PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Are tortoises important seed dispersers in Amazonian forests?

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Abstract According to most studies on seed dispersal in tropical forests, mammals and birds are considered the main dispersal agents and the role played by other animal groups remains poorly explored. We investigate qualitative and quantitative components of the role played by the tortoise *Chelonoidis denticulata* in seed dispersal in southeastern Amazon, and the influence of seasonal variation in tortoise movement patterns on resulting seed shadows. Seed shadows produced by this tortoise were estimated by combining information on seed passage times through their digestive tract, which varied from 3 to 17 days, with a robust dataset on movements obtained from 18 adult *C. denticulata* monitored with radio transmitters and spoon-and-line tracking devices. A total of 4,206 seeds were found in 94 collected feces, belonging to 50 seed morphotypes of, at least, 25 plant genera. Very low rates of damage to the external structure of the ingested seeds were observed. Additionally, results of germination trials suggested that passage of seeds through *C. denticulata*'s digestive tract does not seem to negatively affect seed germination. The estimated seed shadows are likely to contribute significantly to the dispersal of seeds away from parent plants. During the dry season seeds were dispersed, on average, 174.1 m away from the location of fruit ingestion; during the rainy season, this mean dispersal distance increased to 276.7 m. Our results suggest that *C. denticulata* plays an important role in seed dispersal in Amazonian forests and highlight the influence of seasonal changes in movements on the resulting seed shadows.

Keywords *Chelonoidis denticulata* ·
Yellow-footed tortoise · Amazon forest · Frugivory ·
Seed dispersal

Introduction

Seed dispersal represents a critical stage in plant reproduction (Terborgh 1990; Herrera et al. 1994). Failure in this process can jeopardize the establishment and survival of seedlings, since seeds and seedlings that are close to the mother plant may have an extremely low chance of escaping from pathogens and predators (Janzen 1970; Connell 1971; Wills et al. 1997; Harms et al. 2000; Howe and Miriti 2000; Fragoso et al. 2003).

Schupp (1993) defined the efficacy of a dispersal agent as its contribution to the reproductive success of a plant, which is determined by a quantitative component, related to the number of dispersed seeds, and by a qualitative component, related to seed treatment by the disperser and with the spatial pattern of seed deposition. Terborgh (1990) listed three main characteristics of large-bodied birds and mammals which, generally, make them more effective dispersal agents of plant species of mature forests than other animals: tendency to be more selective towards large-seeded fruits, higher consumption per feeding bout, and tendency to transport the seeds farther before regurgitating or defecating them. Wehncke et al. (2003), arguing about

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the role of capuchin monkeys (*Cebus capucinus*) as seed dispersers, added two other characteristics which appear to make this species especially efficient for this ecological process: a predominantly frugivorous diet, including fruits of many plant species; and the scattered deposition of feces, reducing seed and seedling mortality rates through a density-dependent mechanism.

Mammals and birds are considered the main seed dispersal agents in tropical forests (Terborgh 1990; Jordano 2001; Herrera 2002), where most plants have fruits adapted to animal dispersal (Howe and Smallwood 1982; Gautier-Hion et al. 1985; Webb and Peart 2001). Although studies conducted in arid regions indicated that tortoises of the family Testudinidae may be effective seed dispersal agents (Cobo and Andreu 1988; Varela and Bucher 2002; Liu et al. 2004), in tropical forests the role played by this group in seed dispersal has received little attention (see Strong and Fragoso 2006; Guzmán and Stevenson 2008).

Throughout the Amazon basin there are only two species of truly terrestrial chelonians (Testudinidae), the tortoises *Chelonoidis denticulata* and *Chelonoidis carbonaria* (Ernst and Barbour 1989). Both species have similar ecologies, morphologies and body sizes, with mean linear carapace length of wild adult individuals varying from 30.4 to 37.8 cm for *C. denticulata* and from 29.5 to 32.2 for *C. carbonaria* (Castaño-Mora and Lugo-Rugeles 1981; Pritchard and Trebbau 1984; Moskovits 1988; Jerozolimski 2005). Their distributions overlap in many areas, although *C. carbonaria* occurs in a wider variety of habitats, including open vegetation such as cerrado, whereas *C. denticulata* seems to be more dependent on humid forests (Jerozolimski 2005). In spite of their wide geographical range, relatively high abundance and their frequent use by many traditional human communities as a food source (Milton 1991; Mena et al. 2000; Souza-Mazurek et al. 2000; Peres and Nascimento 2006), very little is known about their wild populations (Pritchard and Trebbau 1984; Moskovits 1988). Although fruits seem to constitute an important item in their diets (Moskovits 1998; Josseaume 2002) and the passage through their digestive tract does not seem to negatively affect seed viability (Moskovits 1998), only recently did Strong and Fragoso (2006) and Guzmán and Stevenson (2008) suggest that these two tortoise species may be effective dispersal agents.

The aim of this study was to provide a robust evaluation of the role played by the tortoise *C. denticulata* in seed dispersal in an Amazonian forest through the analysis of qualitative and quantitative aspects of this interaction. More specifically, we focused on the following questions:

1. What is the relative importance of fruits in the diet of *C. denticulata* and what species are ingested?
2. Does passage through the tortoise digestive tract affect seed viability?
3. What is the seed passage time in the digestive tract of *C. denticulata*?
4. What is the seed shadow produced by *C. denticulata*, combining data on average movement capacity of monitored tortoises and seed passage time through the digestive tract?
5. Are the seed shadows produced in the rainy season different from the seed shadows produced in the dry season?

