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Conservation puzzle: Endangered hyacinth macaw depends on its nest predator for reproduction

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ABSTRACT

In the Pantanal wetlands of Central Brazil, the endangered hyacinth macaw (*Anodorhynchus hyacinthinus*), the largest psitacid in the world, makes its nest almost exclusively in natural hollows found in the manduvi tree (*Sterculia apetala*). The recruitment of manduvis greatly depends on the seed dispersal services provided by the toco toucan (*Ramphastos toco*), responsible for 83.3% of the seed dispersal. The toco toucan, however, is responsible for about 53% of the preyed eggs, resulting in a case of conflicting ecological pressures in which the reproduction of the hyacinth macaw is indirectly dependent on the seed dispersal services of its nest predator. The case illustrates the intricacies of biotic interactions in species-rich environments where species may be tied by indirect, subtle ecological links which conservationists should be aware of.

1. Introduction

Hyacinth macaw (*Anodorhynchus hyacinthinus*) is the largest psitacid in the world, currently considered endangered because the remaining small populations are undergoing very rapid reductions as a result of illegal trapping and habitat loss (Snyder et al., 2000; BirdLife International, 2004). As a large, secondary cavity nester, hyacinth macaws need large, pre-existing tree holes for nesting (Guedes and Harper, 1995). Because such nesting sites are naturally scarce, their availability is an additional conservation problem (Guedes and Harper, 1995; Snyder et al., 2000).

In the Pantanal wetlands of central South America, home of the largest population of hyacinths, manduvi trees (*Sterculia apetala* (Jacq.) Karst; Malvaceae) provide the bulk (95%) of nesting sites (Guedes and Harper, 1995). Competition for nest cavities with other cavity-nesting birds (approximately 17 bird species use manduvi cavities for reproduction; Guedes, 2002), mammals, and even honey bees is intense (Snyder et al., 2000). Competition among breeding hyacinth macaw pairs is exacerbated because only trees older than 60 years produce cavities large enough to be used by the macaws (Santos et al., 2006). Provisioning of nesting boxes is thus a conservation strategy that is

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being used for the species (Snyder et al., 2000; Guedes, 2004).

The manduvi is one of the tallest trees in the Pantanal (20–35 m height), where it grows in forest patches (semideciduous and gallery forest) that cover only 6% of the vegetation area of the Pantanal (Silva et al., 2000). From July to September manduvi trees produce large fruits that open to expose three to eight bird-dispersed seeds (23.8 mm length × 14.2 mm wide, $n = 20$) with an oily aril. The species is not safe from threats, because the traditional extensive cattle ranching, the main economic activity in the Pantanal, is being rapidly replaced by more intensive ranching models, leading to the degradation of the natural vegetation through deforestation and forest fragmentation (Seidl et al., 2001; Harris et al., 2005). The intensive cattle ranching represent a problem for recruitment in manduvi populations because cattle trample and eat manduvi seedlings, thus reducing seedling densities in areas with high cattle load (Johnson et al., 1997).

The surmounting importance of manduvis to a critical phase of the life cycle of hyacinth macaws stimulated us to study the seed dispersal of this tree. The results surprisingly revealed a system of conflicting ecological pressures in which the availability of nesting sites for hyacinth macaws is directly dependent on the seed dispersal services of its major nest predator, the toco toucan (*Ramphastos toco*).

2. Methods

2.1. Study area and observations of seed dispersers

The study took place at Fazenda Rio Negro (19°34′29″S; 56°14′37″W), located in the Nhecolândia region of the Brazilian Pantanal. The Pantanal is a UNESCO Biosphere Reserve and a Brazilian National Heritage site of international relevance according to the RAMSAR Wetlands Areas Convention. Fazenda Rio Negro is a well-preserved private ranch of 7500 ha free of cattle since 2001, with habitats that represent the main vegetation types of Pantanal (Prance and Schaller, 1982), including *cerrado* – the Brazilian savanna, gallery and semideciduous forests.

Observations on 12 fruiting manduvi trees were carried out annually from 2002 to 2005 during the period of fruit maturation. In total, 89 observation sessions, lasting from 1 to 5 h, were made for a total of 255 h. Observation sessions were evenly distributed from 06:00 to 18:00 h. During observations, the observer seated quietly in a concealed position 20–40 m from the focal plant, recording continuously the species that visited the plant as well as their behavior (i.e., if they swallowed whole seeds or only took pieces of aril, or if the seeds were cracked) and the number of seeds they removed from plants or preyed on. To correlate fruit crop with visitation rate (i.e., number of visits/hour of observation), the total number of fruits (mature or not) on the trees were recorded at the beginning of each observation session.

