EXTENSIVE CONSUMPTION OF *Tabebuia aurea* (MANSO) BENTH. & HOOK. (BIGNONIACEAE) NECTAR BY PARROTS IN A TECOMA SAVANNA IN THE SOUTHERN PANTANAL (BRAZIL)

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ABSTRACT

Neotropical parrots forage for various food items such as seeds, fruit pulp, flowers, young leaves, and even arthropods. While foraging, many species wander over large areas that include both open and closed habitats. In this study, I examined parrot foraging activity during a brief synchronous and massive flowering in August 1998 in a tecoma savanna (dominated by *Tabebuia aurea*) in the southern Pantanal. Six parrot species, ranging from the small *Brotogeris chiriri* to the large *Amazona aestiva*, foraged for *T. aurea* nectar, but *Nandayus nenday* was by far the major nectar consumer, and the results of each of their visits, like those of the other species, was damage of a substantial proportion of the existing flower crop. Parrots foraged mostly during the afternoon, when nectar concentration tended to be higher. Nevertheless, compared to bird-pollinated flowers, which produce copious nectar, *T. aurea* had a smaller mean nectar volume per flower. Hence, presumably the amount of damage wreaked by these parrots resulted from their efforts to obtain part of their daily energy and water requirements. Thus, the synchronous and massive flowering occurring in such a brief period in the dry season may be related to, among other factors, the necessity of satiating predators such as parrots, which are still abundant in the Pantanal.

Key words: parrots, Pantanal, flowering, Tabebuia aurea, Nandayus nenday.

RESUMO

Consumo massivo do néctar de *Tabebuia aurea* (Manso) Benth. & Hook. (Bignoniaceae) por psitacídeos em uma savana de ipês (Paratudal) no Pantanal Sul (Brasil)

Papagaios e periquitos neotrópicos utilizam amplamente recursos como frutos e sementes. No entanto, flores, brotos e mesmo artrópodes podem ser alternativas alimentares importantes. Usualmente, essas aves forrageiam por amplas áreas, que incluem tanto formações vegetais abertas como fechadas. Neste estudo examinei o padrão de consumo de néctar por psitacídeos em uma savana dominada por ipês-amarelos (*Tabebuia aurea*) durante um episódio de floração massiva e sincrônica no sul do Pantanal em agosto de 1998. Seis espécies de psitacídeos, incluindo desde o pequeno periquito *Brotogeris chiriri*, até o papagaio *Amazona aestiva*, consumiram intensamente o néctar das flores dos ipês. *Nandayus nenday*, de longe, explorou a maior proporção do total de flores utilizadas, e bandos desse periquito, bem como das outras espécies, destruíam, a cada visita, parcela substancial das flores presentes em uma dada copa. Os psitacídeos consumiram néctar com maior freqüência durante a tarde, principalmente no final, quando a concentração tendeu a ser maior. O volume, no entanto, foi comparativamente baixo em relação às flores de espécies polinizadas por pássaros. Dessa forma, aparentemente, os psitacídeos foram acentuadamente destrutivos ao explorar *T. aurea*, uma vez que o néctar de muitas flores era requerido para suprir parte da demanda diária de energia e água dessas aves. Portanto, a floração massiva

e sincrônica em *T. aurea* durante curto período no auge da estação seca, dentre outros fatores, pode estar voltada a saciar predadores, como os psitacídeos, ainda abundantes no Pantanal.

Palavras-chave: Psitacidae, Pantanal, floração, Tabebuia aurea, Nandayus nenday.

INTRODUCTION

Dry neotropical woody vegetation usually sheds leaves and flowers from the middle to late dry season (Frankie et al., 1974; Bullock & Solis-Magallanes, 1990; Ramirez, 2002). Furthermore, many tree species briefly flower synchronously and massively, potentially to enhance the attraction of pollen vectors and/or to avoid losing too many flowers to nectar robbers (Janzen, 1971; Augspurger, 1981). Although in markedly seasonal habitats such intensive flowering tends to occur during part of dry season, fleshy fruit production sharply declines in this period (Griz & Machado, 2001; Ramirez, 2002). Thus, fruit scarcity imposes on heavy frugivores either dietary shifts, in which other plant materials are used, or forces displacement to more favorable areas (Terborgh, 1986; van Schaik et al., 1993). As flowers may be abundant while fleshy fruits are scarce, some frugivores rely mostly on nectar up to the return of fruit availability (Terborgh, 1986).