Materials and methods

Study site

This study was conducted in the southern state of Pará, in the territory of the Kayapó village of A'Ukre (7°41′15″S, 51°52′25″W), which is located in the Kayapó Indigenous Land (KIL) along the Riozinho river, a second-order tributary of the Xingu river. The KIL region is an area of transition between the Amazon forests and the cerrado of central Brazil, and in spite of the dominance of semi-deciduous forests, patches of cerrado and of more open and deciduous vegetation associated with granitic rock outcrops are common in the area (Hecht and Posey 1989; Zimmerman et al. 2001). The altitude varies from 200 to 500 m above sea level. The weather is hot and humid and mean annual rainfall is around 2,100 mm, with a marked dry season beginning at the end of May and extending till the end of August, during which the mean monthly rainfall is under 70 mm.

Nine field trips were conducted from December 1998 to December 2001, totaling 426 days of field work. Most data were obtained in the 8,000-ha Pinkaiti wildlife reserve (7°46′14″S, 51°57′43″W; Zimmerman et al. 2001), which is located 12 km southwest of the village of A'Ukre and has a history of little anthropogenic disturbance and no commercial logging. Although the dominant vegetation in the reserve is mixed and open semi-deciduous forest, with mean canopy height around 18 m (Baider 2000), it is characterized by a mosaic of different forest types, including areas of vine forest with very low and discontinuous canopy (approximately 7 m high) and forests with continuous canopy over 35 m high, such as in Brazil nut (*Bertholletia excelsa*) groves (Lambert et al. 2005).

Importance of fruits in the diet of *C. denticulata*

We evaluated the importance of fruits in the diet of *C. denticulata* by analyzing their frequency and relative volume in feces of tortoises captured in the Pinkaiti reserve

for the study of movement capacity, and opportunistically, in other parts of the A'Ukre village territory (within 30 km of the village), during traditional Kayapó hunting trips conducted between 1999 and 2001. We tested for seasonal changes in fruit frequency using the Fisher exact test and for seasonal changes in fruit volume using the Mann–Whitney U-test (Zar 1996). For all tests we used a significance level of 5%. Fruits collected during fruit censuses conducted along 4 km of trails in the Pinkaiti reserve, and sporadically in other areas of the A'Ukre territory, were identified by Manoel Cordeiro from Embrapa Amazônia Oriental and used as reference for comparison with seeds found in tortoise feces.

We estimated the number of seed species that *C. denticulata* ingests in the rainy season using the jacknife estimator (Quenouille 1956) and used the interpolation method proposed by Burnham and Overton (1979) to choose its most appropriate order.

Effect of the passage through *C. denticulata* digestive tract on seed structure and viability

The effect of the passage through the tortoise digestive tract on seed morphological structure was evaluated visually for seed species found in four or more fecal samples (Table 1): *Spondias mombim* ($n = 25$), *Attalea maripa* ($n = 8$), *Tetragastris altissima* ($n = 44$), *Jacaratia spinosa* ($n = 2,073$), *Porouma guianensis* ($n = 112$), *Brosimum lactescens* ($n = 158$), *Clarisia ilicifolia* ($n = 211$) and *Celtis* sp. ($n = 17$). All crushed seeds and seeds with cracked coats were classified as damaged and their proportion was recorded for each seed species.

To evaluate the effect of passage through the tortoise's digestive tract on seed viability, germination tests were performed with seeds of two species consumed by the tortoise and abundant at the time of the experiment: *Genipa americana* (Rubiaceae) and *J. spinosa* (Caricaceae). Ripe

Table 1 Mean dimensions of the identified seeds found in feces of *Chelonoidis denticulata* ($n = 94$) collected in the territory of the Kayapó village of A'Ukre, southeastern Amazonia, total number of seeds and number of feces in which the seed type was found

Family	Species	Length (mm)	Width (mm)	No. seeds/ no. feces
Anacardiaceae	*Spondias mombin*	26.5	15.7	25/8
Annonaceae	*Xylopia amazônica*	6.7	4.6	1/1
Arecaceae	*Attalea maripa*[a]	40.2	17.2	8/4
Bromeliaceae	*Ananas ananassoides*	4.0	2.5	713/2
Burseraceae	*Protium* sp.	7.5	6.4	1/1
Burseraceae	*Tetragastris altissima*	18.0	10.6	44/5
Caricaceae	*Jacaratia spinosa*	8.0	5.1	2073/30
Cecropiaceae	*Cecropia* sp.	2.6	1.5	28/3
Cecropiaceae	*Pourouma guianensis*	13.0	8.2	112/5
Cecropiaceae	*Pourouma* sp.	18.6	10.0	3/2
Leguminosae-Minosoideae	*Inga* sp.	12.0	7.7	5/2
Memecylaceae	*Mouriri* sp.	10.6	7.8	3/2
Moraceae	*Brosimum lactescens*	8.4	10.2	158/3
Moraceae	*Castilla ulei*	8.7	7.8	13/1
Moraceae	*Clarisia ilicifolia*	10.3	8.4	211/4
Moraceae	*Fícus* sp. 1	1.6	1.3	207/3
Moraceae	*Fícus* sp. 2	1.7	1.1	9/1
Moraceae	*Helicostylis tomentosa*	7.8	6.6	17/3
Moraceae	*Sorocea* sp.[b]	3.9	4.7	32/2
Myrtaceae	*Eugenia* sp.	5.7	4.0	1/1
Myrtaceae	*Psidium* sp.[b]	5.1	4.2	59/2
Myrtaceae	Unidentified	8.0	6.1	1/1
Quiinaceae	*Quiina paraensis*	15.6	9.1	11/1
Rubiaceae	*Genipa americana*	11.6	8.5	16/3
Rubiaceae	*Geophila cordifolia*[b]	4.0	2.3	25/3
Rubiaceae	*Guettarda* sp.	12.3	15.2	12/2
Sapotaceae	*Pouteria macrophylla*	16.1	12.7	1/1
Sapotaceae	Unidentified	8.7	6.4	12/1
Ulmaceae	*Celtis* sp.	10.4	6.9	17/6