2.2. Disperser densities

We performed a chi-square test to examine the relationship between the frequency of visitation and the abundance of toco toucans and chestnut-eared aracaris, *Pteroglossus castanotis*, the main seed dispersers of the manduvi (see below). To test the null hypothesis that bird species visitation was proportional to their abundance, we set the expected frequency equal to the density of each species in the study area. Densities were assessed by counting birds along four variable width transects (2.3, 2.3, 2.5 and 3.4 km long) established in the habitats where manduvis occur. Each transect was sampled once or twice a month from 2002 to 2005 totaling 182 km for the whole study period. The same transect was not sampled in the same week twice to improve the independence of data. Sampling occurred in the early morning avoiding rainy days. Transects were sampled keeping a constant walking speed at ca. 1 km/h, with stops to look around for animals (Buckland et al., 1993). For every sighting of a group or a single individual bird, we noted the species, number of individuals, and the perpendicular distance of the animal to the transect, which was obtained directly with a measuring tape or indirectly with compass and a measuring tape (Buckland et al., 1993). Densities were calculated using the software DISTANCE (http://www.ruwpa.st-and.ac.uk/distance/).

2.3. Manduvi recruitment

To assess the recruitment spatial pattern in the manduvi population in relation to putative parent plants, we surveyed all manduvi seedlings (defined as plants with <30 cm height) and adults (plants >13 m height, corresponding to the minimum height of the trees where hyacinths make their nests; Guedes and Harper, 1995) along four transects with 800 m length × 20 m width crossing the semideciduous forest. Transects were separated from each other by 2 km on average. The distance from each plant (seedlings and adults) to the most likely parent plant (i.e., the nearest adult tree) was measured with a measuring tape up to 30 m. Because 30 m was the minimum distance separating neighbouring macaw breeding pairs (see below), plants beyond this distance were lumped together in a single category (>30 m). Notice that the procedure adopted here is a conservative approximation to recruitment distances because the actual parent of a given plant may be farther away than its nearest adult tree.

2.4. Nest predation

In 1995, and annually from 1999 to 2003, NMRG monitored a total of 346 hyacinth macaw nests (152–310 each year) by climbing trees and checking nest contents. Events of nest predation were assigned to a given predator based on (i) direct observations of animals assaulting nests, (ii) signs (e.g. feathers, hairs, marks on the egg shell) left behind by predators, and (iii) the occupation by potential predators of recently preyed nests. It should be noticed that this method underestimates the relative importance of toco toucans as nest predators because, contrary to other potential predators, they could swallow whole eggs leaving no sign behind.

Mean ± SD are presented throughout the paper.

3. Results

A total of 14 bird species fed on manduvi fruits (Table 1). Half these birds were psitacids that cracked and preyed on the seeds. The remaining species were either gape-limited and unable to swallow whole seeds (e.g. plush-crested jay *Cyanocorax chrysops* and silver-beaked tanager *Ramphocelus carbo*), or pulp-consumers that only picked off pieces of aril and rarely carried away a seed in the bill for further consumption (e.g., purplish jay *Cyanocorax cyanomelas*, and crested oropendola *Psarocolius decumanus*). Toco toucans and chestnut-eared aracaris were the only legitimate seed dispersers, swallowing whole seeds and removing them from the vicinity of fruiting plants. However, in comparison with aracaris, toucans visited plants more frequently than expected based on their densities (toucan: 4.6 ± 1.41 birds/km^2, $n = 34$; aracari: 1.3 ± 0.74 birds/km^2, $n = 4$; $\chi^2 = 25.54$, df = 1, $p < 0.001$). Toco toucans made the bulk of visits to fruiting plants (63.5%; aracari: 7.6%; $n = 795$), and removed most of the seeds (86.3%, $n = 447$) (Table 1). We found a positive relation between fruit crop and visitation rate of toco toucans ($R^2 = 0.16$, $p = 0.016$; Fig. 1). Such relationship did not hold for aracaris ($R^2 = 0.04$, $p = 0.23$), seed predators or pulp-consumers (all $p > 0.50$).

The frequency of seedlings decreased with distance from adults, whereas the majority (51%, $n = 49$) of adults were >30 m from the nearest adult tree, and none was within the 5-m average crown radius of adult manduvis (Fig. 2). This distribution pattern revealed that removal of seeds from the immediate vicinity of parent plants is necessary for the recruitment of manduvis.

Toco toucans, purplish jays, white-eared opossums (*Didelphis albiventris*), and coatis (*Nasua nasua*) preyed on hyacinth macaw eggs (Table 2). A total of 23.7% of the 582 eggs monitored were lost to predators. Toco toucans were the main egg predators, responsible for the predation of 12.4% ± 2.7% of all the eggs monitored and 53.5% ± 12.9% of the eggs preyed annually (Table 2).

