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SEED PREDATION OF *COURATARI GUIANENSIS* (LECYTHIDACEAE) BY MACAWS IN CENTRAL AMAZONIA, BRAZIL

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Resumo. – Predação de sementes de *Couratari guianensis* (Lecythidaceae) por araras na Amazônia central, Brasil. – Os psitacídeos são importantes predadores de pré-dispersão de sementes nas florestas Neotropicais. No entanto, dados sobre a intensidade de predação de sementes por estas aves são limitados. Neste estudo apresento resultados sobre a destruição de culturas de *Couratari guianensis* por araras na Amazônia central, Brasil. As araras destruíram 99% da cobertura de frutos de três árvores de *C. guianensis*. Os frutos ainda estavam imaturos e as observações sugerem que as sementes imaturas, que escaparam à predação, não deverão ser viáveis. Este nível de destruição de cultura é elevado quando comparado com outros estudos envolvendo psitacídeos. A extensão da destruição poderá resultar da escassez de fontes de alimentação alternativas e sugere que os frutos de *C. guianensis* poderão ser um recurso importante para as araras da área de estudo na época de seca.

Abstract. – Psittacids are important pre-dispersal seed predators in Neotropical forests. However, little data on the intensity of seed predation by these birds are available. Here I report observation of crop damage by macaws on *Couratari guianensis* trees in central Amazonia, Brazil. Macaws destroyed 99% of the fruit crop in the canopy of three *C. guianensis* trees. Fruits were still immature and observations suggest that unripe seeds which escaped predation were unlikely to be viable. This level of crop damage is high compared with other studies involving psittacids. The extent of crop damage may result from a scarcity of alternative food sources and suggests that fruits of *C. guianensis* may be an important dry season resource for macaws in the study area. *Accepted 11 April 2008.*

Key words: Neotropical forest, phenology, pre-dispersal, *Couratari guianensis*, Psittacidae, resource abundance, seed loss, seed predation, seed predators.

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INTRODUCTION

Seed predators ingest seeds as an important part of their diet on a year-round or seasonal basis (Norconk *et al.* 1998). This is an abundant guild in tropical ecosystems and includes animals from a wide variety of taxonomic groups such as fishes, birds, mammals and insects (Janzen 1971). Where seed predators can cause high levels of seed mortality (e.g., Peres 1991), they may comprise an ecologically important group due to the impact they may have on forest structure (Silman *et al.* 2003) and evolution of phenological patterns (Brody 1997). This guild is further divided into two groups: “pre-dispersal” and “post-dispersal” seed predators, where pre-dispersal predators remove and ingest immature and mature seeds from the tree crowns and post-dispersal predators ingest mature seeds that have fallen to the ground (Janzen 1971).

In Neotropical forests, psittacids (parrots, macaws and parakeets) have been recognised as important pre-dispersal seed predators (Higgins 1979, Janzen 1981, Galetti & Rodrigues 1992, Fransisco *et al.* 2002, Trivedi *et al.* 2004, Renton 2006). Macaws (*Ara* spp.) in particular are capable of extracting and consuming well protected seeds by using their strong beaks (e.g., Norconk *et al.* 1997). Macaws occur over a range of forested habitats throughout the Neotropics and nest in cavities of tall trees (Forshaw 1989). In the Amazon basin, floodplain forests appear to be preferred nesting sites (Renton 2004, pers. observ.) and Renton (2006) suggests that this preference may be linked to nestling diets which consist mainly of seeds from trees characteristic of floodplain habitats. Seeds are also the main food item for adult macaws, constituting more than 76% of the diet (Renton 2006). Nevertheless, despite their important role as a major seed predator in Neotropical forest regions and the potential impact this may have on the structure and

maintenance of forests (e.g., Terborgh 1992, Silman *et al.* 2003), little data on the intensity of pre-dispersal seed predation by these birds are available. In fact, except for a recent study of macaw seed predation on immature fruits of the Brazil nut tree (*Bertholletia excelsa*; Trivedi *et al.* 2004), studies of macaw seed predation appear to be completely lacking in the literature. Instead studies have focused on diet and the identification of food plants (e.g., Renton 2006, Berg *et al.* 2007). In this paper, I report on seed predation by macaws on an Amazonian tree, *Couratari guianensis*, which is a large wind-dispersed Lecythydaceae occurring in upland Amazonian forests. However, firstly I present details of the morphological characteristics of the fruits and seeds of the species.