[a] Species found in both wet and dry seasons

[b] Species found only in feces from the dry season

fruits of these two species were offered to six individuals of *C. denticulata* at the Pinkaiti research station. The seeds obtained from their feces (*G. americana*, n = 48; *J. spinosa*, n = 286), as well as a similar number of seeds extracted from ripe fruits (*G. americana*, n = 60; *J. spinosa*, n = 180), were planted at a depth of 3 mm in plastic bags filled with local soil. *Duroia* sp. (Rubiaceae) fruits were also offered to the tortoises; however, due to the small number of fruits obtained, only ingested seeds were planted (n = 5). The plastic bags were placed in a natural gap in the surrounding forest and germination rates were recorded after 1 and 8 months, when the samples was examined for both germinating and ungerminated seeds. Comparison between the germination rates of ingested seeds with seeds planted directly from ripe fruits were performed with the *G*-test (Zar 1996).

Seed passage time through *C. denticulata*'s digestive tract

We estimated seed passage time through *C. denticulata's* digestive tract from six individuals kept for 30 days in an enclosure at the Pinkaiti research station. Every morning, different food items reported by the Kayapó Indians to be consumed by tortoises—such as fruits, fungi and leaves—were offered to the tortoises. Additionally, every 4 days, papaya (*Carica papaya*) and banana (*Musa* sp.) pulp mixed with a single kind of seed were offered to the tortoises from 0700 to 0900 hours. A total of six types of seeds, with sizes varying from 3 to 7 mm long, including the seeds of *G. americana*, *J. spinosa* and four types of hard-coated exogenous seeds, were used and the same seed type was only re-offered to the tortoises after 24 days.

The enclosures were checked for the presence of feces every 2–3 h daily, from 0600 to 2200 hours and whenever a feces was collected at 0600 hours, we assumed it was produced at 0200 hours of the same morning. Each feces was washed in running water over a 0.5-mm sieve to find the seeds and the relative frequency of each passage time interval (1-day intervals) was calculated.

C. denticulata's movement capacity

We evaluated *C. denticulata's* movement capacity by monitoring 18 radio- or spool-and-line-tracked individuals found in the Pinkaiti reserve, where tortoises are not hunted. Tortoises found in the area were taken to the research station for attachment of a transmitter and/or a thread device to their carapace and, a maximum of 1 day later, released in the place of capture. We used a RA-2A Telonics receiver and ATS transmitters (model 16 M, weight 25 g) fixed with epoxy resin to the lower posterior area of the tortoise carapace, slightly displaced to one side.

Transmitters with epoxy resin weighed, on average, 2.4% of the animal's body weight, ranging from 0.8%, in a 5,925-g adult individual to 8.6%, in one 525-g juvenile. Additionally, due to a limited number of transmitters, we also used thread devices made with 457-m-long bobbins of polyester thread placed in plastic cylinders (31 mm diameter, 50 mm long, weight 20 g) following the methods described by Miles et al. (1981). The thread devices were fixed with duct tape and contact adhesive to the tortoise carapace in the same position of the transmitters or, for individuals which already had a transmitter, slightly displaced to the opposite side. The thread devices with duct tape and contact adhesive weighed, on average, 0.7% of the animal's body weight, ranging from 0.5 to 1.0%. The free extremity of the polyester thread was fixed to a tree near the place where the tortoise was released. The transmitters and the thread devices did not increase the height or width of the tortoise carapace, therefore avoiding interference with movements in the forest understory. When the 457 m of polyester thread was unraveled, a new bobbin of thread was placed in the cylinder without moving the tortoise from its location. To further minimize interference with tortoise behavior, the released tortoises were captured again only at the end of the study, when the transmitters and thread devices were removed. Therefore, we collected feces from monitored tortoises exclusively when they were kept in the research station for attachment or removal of transmitters and thread devices at the beginning and at the end of the monitoring period.

Whenever possible, we located the monitored tortoises every day; however, due to difficulties in finding them in the forest on occasion, 3 days was the most frequent time interval between successive locations. In cases when an individual was not observed directly, its location was confirmed by triangulation (see White and Garrott 1990). Because the minimum and maximum seed passage time through the *C. denticulata* digestive tract we recorded was 3 and 17 days, respectively, we analyzed movement distance only within this time interval. All linear distances between locations of each monitored tortoise were organized in 1-day time intervals, from 3 to 17 days.