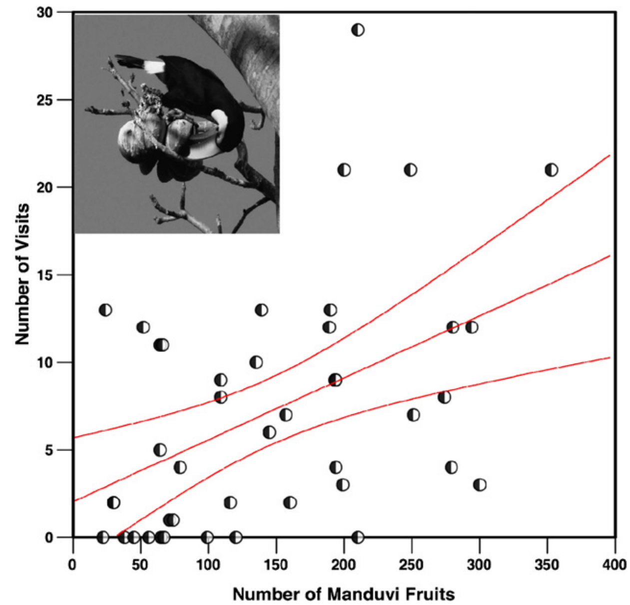

Fig. 1 – Relation between the number of fruits and the number of visits made by toco toucans (*Ramphastos toco*) to fruiting manduvi trees (*Sterculia apetala*) at the Brazilian Pantanal. Depicted are the regression line and the 95% confidence interval. The picture shows a toco toucan inserting its bill into a semi-opened manduvi fruit to feed on the arilate seeds.

4. Discussion

Among birds, habitat and feeding specializations are good predictors of the risk of extinction (Sekercioglu et al., 2004). Hyacinth macaws scores high in what concerns feeding specialization, eating exclusively the fruits of two palm species, *Attalea phalerata* and *Acrocomia aculeata* (Guedes and Harper, 1995). It also scores high in nest site specialization, selecting

Table 1 – Bird species that visited manduvi (*Sterculia apetala*) trees (defined as each arrival of a bird or group of birds to a fruiting plant) and the number of seeds removed from the adults (either swallowed or carried away in the bill) recorded during 255 h of observations on 12 fruiting plants from 2002 to 2005 in the Brazilian Pantanal

Species	No. of visits/No. of seeds removed from plants				
	2002	2003	2004	2005	Total
Ortalis canicollis	2/0	0/0	1/0	4/0	7/0
Amazona aestiva	1/0	21/0	1/0	0/0	23/0
Ara chloroptera	4/0	5/0	13/0	1/0	23/0
Aratinga aurea	0/0	3/0	0/0	0/0	3/0
Aratinga leucophtalmus	0/0	1/0	3/0	0/0	4/0
Brotogeris versicolurus	2/0	59/0	36/0	8/0	105/0
Myiopsitta monachus	0/0	5/0	0/0	2/0	7/0
Propyrrhura auricollis	0/0	4/0	0/0	5/0	9/0
Pteroglossus castanotis	1/0	31/21	24/37	5/0	61/58
Ramphastos toco	23/4	333/266	39/21	110/95	505/386
Cyanocorax chrysops	0/0	2/0	0/0	0/0	2/0
Cyanocorax cyanomelas	3/1	4/0	19/0	3/0	29/1
Psarocolius decumanus	1/0	8/0	3/2	1/0	13/2
Ramphocelus carbo	0/0	3/0	1/0	0/0	4/0
Total	37/5	479/287	140/60	139/95	795/447

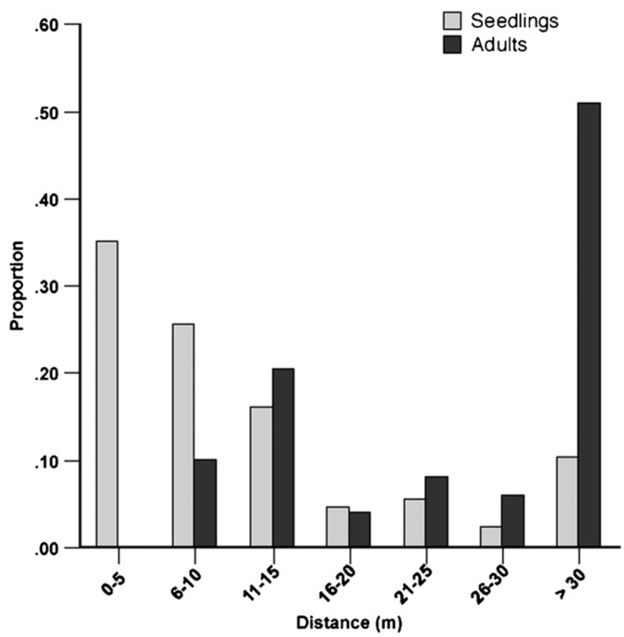

Fig. 2 – Frequency distribution of seedlings (<30 cm height, *n* = 125) and adults (>13 m height, *n* = 49) of manduvi (*Sterculia apetala*) in relation to distance to the nearest adult plant. Plants were sampled 10 m off both sides of four transects totaling 3.2 km.

predominantly manduvi tree holes to set their nests. Given the current land use trends in the Pantanal (Seidl et al., 2001; Harris et al., 2005), these specialized relationships make hyacinth macaws especially vulnerable to extinction.