METHODS

This study was conducted at Lago Uauaçu which is located in the lower Rio Purús region (04°14'S, 62°23'W) of central Amazonia, Brazil. The region incorporates a large interdigitated mosaic of unflooded (*terra firme*) and flooded forests inundated by white-water (*várzea*) and black-water (*igapó*) on a seasonal basis for as long as 6 months of the year. Lago Uauaçu itself is a large crescent-shaped black-water lake fed entirely by rainfall collected in an internal catchment consisting primarily of upland *terra firme* forest. There is a pronounced seasonal variation in rainfall, with July through October being the driest months, and February through June the wettest (Haugaasen & Peres 2006). A recent 4-year phenological study at Lago Uauaçu showed that mature fruit production of trees in the region is highly seasonal and not completely synchronous across forest types. In *terra firme*, most trees fruited at the onset and through to the middle of the rainy season (December–March). Mature fruit production in both *várzea* and *igapó* started at the onset

of the high-water season (January) and continued throughout the rainy season (Haugaasen & Peres 2005). Large inter-annual variations in fruiting intensity at the community level were also observed (Haugaasen & Peres 2005).

Three species of large macaws, Red-and-green (*Ara chloropterus*), Scarlet (*A. macao*), and Blue-and-yellow (*A. araranna*), have been recorded in the study area (Haugaasen & Peres 2008). In early November 2006, a group of approximately 20 macaws (Scarlet or Red-and-green) was observed in the canopy of a *Couratari guianensis* tree in *terra firme* forest north of the lake. The macaws were considered consuming the seeds from immature fruits in the tree crown based on the large number of fruits and their winged seeds (and wings with their seeds missing) which were scattered on the ground underneath the tree. Two additional *C. guianensis* trees which had experienced similar seed predation by macaws based on fruits and seeds on the ground were encountered south of the lake on the following day. Walks on the trails where the trees were found were performed either daily or every other day for several weeks both before and after the observations, which indicate that the predation events in each tree were brief and occurred over a maximum period of 2 days.

Subsequently, I collected all fruits handled by macaws from underneath the crowns of the three trees. Determining the crop damage caused by macaws was facilitated by the fact that all fruits found on the ground had been detached from the trees by macaws. Fruits that were handled by macaws were easily recognised by the characteristic beak marks found on the individual capsules containing the seeds (pyxidia) and the column-like structure (columella) usually released to naturally liberate the seeds. Those which escaped attack remained attached to the trees for around 6 months (until June–July) after seed emer-

gence. Fruits were also still immature and we can therefore safely assume that all fruits contained a full set of seeds. Likewise, fruits detached from trees were clearly distinguishable from previous crops. Virtually the entire fruit crop could therefore be carefully examined, although a small number of fruits may have been removed by rodents.

Having collected the fruits, they were then counted and categorised as either open (if the lid covering the pyxidium, the operculum, was missing) or closed (if the operculum was sealed), and a randomly selected set of fruits from each tree were measured and weighed; seeds were counted and measured. Careful inspections of the tree crown with 10 x 40 binoculars determined the number of fruits still remaining in the tree crowns. This was feasible as the trees were without leaves. Fruit and seed measurements were taken with a digital calliper and scale and differences between trees were analysed using ANOVA.

Couratari guianensis is a widespread species in Neotropical *terra firme* forests (Mori & Prance 1990); it is buttressed and may reach 50 m in height. However, little seems to be known about the general phenology of the species. There appears to be a consensus on that this species is seasonally deciduous and sheds all its leaves in a single leaf changing event in the wet season, during which the tree is also seen in bloom (Lepsch-Cunha *et al.* 1999, Marin & Flores 2002). This is not entirely consistent with observations at Lago Uauaçu which appear to suggest that this species changes leaves towards the end of the dry season (September–October), since only emerging new leaves were observed in the canopy at the time of the macaw seed predation. New leaves therefore emerged in early to mid-November in the study area, when the fruits were in the later stages of fruit maturation. Thus, the trees carried immature fruits throughout the dry season which appears to