Seed shadows produced by *C. denticulata*

We combined data on tortoise movement patterns with data on gut passage rates for ingested seeds to generate the probabilities of deposition of seeds ingested by *C. denticulata* at different distances from the feeding site (herein called "seed shadows"), using the method described by Murray (1988) and by Holbrook and Smith (2000). This method assumes that the behavior of a tracked tortoise after leaving any mapped location does not differ significantly from that after ingesting a fruit. Therefore, any location of

a monitored tortoise could be used as a potential site of fruit ingestion for calculating the seed shadow. We grouped the recorded distances between all mapped locations for each of the 18 individuals of *C. denticulata* monitored at 1-day intervals, from 3 to 17 days. We then calculated, for each monitored tortoise, the mean distance between locations for each time interval. Grouping the data from all 18 monitored individuals by calculating the mean of the mean distance for each time interval, we obtained the probability of different movement distances for each time interval considered. Therefore, we avoided pseudo replication because data from every monitored tortoise contributed equally to the calculation of the mean distance between locations for each time interval.

To estimate the seed shadow produced by *C. denticulata*, the relative frequency of each distance category for each time interval was multiplied by the probability of the specific seed passage time. Then, summing the results for each distance interval (<50 m, 50–100, >100–150, >150–200, and so on) over all 17 time intervals, yielded the overall dispersal probability for each distance class (D_d), expressed by the following formula:

$$D_d = \Sigma(L_t P_t)$$

where *d* varies in intervals of 50 m, from 0 to 1,150 m; *L* is the probability of a tortoise being at distance class *d* from a fruiting plant (mapped location) after *t* days (*t* varies in 1-day intervals, from 1 to 17 days); and *P* is the probability of an ingested seed being released through defecation after the time interval *t*. Finally, we built a histogram of seed deposition probability as a function of the distance from the site of seed ingestion.

Results

Importance of fruits in the diet of *C. denticulata*

A total of 94 feces of *C. denticulata* were collected; 39.4% from feces obtained from tortoises found in the Pinkaiti reserve and 60.6% obtained opportunistically from tortoises hunted by the Kayapó Indians, in other areas of the A'Ukre village territory. Most of the feces (84%) were collected during the rainy season (October–March). Fruits were the second most frequent and abundant item found in the feces, after non-reproductive plant parts (leaf and stem). Fruit frequency in feces did not differ significantly between wet and dry seasons (*P* = 0.059). However, in the rainy season fruit volume in feces was significantly higher than in the dry season (*U* = 381, *P* = 0.024). Fruit parts (mainly seeds) were present in 77.2% of the feces collected during the rainy season and represented, on average, 29.8% of their

volume. In contrast, they were present in 53.3% of the 15 feces collected during the dry season and represented, on average, only 4.7% of feces volume.

We recorded a total of 50 seed morphotypes in the 94 feces of *C. denticulata*. Of these, 58% were identified as belonging to 26 genera within 15 plant families (Table 1). In the 79 feces obtained in the rainy season, we found a total of 4,099 seeds belonging to 48 different morphotypes, and each feces had from zero to eight seed morphotypes. In the 15 samples obtained in the dry season, we found a total of 107 seeds belonging to three different morphotypes and each feces had at most one seed morphotype. The sizes of the seeds found in the feces varied from tiny *Ficus* sp. seeds (approximately 1.5 mm long) to seeds of the *Attalea maripa* palm (approximately 40 mm long). The most frequent seed species found in the feces was *J. spinosa*, followed by *S. mombin*, *Celtis* sp. and *T. altissima* (Table 1). The estimated number of seed species consumed by *C. denticulata*, generated by the interpolation of the second- and third-order jacknife estimators, was 97.6 (±14.6) or between 69 and 126 seed species (morphotypes) if the 95% confidence interval is considered.

Seed damage and germination rates

Rates of damage to seed structure after passage through *C. denticulata*'s digestive tract were very low, reaching more than 5% in only one of the eight species evaluated (*C. ilicifolia*, 5.7% of seeds damaged). *J. spinosa*, the most abundant seed species found in fecal samples had 4.8% of seeds damaged, while *B. lactescens* and *T. altissima* had 3.8 and 4.3% of seeds damaged, respectively. None of the seeds of *S. mombim*, *A. maripa, P. guianensis* or *Celtis* sp. found in fecal samples were damaged.

The germination rates for *G. americana* seeds ingested by *C. denticulata* (62.5%) did not differ significantly from the germination rates obtained from *G. americana* seeds sown directly from ripe fruits (68.3%; *P* = 0.72). However, none of 466 seed planted of *J. spinosa* germinated. Three of five seeds of *Duroia* sp. obtained from feces of *C. denticulata* germinated. At the end of the experiment we found no ungerminated seeds in the plastic bags where they were sown, indicating decomposition or predation.

