Can Seeds Help to Expel Parasites? A Comment on the Garber-Kitron (1997) Hypothesis

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Introduction

Like many other primates, moustached and saddle-back tamarins (*Saguinus mystax* and *Saguinus nigrifrons*; previously *Saguinus fuscicollis nigrifrons*; Matauschek *et al.* 2011) are seed dispersers for a large number plant species whose fruits they exploit for food (Culot 2009; Garber 1986; Knogge and Heymann 2003). Tamarins consistently swallow seeds (*ca.* 95 % of fecal samples contain seeds) that are often very large in relation to the tamarins' body size (Garber and Kitron 1997; Knogge and Heymann 2003). Mean length and width of seeds ($\pm$ SD) recovered from feces was 1.75 ± 0.59 cm (maximum: 2.35 cm) and 0.74 ± 0.32 cm (maximum: 1.31 cm) in *Saguinus mystax*, and 1.74 ± 0.56 cm (maximum: 2.33 cm) and 0.75 ± 0.31 cm (maximum: 1.35 cm) in *S. nigrifrons* (Knogge and Heymann 2003). Heymann (1992) speculated that large seeds may function physiologically as a kind of "roughage" and that the lack of continuous gut stimulation may be one cause of the high prevalence of gastrointestinal diseases in captive tamarins (Clapp *et al.* 1988; Gozalo and Montoya 1992), which contrasts to the low prevalence in wild tamarins (Wood *et al.* 1989).

Seeds do not provide a nutritional benefit but rather are ballast that occupies much space in the gastrointestinal tract (Garber and Kitron 1997). Therefore, seeking an adaptive explanation of seed swallowing, Garber and Kitron (1997) proposed dislodging and expelling intestinal parasites, particularly the highly damaging acanthocephalan hookworm *Prosthenorchis elegans*, as the major function. Huffman (1997; see also Huffman and Caton 2001; Huffman *et al.* 1996) and Wrangham (1995) had provided evidence for the mechanical expulsion of parasites through swallowing of entire leaves in chimpanzees (*Pan troglodytes*). Garber and Kitron (1997) based their argument on the high prevalence (and lethality; Cosgrove *et al.* 1968) of *Prosthenorchis elegans* infections in captive tamarins and low prevalence in

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the wild. Under the Garber–Kitron hypothesis, the following predictions can be made:

- 1) At the group level, the prevalence of infections with *Prosthenorchis elegans* should correlate negatively with the proportion of fecal samples per group that contain seeds.
- 2) At the individual level, individuals infected with *Prosthenorchis elegans* should swallow seeds more often than noninfected individuals. Because rates of seed swallowing itself are difficult to determine, I use the number of fecal samples per individual containing seeds as a surrogate variable.

I used data from field studies of a population of *Saguinus mystax* and *S. nigrifrons* at the Estación Biológica Quebrada Blanco (EBQB), in northeastern Peruvian Amazonia since 1994 to test these predictions.

Methods

Müller (2007) and Wenz *et al.* (2010) conducted parasite analyses on three mixed-species groups of *Saguinus mystax* and *S. nigrifrons* at EBQB in 2002–2003 and 2007, respectively. Wenz *et al.* (2010) also examined a mixed-species group of *Saguinus mystax* and *S. nigrifrons* living close to Diamante, a village *ca.* 1.5 km from EBQB. Müller (2007) analyzed 430 fecal samples randomly selected from a total of 1907 samples, with 4–16 samples from nonconsecutive days per individual. Wenz *et al.* (2010) examined a total of 356 samples, at least three samples per individual from nonconsecutive days. Müller (2007) noted the presence or absence of seeds >0.5 cm length in samples selected for analyses. Both studies determined the prevalence of several gastrointestinal parasites, including *Prosthenorchis elegans*, in individually assigned fecal samples (for methodological details see Müller 2007 and Wenz *et al.* 2010). I used prevalence data from Müller (2007) and calculations of the proportion of faecal samples containing seeds from Müller’s original data. To test prediction 1 I used Kendall’s τ , which allows correlation analyses with small sample sizes, in WinSTAT® version 2009.1. To test prediction 2 I used the Mann–Whitney *U*-test in Statistica 9.0 (StatSoft 2009) to compare the proportion of samples containing seeds between infected and noninfected individuals.

