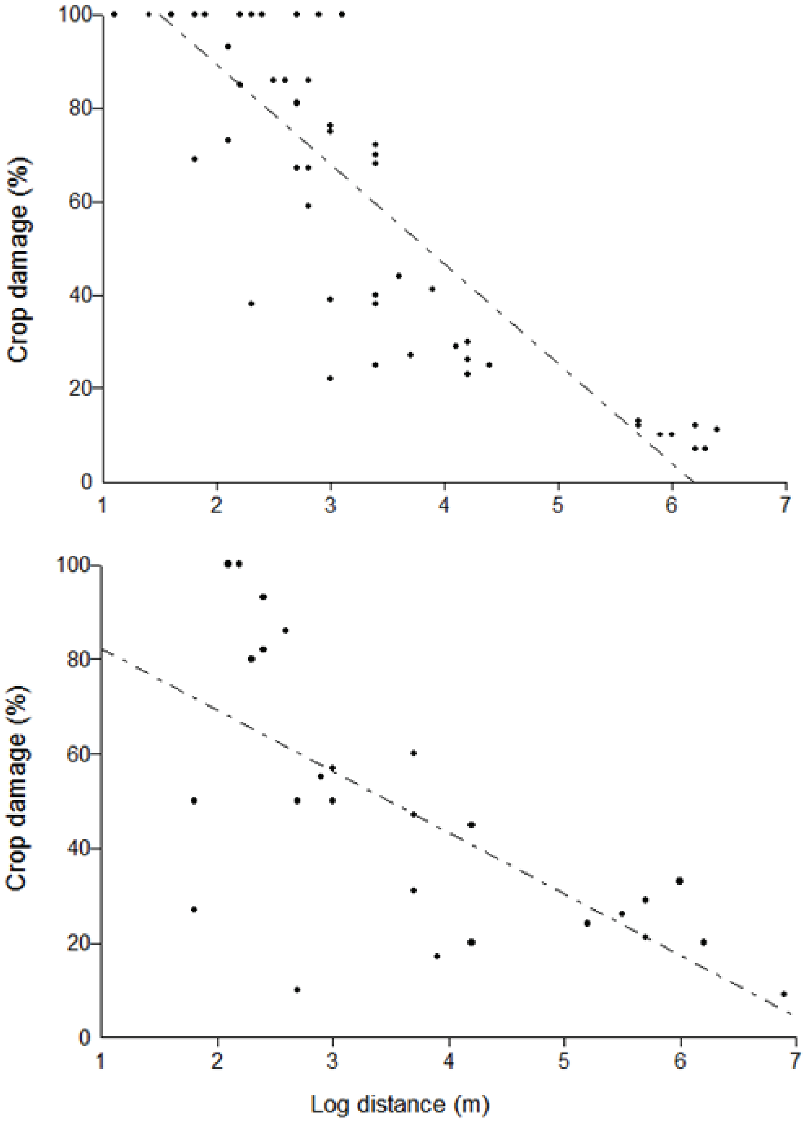

FIG. 2. *Caryocar brasiliense* crop loss (%) to macaws as a function of the distance from the nearest damaged conspecific tree, during the fruiting periods of 2004/2005, and 2005/2006 (below). The distances between damaged trees (Emas National Park, State of Goiás, Brazil) were Log_{10} transformed.

zona aestiva, *Diopsittaca nobilis*, and *Alipiopsitta xanthops*, pers. observ.) found in ENP to access the Pequi seeds. Presumably, for these smaller parrots the efforts required to pierce fruits to access seeds may be discouraging (Kiltie 1982, Peres 1991).