Seed passage times in the digestive tract of *C. denticulata*

A total of 43 feces were collected from the six *C. denticulata* individuals kept in an enclosure to estimate seed passage times. Seed passage times through *C. denticulata*'s digestive tract varied from 3 to 17 days (mean 8.3 days; Fig. 1).
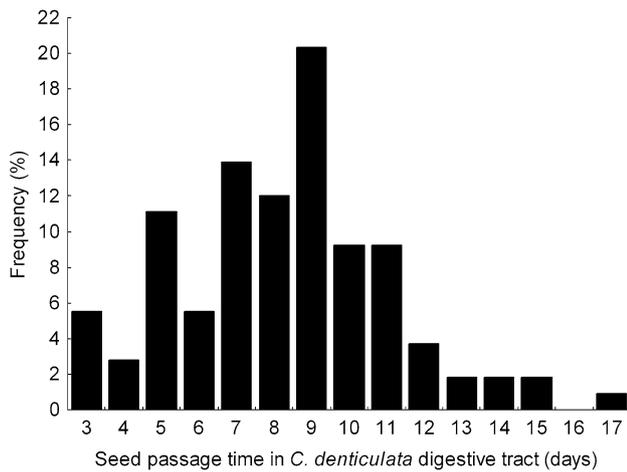
Fig. 1 Frequencies of seed passage times in the digestive tract of *Chelonoidis denticulata*, obtained from six *C. denticulata* individuals kept in an enclosure at the Pinkaiti reserve

Movement capacity of *C. denticulata*

Thirteen individuals of *C. denticulata* were monitored during the dry season, 14 were monitored during the rainy season and nine were monitored during both seasons (Table 2). Notwithstanding the great variance in *C. denticulata* movements, mean linear distances between locations were always smaller in the dry season for all time intervals analyzed. For time intervals of 3 to 17 days, mean linear distance between locations varied from 171.9 to 392.3 m in the rainy season and from 93.0 to 258.8 m in the dry season (Fig. 2).
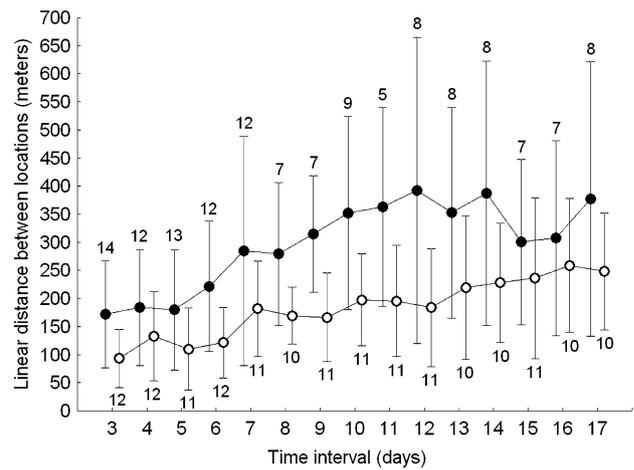

Fig. 2 Mean linear distance between locations for *C. denticulata* individuals monitored at the Pinkaiti reserve for time intervals from 3 to 17 days, for the rainy (*black circles*) and dry (*white circles*) seasons. Values are means ± 1 SD. Sample sizes (number of tortoise individuals) for each time interval are indicated above and below the SD bars for the rainy and dry seasons, respectively

Seed shadows produced by *C. denticulata*

On average, seeds ingested in the rainy season are dispersed 276.7 m from the place of fruit consumption, whereas in the dry season they are dispersed, on average, 174.1 m from where they are consumed. During the rainy season 91.2% of the seeds ingested by *C. denticulata* are expected to be dispersed at distances greater than 100 m from theit place of ingestion and 38.1% are dispersed at

Table 2 Information on the *C. denticulata* individuals monitored at the Pinkaiti reserve in the dry (*D*) and rainy (*R*) seasons

Season	Sex	Weight (kg)	CLC (cm)	Monitoring duration (days)	Number of locations
D	M	2.24	26.1	34	5
D	M	2.80	26.0	55	17
D	F	3.75	29.2	26	9
D	F	1.80	22.1	6	6
R	M	4.80	33.3	21	9
R	M	2.70	26.5	64	7
R	M	2.33	25.6	9	9
R	F	3.15	27.6	66	10
R	F	2.21	24.8	29	4
DR	M	2.75	26.5	343	16
DR	M	2.83	28.0	529	21
DR	M	2.95	27.6	387	45
DR	M	3.68	30.0	884	74
DR	M	3.85	31.4	406	40
DR	F	2.97	26.5	154	33
DR	F	5.83	32.0	578	64
DR	F	5.30	34.0	375	28
DR	F	3.45	29.0	274	19

CLC Carapace linear length, *D/R* tortoise monitored in both dry and rainy seasons, *M* male, *F* female
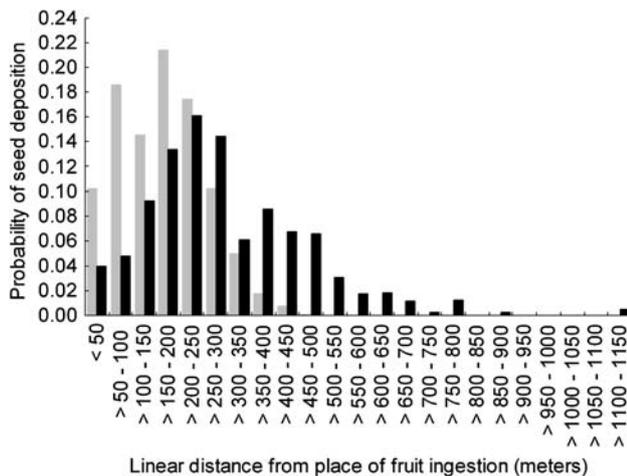
Fig. 3 Probability of seed deposition as a function of distance from the place of fruit ingestion by *C. denticulata*, during the rainy (*black bars*) and dry (*grey bars*) seasons

distances over 300 m. During the dry season, however, these percentages fall to 71.2 and 7.5%, respectively (Fig. 3).