Many parrot species forage over large areas composed by a mosaic of habitats that may range from dry to wet vegetation, as well as from savannas to dense forests (Roth, 1984; del Hoyo et al., 1997; Renton, 2001). Such birds usually exploit massive and varied resources as they become available; hence, their diets are often markedly seasonal. Thus, flowers may be a useful food item during a substantial portion of the dry season, when fruit production is reduced (Cannon, 1984; Galetti, 1993; Wermundsen, 1997; Ragusa-Netto, 2004). Apparently, flowers are particularly important for some neotropical parakeet species that recently have been recorded pollinating tree species (Vicentini & Fischer, 1999; Cotton, 2001; Ragusa-Netto, 2002), or destroying a very large proportion of flower crop to access the nectar (Galetti, 1993; Cotton, 2001; Ragusa-Netto, 2002).

The Pantanal is a large floodplain whose semiarid vegetation is a mosaic in which grassy areas are interspersed with savannas and patches of deciduous forest (Pott & Pott, 1994). Among the savannas are the tecoma savanna (*Paratudal*) dominated by *Tabebuia aurea* (Manso) Benth. & Hook. (Bignoniaceae), which presents a synchronous and massive flowering, usually between July and September (Barros, 2001). In this study I describe the extensive use of *T. aurea* nectar by parrots in a tecoma savanna in the southern Pantanal during a massive flowering from the middle to the late dry season in 1998.

METHODS

Study site

This study was carried out in the southern Pantanal flood plain in a tecoma savanna cut by the Miranda River (19°35'S, 57°2'W; altitude ± 100 m; 80-100 km east of Corumbá, Mato Grosso do Sul State). The vegetation in the area is a mosaic of the dense Miranda river gallery forest, patches of deciduous forests interspersed with open grassy areas, and both palm (dominated by Copernicia alba) and tecoma savanna (dominated by Tabebuia aurea). In the latter, trees are 4-8 m high, although some individuals may reach 12 m. Trees develop on small mounds (\pm 0.5-1.0 m) where they remain safe in floods. Such mounds are interspersed with open grassy areas, in which common species are Panicum laxum, Hymenachne amplexicaulis, and Hemarthria altissima. Individuals of Byrsonima orbignyana are often mixed with T. aurea, although in smaller number (Oliveira, 1993). T. aurea trees loose their leaves just before flowering, generally from the middle to the late dry season. Annual rainfall is around 1,000 mm, mostly from November to March (wet season). In this period average temperature is 27°C, while in the dry season (April to October) average temperature is 20°C. In the cold months (June-July) frosts may occur. In this area of the Pantanal, flood pulses typically occur from January to March. During floods, standing water in the tecoma savanna rises to 1.0 m.

Field procedures

In order to evaluate parrot foraging activity in the tecoma savanna, I used three 10 km permanent access trails (separated each from the other by 5 km). From August 2 to 10 of 1998, during a massive and synchronous flowering I walked these trails from 6 to 18 h to examine daily foraging activity of parrots, their rate of flower use, and the proportion of flower crop damage at every parrot

visit. Whenever parrots were detected arriving at a flowered crown, I observed them foraging for nectar until they flew away. I then noted time and date, length of visit, number of parrots and, for the most visible individuals (2 to 5), I recorded the number of flowers exploited per minute. To evaluate the proportion of flower crop damage per visit, I estimated the total of flowers destroyed by a flock during a visit using the following calculations: mean number of flowers used per min. by a species x time of visit x flock size. Also, the remaining flower crop size was estimated (following Chapman *et al.*, 1992), and the result added to the number of destroyed flowers. From this total I calculated the percentage of crop damaged by parrots at every visit.

To sample nectar availability and concentration (during day 4), at the beginning of each hour (from 7 to 17 h) I took 10 flowers from three trees and measured nectar volume (with a microsyringe) and concentration (with a hand refractometer). Both results (mean volume and concentration) were correlated (Spearman correlation) with the hourly parrot-foraging activity.

RESULTS

I totaled 60 h of direct observations on parrot foraging activity when most crowns were intensely flowered and, therefore, apparently Tabebuia aurea was experiencing a flowering peak. My records show a total of 74 parrot visits to flowered crowns of T. aurea. Nandayus nenday made the most visits (54%), while large parrots (Amazona aestiva and Propyrrhura auricollis) visited the crowns only a few times (each species: 5% of visits; Table 1). Parrots visited crowns in flocks that ranged from two to 15 individuals, although usually 2-4 individuals foraged for nectar (Table 1). During most visits parrots spent from five to 10 min. drinking nectar, but A. aestiva spent 15 min. or even more, while P. auricollis rarely foraged for more than 5 min. at a given crown (Table 1). Parrots removed the flowers and pierced the calvx to drink the nectar. Only A. aestiva sometimes ate the petals in addition to drinking the nectar. These parrots together with Brotogeris chiriri exhibited the highest rates of flower exploitation per minute (11-12 flowers), while the other species exploited 6-7 flowers per minute (Table 1). As parrots visited flowering crowns in flocks during several minutes and destroyed numerous flowers per minute, every foraging bout resulted in substantial crop damage.