The evaluation of crop damage during two consecutive fruiting periods showed obvious differences related to fruit production. Macaws responded positively to the massive fruiting period, depredating an uncommon proportion of fruit crops (Janzen 1972, Howe 1980, Coates-Estrada *et al.* 1993, Trivedi *et al.* 2004). In fact, the intensity of use of food resources by mobile and flexible seed predators, such as parrots, likely reflects the spatial and temporal variation in resource availability (Moeremburgh & Levey 2003, Berg *et al.* 2007). Potential food items produced in moderate amounts may be rarely used or neglected at all. However, when items are available in large numbers they may represent a major source of food (Bonadie & Bacon 2000, Ragusa-Netto 2006, 2007, 2008). The influence of resource availability on the seed predation rate was also suggested by the propensity of Blue-and-Yellow Macaws to forage on the more productive trees, even when fruit production was moderate. Moreover, crop damage caused by them was positively related to fruit crop size, which complies with the prediction of enhanced predation rates according to seed density and a respective decrease as a function of the distance of seed source (Janzen 1970). In this respect, a density-dependent effect emerged in the relationship between both species, regardless of the amount of fruit production. Although the absence of this effect might be expected when fruit production was higher, it is important to note that from mid-December to February macaws relied almost exclusively on Pequi seeds due to the unavailability of other important fruits (JRN unpubl.). Moreover, in this period young macaws foraged together with their parents (pers. observ.). This potential increment of macaw population size presumably enhanced the demand for these nutritive seeds. However, only a long term study may clarify the absence of a satiation effect, because fruit production in both studied years might have been below the threshold of swamping macaws.

The intensity of crop damage caused by macaws was inversely related to the distance between depredated fruiting trees. The tendency for higher depredation rates on neighboring trees suggests that macaws searched for patches of fruiting Pequis rather than for trees only according to their fruit crop size. In fact, in seasonal forests and also in the seasonal cerrado, tree species are distributed in clumps (Hubbel 1979, Ribeiro & Walter 1998, pers. observ.). Moreover, within the ENP Blue-and-Yellow Macaws often established communal roosts at *Mauritia* stands when important plant species were fruiting (JRN unpubl.). Presumably, to compensate the efforts of daily trips to foraging areas, macaws performed feeding routes including patches of fruiting Pequis, which might provide adequate nutritional and energetic reward (Graham 2001). Such a foraging pattern is consistent with the prediction that herbivores are more likely to find food plants in dense stands than when sparsely distributed, and predators should concentrate their activities in areas where foraging success is expected (Schupp 1988b). Then, seed predation tends to increase according to the density of conspecific adult trees, as the proportion of habitat exposed to specific predators enhances with tree density (Schupp 1992). The inverse relationship between proportional crop loss by parrots and distance of fruiting conspecifics was found both in wet (Coates-Estrada *et al.* 1993) and dry forests (Villaseñor-Sánchez *et al.* 2010), suggesting also that parrots actively searched for patches of fruiting trees.

The potential of an enhanced seed predation rate on Pequi patches points out the importance of further studies focusing on the proportional crop loss to macaws in a density gradient of Pequi trees. Such studies, besides the present one, might provide important clues for the management of Pequi to avoid conflicts between humans (either farmers or harvesters) and macaws. In Central Brazil, locals have been harvesting Pequi fruits in extensive cerrado remnants, and recently farmers are developing Pequi orchards to improve fruit production to supply the increasing demand of fruits for the food industry (Silva *et al.* 2001). To prevent potential conflicts we urgently need to formulate conservation plans.

The Blue-and-Yellow Macaw is yet locally abundant in the Cerrado. This generalist is one of the most abundant members of the genus *Ara* (del Hoyo *et al.* 1997, Sick 1997, Karubian *et al.* 2005), persisting even in fragmented landscapes (Ragusa-Netto 2006). It is important to consider that the ENP is a large remnant within a matrix of agricultural and pastureland areas. Perhaps, the importance of highly nutritive food resources in this area is higher than in large and continuous areas (Trivedi *et al.* 2004, Ragusa-Netto 2006). The Brazilian Cerrado exhibits one of richest florae of the world, in which the Pequi is a prominent species (Ribeiro & Walter 1998). The rate of fruit crop loss to macaws suggests a high impact caused by an abundant pre-dispersal seed predator on a common tree species. Such severe selective pressure may avoid that a species will become dominant at a particular site and promotes maintenance of diversity (Janzen 1970, Augspurger 1981). Therefore, the results presented here suggest that the interactions between seed predators and their food plants play an important role for the maintenance of diversity in the Cerrado.

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