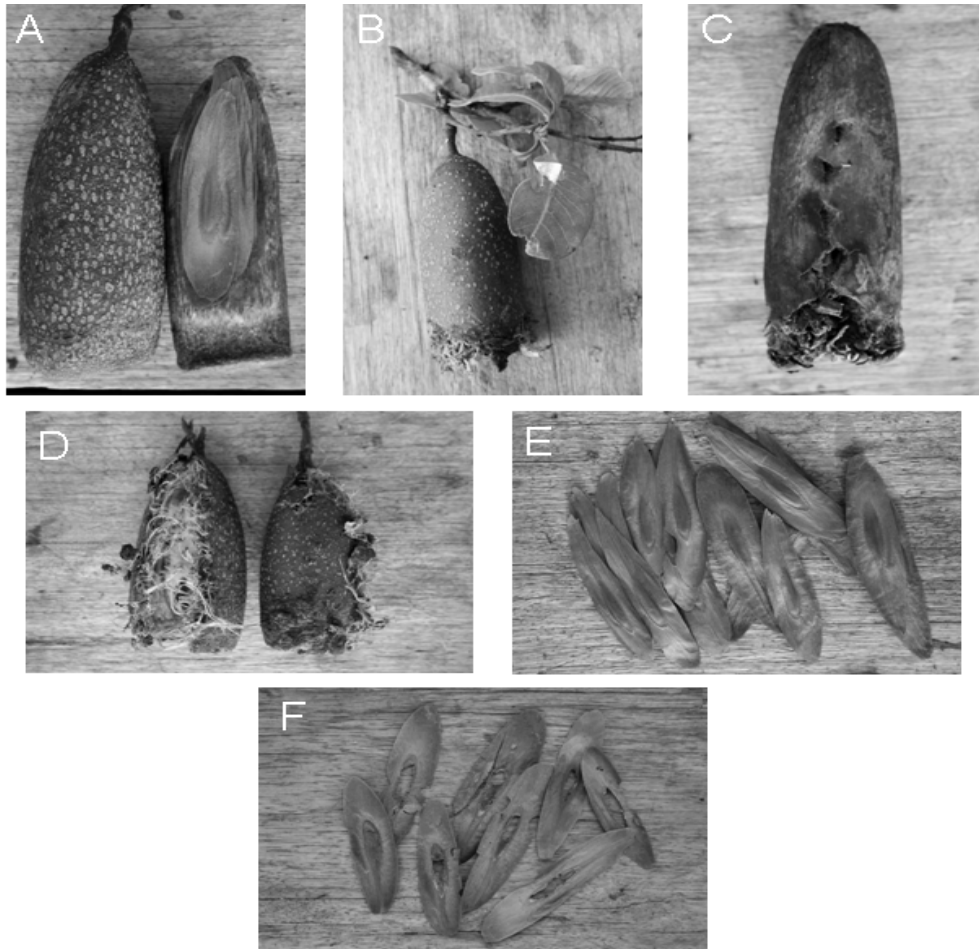


FIG. 1. Characteristics of *Couratari guianensis* fruits predated by macaws: (A) pyxidium closed by operculum (left) and triangular columella with winged seeds neatly arranged (right), (B) pyxidium opened by loosening the operculum, (C) triangular columella with prominent beak marks, (D) pyxidium opened by severing the pericarp wall, (E) intact winged seeds, (F) wings with their seeds removed.

be consistent with other species from the Lecythidaceae family (Peres 1991, Lepsch-Cunha & Mori 1999). Marin & Flores (2002) state that crops are annual, but this is uncertain as a number of adult individuals of the same species failed to produce fruits at Lago Uauaçú on a yearly basis during an extensive phenological study previously undertaken in the study area (Haugaasen & Peres 2005,

unpubl. data). Our observations suggest that this species portrays a multi-annual fruiting cycle where different individuals may fruit in different years.