The present study revealed that the reproduction of hyacinth macaws is indirectly linked to another specialized interaction involving manduvi trees and toco toucans. Evidences suggest that this is indeed a specialized interaction and that manduvi fruits are a specially prized resource for toucans. Despite the presence of other large frugivorous birds in the study area occurring in high densities (e.g., Chaco Cachalaca, *Ortalis canicollis*, 36.3 birds/km^2; Blue-throated Piping Guan, *Pipile cumanensis*, 11.7 birds/km^2; Galetti et al. unpubl. data), toco toucans are by far the main seed remover, visiting manduvi fruiting trees more frequently than expected by its abundance. The positive relationship between fruit crop and visitation rate by toco toucans suggests that toucans actively track manduvi fruiting trees across the landscape looking for fruits. Toco toucans sometimes work for several minutes to force with their strong mandibles semi-opened capsules of manduvi fruits to feed on the arilate seeds (see inset in Fig. 1). Finally, during nest monitoring, NMRG observed toucan nests completely lined up with regurgitated (i.e., intact seeds without aril) manduvi seeds, indicating that seedlings are offered to nestlings.

Toco toucans are strong fliers that cross open areas when moving from one forested patch to another (Yabe and Marques, 2001). They are, therefore, likely to promote long distance dispersal of manduvi seeds and its importance for the reproduction of hyacinth macaws is twofold. First, they are the most frequent seed disperser promoting the recruitment of the tree that represents the main nesting site for the macaws. Seeds deposited beneath manduvi trees are preyed upon by peccaries and agoutis (Donatti et al., 2007). Second, toco toucans spread out the seeds, thus avoiding the clumping of adult manduvis, which is of special importance because hyacinth macaws do not place their nests close to each other. The minimum distance between two neighbouring breeding pairs is 30 m, even though suitable nesting holes were occasionally close to each other, sometimes in the same tree (NMRG unpubl. data).

Although indirectly vital for the reproductive success of hyacinth macaws, toco toucans are responsible for about 53% of the preyed eggs. In addition, toco toucans may also take over hollows occupied by hyacinth macaws and kill macaw nestlings (Guedes, 2002, 2004). Therefore, the negative impact of toco toucans as nest predators must be weighted against its positive role as the main seed disperser of manduvis, and a conservation biology puzzle then derives: any conservation plan for hyacinth macaws must take into account the toucans, which would not normally be done because of their predator status and because toco toucans are not particularly threatened; the species is considered as "Least Concern" by IUCN (BirdLife International, 2004).

The macaw-toucan-manduvi relationship reported here exemplifies the intricacies and far-reaching effects of biotic interactions that make species ecologically tied by sometimes unsuspected, indirect links (Wootton, 1994). Be aware of these links is mandatory for proper management and conservation of endangered species.

Table 2 – Number of nests and eggs of *Anodorhynchus hyacinthinus* monitored in 1995 and from 1999 to 2003 in the Brazilian Pantanal, with information on the number of eggs preyed on and the relative importance of toco toucans (*Ramphastos toco*), purplish jays (*Cyanocorax cyanomelas*), white-eared opossums (*Didelphis albiventris*), coatis (*Nasua nasua*), and unknown agents as egg predators

Predator/years	1995	1999	2000	2001	2002	2003	Total
Nests monitored[a]	152	310	195	325	234	238	346
Eggs monitored	83	82	118	96	117	86	582
Preyed eggs	17	25	34	17	27	18	138
Toucans	13 (76.5)	12 (48.0)	15 (44.1)	8 (47.0)	12 (44.4)	11 (61.1)	71 (51.4)
Jays	2 (11.8)	4 (16.0)	8 (23.5)	6 (35.3)	4 (14.8)	2 (11.1)	26 (18.8)
Opossuns	0	2 (8.0)	4 (11.8)	0	4 (14.8)	2 (11.1)	12 (8.7)
Coatis	0	0	2 (5.9)	0	0	2 (11.1)	4 (3.0)
Unknown predators	2 (11.8)	7 (28.0)	5 (14.7)	3 (17.6)	7 (25.9)	1 (5.6)	25 (18.1)

Percentages in relation to the total number of eggs preyed on in each year are in parentheses.
a Refers to the total number of individual nests monitored, many of them accompanied for multiple years.

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