Discussion

Seed dispersal studies have suggested so far that mammals and birds are the main dispersal agents in tropical forests (Terborgh 1990; Jordano 2001; Herrera 2002), whereas the role played by other groups has remained poorly explored. Our results demonstrate that a reptile species, *C. denticulata*, possesses several essential characteristics which make it an important seed dispersal agent in Amazonian forests.

Diversity of dispersed seeds

We found 50 morphotypes of seeds ingested by *C. denticulata*, but a jacknife estimator indicated that this tortoise species may ingest seeds from more than 100 plant species, highlighting the frequency of this animal–plant interaction. Strong and Fragoso (2006) found seeds of 11 plant species in only 19 fecal samples of *C. denticulata* and *C. carbonaria* from Maracá Island, northwestern Brazil, while Guzmán and Stevenson (2008) found a diversity of seeds similar to the one found in this study, in fecal samples of *C. denticulata* (55 species) in the Peruvian Amazon, a site located almost 2,000 km southwest from our study site. This suggests that *C. denticulata* should interact with a high number of plant species throughout its geographic range.

The recorded number of plant species whose fruits are consumed by *C. denticulata* is similar to the number recorded for many species of mammals and birds. Yumoto

et al. (1999) found 17 seed species in 176 feces samples of red howler monkeys (*Alouatta seniculus*) and woolly monkeys (*Lagothrix lagotricha*), in the Colombian Amazon; Wehncke et al. (2003) found 67 seed species in 174 feces samples of capuchin monkeys in the Barro Colorado Island, Panamá; Poulsen et al. (2002) recorded the consumption of approximately 50 fruit species by the hornbills *Ceratogymna atrata* and *Ceratogymna cylindricus* in the Dja reserve, in Cameroon. Among secondary dispersers, Fragoso and Huffman (2000) found 39 seed species in tapir (*Tapirus terrestris*) feces in a 14-month-long study on Maracá Island (northwestern Brazil), and Silvius and Fragoso (2003) found, by radio-tracking red-rumped agoutis (*Dasyprocta leporina*), that they consumed pulp, seeds and seedlings of 19 plant species.

Size constraints for seed dispersal

Besides consuming a great diversity of seeds, *C. denticulata* might also disperse many seed species which are only dispersed by a few dispersal agents. Some seed species found in *C. denticulata* feces, such as the seeds of *A. maripa* (mean length of 40.2 mm) and of *S. mombim* (mean length of 26.5 mm), are significantly larger than the biggest seed species found by Yumoto et al. (1999) in feces of woolly monkeys, which had a mean length of 21.3 mm. Endozoic dispersal of *A. maripa*, for instance, seems to be performed by very few animal species, including the spider monkey, *Ateles belzebuth* (Silvius and Fragoso 2002; Fragoso et al. 2003), and the tapir (Fragoso 1997). Wheelwright (1985) conducted a study on the frugivorous bird community of a lower montane forest in Costa Rica, which included 70 bird species and 171 plant species, and found that ingestion of large fruits (>20 mm in diameter) was limited to a very few large and broad-gape bird species.

What is the role of other secondary seed dispersers compared to that of tortoises? Among the invertebrates, ants and dung beetles are known to be major secondary seed dispersers in tropical forests; however, their role is likely limited to dispersal of small seeds over relatively short distances (Levey and Byrne 1993; Shepherd and Chapman 1998; Gómez et al. 2005). Additionally, some terrestrial vertebrate species considered important seed predators and dispersers, such as the agouti (*Dasyprocta* sp.), appear to interact mainly with a few large-seeded species (Silvius and Fragoso 2003; Jorge and Peres 2005), which limits their influence to a small number of plant species. In contrast to many dispersal agents that show more restricted preferences or constraints to endozoochory, tortoises consume and may disperse seeds of a higher diversity of plant species, including a wider range of seed sizes.

Seed dispersal quality

Because tortoises have a very limited capacity to process their food prior to ingestion (Moskovits and Bjorndal 1990), swallowing most fruits whole, physical damage to ingested seeds is minimal, which is an important condition for effective seed dispersal. In Amazonian forests, very few primate species, including the spider (*Ateles* sp.) and woolly monkey (*Lagothrix lagothricha*) (Stevenson 2000; Link and Di Fiore 2006), might handle seeds in a similar low-impact manner, whereas most frugivorous primates are to a greater degree seed predators (Norkonk et al. 1998). Among secondary dispersers, with the exception of the tapir, most Amazonian ungulates, such as the two species of peccary and two species of brocket deer, mechanically or chemically destroy most of the seeds they eat (Bodmer 1991; Feer et al. 2001).