During their visits, all parrot species damaged a similar proportion of flowers which corresponded to 6-7% of the flower crop available during a foraging bout (Table 1). However, during long visits made by more than four parrots, usually up to 15% of the flower crop was lost, while exceptionally large flocks (15-20 *Nandayus nenday*) damaged almost 30% of the crop in some visits.

Parrots foraged for nectar during the day, including the hot noon hours. However, most foraging activity was recorded during the afternoon, especially from 16 to 17 h (Fig. 1). The two largest parrot species exhibited an inverse hourly pattern of visits, since *A. aestiva* performed all visits from 7 to 8 h, while *P. auricollis* exploited *T. aurea* flowers only during late afternoon. On the other hand, parakeets foraged for nectar all day, although *Aratinga aurea* made no visits in the morning, *Brotogeris chiriri* made only one, and *Myiopsitta monachus* was observed paying two visits in this period. Thus, *N. nenday* was almost the only species that often foraged for *T. aurea* nectar during the morning hours (Fig. 1).

Nectar availability varied hourly, so that the smallest mean volume ($10.0 \pm 8.0 \,\mu l$) was recorded at 7 h, while the highest $(21.0 \pm 9.0 \,\mu\text{l})$ was obtained at 12 h, although mean nectar volume per flower most of time was around 15.0-16.0 µl (Fig. 1). Nectar concentration was also not uniform throughout the day, so that concentration increased from morning (at 8 h, only $14.0 \pm 8.0\%$) to afternoon ($\pm 28.0\%$ most of the time; Fig. 1). Similarly, parrots foraged more often during the afternoon, when nectar concentration tended to be higher. Thus, the hourly pattern of parrot foraging activity and the hourly variation of nectar concentration correlated significantly (r = 0.67, p < 0.05). On the other hand, the hourly variations of nectar volume were unrelated to the hourly pattern of parrot foraging activity (r = 0.48, p = 0.13).

DISCUSSION

In markedly seasonal habitats, wind-dispersed species flower during mid dry season, so that winged seeds may be efficiently dispersed later during windy months. This, flowering pattern was found in several Central and South American *Tabebuia*, that are leafless most of the time while flowering and fruiting (Frankie *et al.*, 1983; Bawa & Webb, 1984; Barros, 2001). During the 1998 dry season, *T. aurea* massively flowered from mid July to mid August, remaining leafless up to fruit maturation during the latter part

of August and early September (pers. obs.), which is the windiest part of the year (source: International Airport of Corumbá). Hence, although on a savanna within a flood plain, *T. aurea* apparently exhibited a flowering pattern like this same genus in forests.

Mobile frugivores often wander over large areas searching for appropriate sources of fruit, since such resources usually exhibit an erratic spatial and temporal pattern of availability (Leighton & Leighton, 1983; Terborgh, 1986; van Schaik et al., 1993). Also, nectarivorous birds are well known for their movements towards variably flowering patches (Feinsinger, 1980; Stiles, 1980, 1985). In neotropical forests many frugivorous vertebrates wander in search of flowers and resort to feeding on nectar in the absence of fleshy fruit during the harshest part of the dry season (Terborgh, 1986; Terborgh & Stern, 1987; Ferrari & Strier, 1992). In spite of the low nutritional value of nectar when compared with fruit rich in fats and/or protein, this resource may be useful to frugivores during harsh periods (Terborgh, 1986). Neotropical parrots that inhabit seasonal areas include flowers and nectar in their diet more often as the dry season progresses (Galetti, 1993; Wermundsen, 1997; Ragusa-Netto, 2004). The parrots recorded using *T. aurea* nectar rely mostly on fruits and seeds. Consequently, none of them are specialized in exploiting nectar, as are the lories and lorikeets (Loriinae) from Australasia and southeast Asia, which present morphological adaptations for efficient use of nectar and pollen (Forshaw, 1989; del Hoyo et al., 1997). Hence, massive T. aurea nectar availability during the driest period of the year, when fruits and seeds are scarce, constitutes an alternative food resource. In the Miranda river gallery forest (southern

Pantanal), most of the parrot species recorded using *T. aurea* nectar heavily also used *Inga vera* nectar during the late dry season when fleshy fruits had almost vanished (Ragusa-Netto, unpublished). Thus, apparently from the middle to the late dry season parrots made substantial use of nectar in this region of the Pantanal, which is annually exposed to a long dry season (early April to late October). Such heavy nectar consumption is very conspicuous particularly in *N. nenday*, since this species was also the major consumer of *Inga vera* nectar (Ragusa-Netto, unpublished), and is probably among the most abundant parakeet in the Pantanal (Sick, 1997).