RESULTS

Couratari fruit and seed characteristics. Fruits of *C. guianensis* consist of a tough, woody and

TABLE 1. Morphological characteristics of fruits from three *Couratari guianensis* trees at Lago Uauaçu, central Amazonia, Brazil.

	Mean fruit length (cm) \pm SE	n	Mean fruit width (cm) \pm SE	n	Mean fruit weight (cm) \pm SE	n	Mean no. of seeds (cm) \pm SE	n
Tree 1	13.17 \pm 0.12 ^a	50	5.51 \pm 0.05 ^a	50	172.48 \pm 4.53 ^a	50	35.42 \pm 1.63 ^a	48
Tree 2	10.63 \pm 0.16 ^b	50	3.83 \pm 0.06 ^b	50	83.42 \pm 3.07 ^b	50	22.02 \pm 1.14 ^b	50
Tree 3	10.99 \pm 0.12 ^b	50	3.94 \pm 0.05 ^b	50	95.84 \pm 3.41 ^b	50	15.84 \pm 0.48 ^c	50

^{a, b, c} Subsets from Tukey's post-hoc test.

TABLE 2. Number of fruits predated, discarded intact or left in the crowns by macaws from three *Couratari guianensis* trees at Lago Uauaçu, central Amazonia, Brazil.

	Fruits opened (%)	Fruits unopened (%)	Fruits left in canopy (%)
Tree 1	1897 (58.7)	1292 (39.9)	46 (1.4)
Tree 2	5669 (59.8)	3807 (40.2)	0 (0)
Tree 3	3840 (66.0)	1830 (31.4)	150 (2.6)
Total	11406 (61.6)	6929 (37.4)	196 (1.0)

fibrous pyriform pyxidium (Fig. 1A) where the pericarp walls are approximately 5.25 ± 0.28 mm thick ($n = 9$). The seeds are winged and lie arranged around a single triangular or quadrangular columella (Fig. 1A) in sets of 1–22 ($n = 451$). The number of seeds per fruit ranged from 8–57 (mean = 24.3 ± 0.95 , $n = 148$). The seeds and their long flattened, membranous wings (Fig. 1E), measured on average $7.6 \pm 0.12 \times 1.92 \pm 0.03$ cm ($n = 100$) and seeds weighed on average 0.187 g ($n = 150$). The pyxidia were 11.6 ± 0.12 cm ($n = 150$) long and measured 4.4 ± 0.85 cm ($n = 150$) at the broadest point. They weighed on average 117.2 ± 47.4 g ($n = 150$).

The size of the pyxidium was highly variable between trees (Table 1). There was consequently a significant difference in length ($F_{2,147} = 100.91$; $P < 0.0001$), width ($F_{2,147} = 347.53$; $P < 0.0001$) and weight ($F_{2,147} =$

168.07; $P < 0.0001$) of the pyxidia between trees, although two trees had similar sizes (Tukey's post-hoc test, Table 1). Similarly, there was a significant difference between trees in the number of seeds contained within each pyxidium ($F_{2,145} = 72.96$; $P < 0.0001$; Table 1).

Macaw fruit predation. Macaws decimated the fruit crop of all three *Couratari* trees. Of the 18,531 fruits produced, 61.6% were opened by the macaws and another 37.4% of fruits were either discarded or dropped with their operculum still intact (Table 2). Careful inspections of the crowns showed that only a small fraction of fruits remained intact (1.0%) and one tree suffered the loss of its entire fruit crop (Table 2).

Fruit handling by macaws. Examination of opened and unopened fruits found on the ground shows that macaws tore the fruits off their pedicel and employed two strategies to open the pyxidia and get to the seeds inside. In some cases, macaws would bite the base of the fruit (Fig. 1B) to loosen the operculum and pull out the columella (Fig. 1C). However, the majority of fruits were opened by severing the pericarp wall the entire length of the fruit (Fig. 1D). A large number of intact winged seeds (Fig. 1E) were found on the ground accompanied by those where the seeds had been removed (Fig. 1F).