C. denticulata uses a wide variety of habitats that vary in topography, drainage and vegetation type (Moskovits 1998; Jerozolimski 2005), which facilitates access to fruits from a wide range of plant species. Furthermore, frequent use of tree fall gaps by *C. denticulata* (Moskovits 1985; Josseaume 2002; Jerozolimski 2005) suggests that this tortoise species could provide high-quality dispersal services to light-demanding plant species (Strong and Fragoso 2006; Guzmán and Stevenson 2008), seeds of many of which we found in *C. denticulata* feces, such as *A. maripa*, *S. mombin*, *J. spinosa* and the three species of the Cecropiaceae family.

In contrast to many species of birds and mammals which live in groups and tend to defecate "collectively" in feeding and resting sites (Wehncke et al. 2003; Russo and Augspurger 2004), tortoises are solitary and scatter the seeds they disperse which likely reduces density-dependent seed and seedling mortality. For example, on Barro Colorado Island, Panamá, Wehncke et al. (2003) recorded lower rates of seed removal from feces of capuchin monkeys than from feces of howler monkeys (*Alouatta palliata*), and concluded that this difference was due to defecation asynchrony among capuchin individuals as well as smaller feces. Additionally, Russo and Augspurger (2004) recorded higher survival rates of *Virola calophylla* seeds dispersed by spider monkeys (*Ateles paniscus*) at in-transit sites, where seed deposition was lower, than in sleeping sites and beneath *V. calophyla* female trees, where seed deposition was higher.

Although the passage times recorded for *C. denticulata* are long compared to those recorded for birds and mammals, which are normally only a few hours and rarely reach a day (Holbrook and Smith 2000; Wehncke et al. 2003; Link and Di Fiore 2006), germination does not seem to be affected after seeds pass through a tortoise gut, a result that has been recorded for other reptile species (Moll and

Jansen 1995; Traveset 1998; Liu et al. 2004). Passed seeds of two of three plant species that were tested, germinated successfully. The single species which failed to germinate in this study, *J. spinosa*, was recorded by Josseaume (2000), in French Guiana, to successfully germinate after passing through *C. denticulata*'s gut, with a germination rate not significantly different from seeds sowed directly from ripe fruits. On the Island of Maracá (northwestern Brazil), Moskovits (1998) reported that four out of six species of seeds ingested by *C. carbonaria* and *C. denticulata* successfully germinated. Strong and Fragoso (2006) evaluated the viability of seeds for the three most abundant species found in feces of these tortoise species by visually examining their embryos and concluded that more than 90% were viable. Additionally, Guzmán and Stevenson (2008) found a mean germination rate of $76 \pm 2.5\%$ for 11 plant species ingested by *C. denticulata* in the Peruvian Amazon. Because the effect on germination of a seed's passage through an animal's digestive tract varies among plant species (Traveset 1998), future research on a greater number of plant species will contribute to a more precise evaluation of the importance of tortoises as seed dispersal agents in Amazonian forests.

Seed passage time

Gut passage times recorded for *C. denticulata* in this study were similar to results obtained by Bjorndal (1989), Josseaume (2000) and Guzmán and Stevenson (2008). However, they differ significantly from the mean minimum passage time of 1.6 days, obtained by Strong and Fragoso (2006). Their result is certainly an underestimation because passage time was calculated from the time of tortoise capture and not from the time of fruit ingestion. Additionally, the fact that these authors obtained data on food passage time from wild tortoises recently captured probably contributed to a further reduction in the recorded passage time, since defecation is stimulated by stress in tortoises (Josseaume 2002).

Because passage rate in an animal digestive tract can be influenced by the size of the ingested seed (Holbrook and Smith 2000), as well as by the composition of other food items ingested together (Bjorndal 1989; Murray et al. 1994; Traveset 1998), experiments to test the influence of different types of food items and the sizes of the ingested seeds on the passage time would contribute to improved seed shadow estimates.

Movement capacity and dispersal distances

Average dispersal distance estimates of 276.7 and 174.1 m obtained for *C. denticulata* during the rainy and dry seasons, respectively, are comparable to the dispersal distance

estimates obtained for mammals and birds considered important seed dispersers in tropical forests (Sun et al. 1997; Yumoto et al. 1999; Wehncke et al. 2003). The average estimated dispersal distances for howler and woolly monkeys obtained by Yumoto et al. (1999) in Colombia, were 316.7 and 327.0 m, respectively. Wehncke et al. (2003) estimated average dispersal distance of 216 m for seed ingested by capuchin monkeys in Barro Colorado Island, in Panamá. The estimates of average dispersal distances for three turaco species in a tropical montane forest in Rwanda, varied from 119 to 229 m and from 156 to 304 m for seeds with short and long retention times, respectively (Sun et al. 1997). Silvius and Fragoso (2003) suggested that agoutis are unlikely to move seeds away from conspecific aggregations because they concentrate their foraging activities in the patches of few large-seeded plants.

Guzmán and Stevenson (2008) estimated the mean dispersal distance for *C. denticulata* in the Peruvian Amazon at 89.6 ($\pm$9.2 m), while in this study we obtained a mean dispersal distance of 276.7 and 174.1 m in the rainy and dry season, respectively. This pronounced difference in average dispersal distances between this and Guzmán and Stevenson's (2008) study may reflect differences in forest characteristics between the two study sites or be due to the fact that these authors removed the monitored tortoise individuals from the forest monthly to collect fecal samples (for typically 1–2 nights), which might have influenced their movement behavior and, therefore, the estimated dispersal capacity. Within the seed passage time recorded in this study, the farthest observed movement for *C. denticulata* was 1,210 m over 12 days by an adult male. Moskovits (1985) recorded 620 m movement for the same species during 17 days on Maracá Island in northern Brazil.