Usually bird-pollinated flowers produce copious and dilute nectar (Bruneau, 1997; Vicentini & Fischer, 1999; Cotton, 2001; Ragusa-Netto, 2002). But, *T. aurea* is pollinated by hymenopterans (Barros, 2001) and, although its nectar concentration is higher, the volume available per flower is comparatively small. Thus, in spite of these unusual features with respect to utility of these flowers to birds, probably the massive flower availability made consuming nectar advantageous, and perhaps by exploiting a very large number of flowers, mainly in the afternoon when nectar concentration tended to be higher, parrots obtained a satisfactory amount of energy.

However, this entailed damage by parrot flocks to a substantial proportion of the flower crop at every visit. These birds, which are well known as important pre-dispersal seed predators in the Neotropics, usually damage from 5% to 10% of a given seed crop (Janzen, 1972; Howe, 1980; Galetti & Rodrigues, 1992), although they may destroy a large proportion or even an entire seed crop of some tree species (Coates-Estrada *et al.*, 1993; Francisco *et al.*, 2002).

TABLE 1

Parrot species recorded foraging (N = 74 foraging bouts) in a tecoma savanna in the southern Pantanal (Brazil): average flock size, proportion of visits to flowered crown, rate of flower use, and crop damage per visit by each parrot species.

Parrot species	Flock size (mean ± sd)	Visits (mean ± sd min.)	Visits (%)	Flowers exploited/min.	Crop damage/visit (%)
Nandayus nenday	4.5 ± 2.9	7.0 ± 5.0	54	$6.5 \pm 2.5 (30)$ *	7.1 ± 4.3
Brotogeris chiriri	3.2 ± 2.0	11.0 ± 8.0	18	11.7 ± 5.8 (17)	7.3 ± 3.9
Myiopsitta monachus	4.5 ± 4.1	8.0 ± 6.0	11	$6.3 \pm 3.1 (12)$	7.0 ± 4.6
Aratinga aurea	2.2 ± 0.4	12.0 ± 7.0	7	$6.8 \pm 3.0 (14)$	6.9 ± 3.4
Propyrrhura auricollis	2.0 ± 0.0	5.0 ± 3.0	5	6.3 ± 1.7 (9)	6.5 ± 4.3
Amazona aestiva	3.0 ± 1.2	15.0 ± 6.0	5	11.7 ± 4.2 (11)	9.6 ± 4.6

^{*}In parentheses, the sample size for flowers exploited per minute.

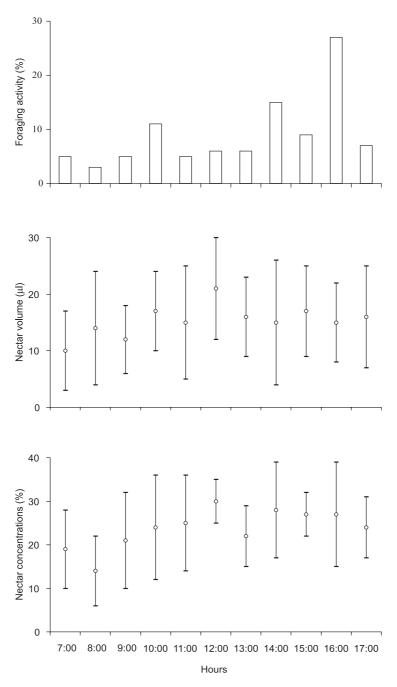


Fig. 1 — From top to bottom: hourly pattern of parrot foraging activity, mean $(\pm sd)$ volume of nectar available per flower, and mean nectar concentration per flower of *Tabebuia aurea*.

Exploiting flowers destructively, parrots potentially reduce the amount of fruit set and act as pre-dispersal seed predators. As at every visit, *T. aurea* trees lost an average of 7% of their flower crops to the parrots, individuals may have suffered reduced fruit production after successive visits.

Although evaluating the major selective forces that cause synchronous and massive flowering in *T. aurea* is out of the scope of this study, a consequence of this flowering pattern may be the maintenance of swamp predators such as parrots, which are still abundant in the Pantanal.

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