Researchers studying seed dispersal by *Saguinus mystax* and *S. nigrifrons* in 1994–1995 (Knogge and Heymann 2003) and reproductive hormones in male (Huck *et al.* 2005) and female (Löttker *et al.* 2004) *S. mystax* in 2000–2001 collected 2470, 369, and 562 fecal samples, respectively. Although these studies did not look for parasites in particular, the presence of adult *Prosthenorchis elegans* would not have been dismissed because they are 2–4 cm long (Mehlhorn 2001) and all samples were examined carefully for other analyses.

Results

We found no adult *Prosthenorchis elegans* in fecal samples in any of the studies. Although we cannot be sure whether individuals examined during the seed dispersal

and hormonal studies were infected with *Prosthenorchis elegans*, the fact that most individuals included in the hormonal studies were also included in the parasitological study by Müller (2007) and the consistency of prevalence of *P. elegans* in the studies by Müller (2007) and Wenz *et al.* (2010) suggest that some proportion of the tamarin population is always infected with *P. elegans*. Interestingly, comparison of the studies by Müller (2007) and Wenz *et al.* (2010) reveals strong intergroup variation in the prevalence of *Prosthenorchis elegans*, with groups living near the human village (group D) and the field camp (group 1) showing the highest prevalence in both tamarin species (Table 1).

The prevalence of *Prosthenorchis elegans* infections did not correlate with the proportion of fecal samples that included seeds (Kendall's $\tau=0.138$, $N=6$, $P=0.349$). The proportion of fecal samples that included seeds >0.5 cm did not differ between infected and noninfected tamarins (median_{infected}=70.0 %, range: 55.6–80.0 %, $N=7$; median_{noninfected}=71.4 %, range: 20–100 %, $N=31$; Mann–Whitney $U=101.0$, $Z=0.26$, $P=0.792$).

Discussion

None of the predictions derived from the Garber–Kitron hypothesis is supported. Another argument against the Garber–Kitron hypothesis results from the fact that *Prosthenorchis elegans* does not move around freely in the intestinal content, but has its spiny head deeply burrowed into the gut mucosa (see Fig. 1 in Müller *et al.* 2010).

Table 1 Prevalence of infections with *Prosthenorchis elegans* in mixed-species groups of *Saguinus mystax* (*Sm*) and *Saguinus nigrifrons* (*Sn*) for details of group composition see Supplementary Tables S1 and S2

Group	Species	Prevalence [%] (no. of individuals infected/no. of individuals examined) ^a		% of fecal samples containing seeds (no. of samples examined) ^b
		Müller (2007)	Wenz <i>et al.</i> (2010)	
1	<i>Sm</i>	33.3 (2/6)	50.0 (3/6)	70.2 (37)
	<i>Sn</i>	50.0 (3/6)	50.0 (2/4)	58.6 (58)
2	<i>Sm</i>	12.5 (1/8)	20.0 (1/5)	48.6 (74)
	<i>Sn</i>	16.7 (1/6)	16.7 (1/6)	68.8 (64)
3	<i>Sm</i>	0.0 (0/7)	0.0 (0/6)	63.6 (77)
	<i>Sn</i>	0.0 (0/5)	0.0 (0/3)	62.3 (61)
D	<i>Sm</i>	–	50.0 (3/6)	–
	<i>Sn</i>	–	57.1 (4/7)	–

Groups 1–3 are from EBQB, group D from the village Diamante

^a The number of individuals examined is identical to group size

^b From samples collected by Müller (2007) in 2002–2003. Figures are lower than the 95 % reported by Knogge and Heymann (2003) and an underestimate, as for the purpose of the parasitological study we only noted whether seeds larger >0.5 cm length were present that might affect quantitative parasitological parameters (such as egg counts per unit faecal matter)

This makes mechanical dislocation and expelling by seeds unlikely or at least quite difficult; dislocation would result in deep wounds in the gut wall. This interpretation is supported by findings of Huffman *et al.* (1996) on the physical effect of leaf swallowing on parasites in chimpanzees: Whereas *Oesophagostomum stephanostomum*, a parasite species with only loose attachment to the intestinal mucosa, was expelled through leaf swallowing, *Strongyloides fülleborni* and *Trichuris trichiura*, both species with firm attachment to the intestinal mucosa, were unaffected.

In conclusion, the curative function hypothesis of seed swallowing is highly unlikely. The alternative hypotheses proposed by Garber and Kitron (1997) — reducing time tamarins spent exposed in the canopy (and thus exposed to aerial predators) and increasing feeding efficiency by swallowing seeds along with the adhering pulp— are more likely, but await testing.

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