DISCUSSION

The size of the pyxidium was highly variable which is consistent with vouchers specimens examined at the Instituto Nacional de Pesquisas da Amazônia (INPA) herbarium and fruits observed in other Lecythidaceae species (pers. observ.). Fruit hardness and size has been shown to determine fruit choice by some granivores in Neotropical forests (e.g., Kinzey & Norconk 1990) and Norconk *et al.* (1997) describe pericarps of *Pradosia caracasana* (Sapotaceae) dropped to the ground by macaws as marginally harder than those that were opened. However, these variables were not measured in this study and it is thus unclear whether fruit size differences within and between trees played a role in fruit choice by macaws or determined whether or not they were dropped intact to the ground.

Seeds of the Lecythidaceae are a major food item for Amazonian parrots (Roth 1984) and the mode in which the macaws opened the *Couratari* fruits clearly portrays how these birds can use their powerful beaks to destructively access even some of the most heavily protected seeds in Neotropical forests (Figs 1B and D). However, observations of foraging behavior on *Couratari* seeds were not conducted and it is therefore not possible to comment on actual predation rates and how many seeds were in fact eaten by macaws. Regardless, inspections during subsequent weeks of fruits which had been dropped to the ground with their opercula sealed showed that seeds were not viable. Additionally, subsequent inspections also showed that the thousands of immature seeds strewn on the ground underneath the trees degraded rapidly and thus did not contribute with reproductive success of parent trees. Macaws therefore inflicted severe seed loss on the trees during their feeding bouts irrespective of whether or not they consumed seeds in the canopy.

A similarly high level of seed predation on

C. guianensis was reported by Peres (1991). High levels of pre-dispersal seed predation have also been observed for other Lecythidaceae species. For example, Peres (1991) estimated that 69.5% of *Cariniana micrantha* seeds were predated by brown capuchin monkeys (*Cebus apella*) and a further 30% was lost as intact fruits were dropped to the ground. This level of seed loss is very similar to that of this study. However, in both cases the remaining fruits were still available to macaws and other seed predators, and more seeds may consequently have been destroyed on subsequent days. Severe pre-dispersal seed loss has also been reported for *Couratari multiflora* (Lepsch-Cunha *et al.* 1999) and *Lecythis usitata* (Prance & Mori 1978).

The common denominator of the above examples is that the seed predation was performed by one or more primate species. Significantly lower seed loss has been reported for cases where psittacine birds were the seed predators. Galetti & Rodrigues (1992) observed that only 8% of the *Albizia* sp. seed crop was lost to Blue-headed Parrots (*Pionus menstruus*) in SE Brazil. *Tetragastris panamensis* lost 6% of its seeds to large parrots (*Amazona* spp.) in Panama (Howe 1980). *Sterculia apetala* lost 10% of its seeds to parrots in Costa Rica, and Brazil nut trees (*Bertolletia excelsa*) in Peru had 9.8% of their crop destroyed by macaws (Trivedi *et al.* 2004). These results contrast with results presented here, though the sample size is limited and it remains unclear how body size, diets and spatio-temporal variability in fruit supply interact.

However, like this study, both Peres (1991) and Lepsch-Cunha & Mori (1999) observed the high pre-dispersal seed predation rates during the dry season. Scarlet Macaws in Belize showed a very narrow diet during dry season months (Renton 2006), and the same is true for Lilac-crowned Parrots (*Amazona finschi*) in Mexico (Renton 2001). It is therefore possible that the high predation

rates observed at Lago Uauaçu and elsewhere are related to reduced resource abundance leading to a greater reliance on a smaller number of fruit patches particularly in low-intensity fruiting years, although further studies are clearly needed to test this hypothesis. Nevertheless, fruiting trees are scarce in the study area during the dry season (Haugaasen & Peres 2005) and *C. guianensis* may consequently provide a potentially important dry season resource for macaws in the region.

If the high level of seed loss described here also takes place at the population level, this could ultimately affect plant recruitment. Peres (1991) found that irregular fruiting outputs between years are common among Lecythidaceae, and this is consistent with observations at Lago Uauaçu (pers. observ.). Peres (1991) suggests that this may emulate masting strategies (Janzen 1974) by swamping seed predators in high production years, with the consequence that seedling recruitment may be entirely confined to mast years. More studies are clearly needed to understand the direct influence of seed predators on the reproductive traits of Neotropical forest trees.

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