The greater distances moved by *C. denticulata* individuals during the rainy season might be associated with mating activities and the apparently higher abundance of animal-dispersed fruits during this period (Moskovits 1985; Jerozolimski 2005; Guzmán and Stevenson 2008), which is supported by the much higher abundance and diversity of seeds found in the fecal samples obtained during this season. The intensification of mating activities during the rainy season (Moskovits 1985) seems to be a consequence of the higher abundance and aggregated distribution of fruits during this period, as the probability of mating encounters should be higher in the vicinity of fruiting trees. Because of the greater distances moved during the rainy season, we predict that the influence of tortoises on gene flow between populations and range expansion of plant species should be stronger in this period.

Terborgh et al. (2002) found, in Cocha Cashu, Peru, that over 95% of the seedlings were within 100 m of a conspecific tree. If this distance is used as a criterion to define seed dispersal events within areas subject to lower mortality rates due to density-dependent mechanisms, tortoises could have a significant contribution to reduce the probability of seed mortality, since 91.2 and 71.2% of the ingested seeds would be dispersed by *C. denticulata* individuals at distances greater than 100 m in the rainy and dry seasons, respectively. Although considerable attention has been given to the places where most seeds are dispersed, normally close to the mother plant, evidence suggests that sites where seed deposition is less frequent might be extremely important for plant reproductive success (Willson 1992). In spite of the difficulties in observing and quantifying long-distance seed dispersal events (Wang and Smith 2002; Nathan et al. 2003), there is a growing body of evidence suggesting that those rare events might be important for our understanding of the patterns of species and populations distribution, habitat colonization, gene flow between populations and even the maintenance of the diversity of tropical forests (Cain et al. 2000; Holbrook and Smith 2000; Nathan and Muller-Landau 2000; Fragoso et al. 2003). Therefore, seed dispersal by *C. denticulata* could potentially contribute to the colonization of new habitats, to the promotion of plant population gene flow, as well as to the distribution of seeds to sites where conspecific seedling density is significantly lower, increasing seedling survival probability by reducing predation rates, herbivory and pathogen infestations (Janzen 1970; Connell 1971; Russo and Augspurger 2004; Norghauer et al. 2006).

Tortoises as important seed dispersers

Why has the role of tortoises as seed dispersal agents been neglected in the Amazon? Although this study, as well as the studies of Strong and Fragoso (2006) and of Guzmán and Stevenson (2008), suggest that the tortoise *C. denticulata* should be considered an efficient seed dispersal agent, as defined by Schupp (1993), and they have most, if not all, the characteristics suggested by Terborgh (1990) and Wehncke et al. (2003) for a high-quality disperser, they have not yet been considered an important seed dispersal agent in tropical forests in the main books and articles published on this subject (see Howe and Smallwood 1982; Terborgh 1990; Jordano 2001; Herrera 2002). Additionally, its sister species, *C. carbonaria*, which occurs in sympatry with *C. denticulata* in many areas of its geographical range, including in the Kayapó territories, probably has a similar ecological role (Strong and Fragoso 2006). In spite of the reduced number of *C. carbonaria* individuals monitored in the Pinkaiti reserve (only 29 locations were obtained from three adult individuals; Jerozolimski 2005), the available data on its movement capacity, together with the high number and diversity of seeds found in their feces—a total

of 3,206 seeds of 23 different morphotypes found in 32 feces—and the comparable seed passage times obtained for this species, varying from 3 to 15 days (mean 8.4 days; A. Jerozolimski 2005), suggest that *C. carbonaria* may also play a significant role in seed dispersal in the Amazon, especially where it attains high densities.

We believe this underestimation of the role of tortoises in seed dispersal can be attributed in part to the difficulty in detecting these species in the forest, due to their cryptic coloration and behavior. For instance, in a Peruvian Amazon forest, the population density of *C. denticulata* obtained from a line-transect method was 60–124 times lower than estimates obtained from mark-recapture methods (Guzmán and Stevenson 2008), which demonstrates the constraints for estimating the abundance of cryptic species based exclusively on visual encounters. Consequently, short-term assessments invariably underestimate tortoise density or even fail to detect this component of the seed dispersal assemblage.

Even considering that, due to ectothermy, tortoises have lower metabolic requirements compared to those of mammals and birds, and, therefore, have lower food consumption rates (Pough 1980; Guzmán and Stevenson 2008), these differences do not appear to justify their omission from the group of relevant seed dispersal agents in the Amazonian forests, especially because their high population densities may compensate for the limited fruit ingestion rate of individuals. On Maracá Island, densities of *C. denticulata* and *C. carbonaria* were estimated to be 20 and 105 individuals km^{-2}, respectively (Moskovits 1985). Peres et al. (2003) estimated the densities of *C. denticulata* and *C. carbonaria* at 5.1 and 11.5 individuals km^{-2}, respectively, in the Arapiuns river basin. Guzmán and Stevenson (2008) recorded densities of 20–30 individuals of *C. denticulata* km^{-2} in the Peruvian Amazon. Within three sampled areas in the A'Ukre territory, *C. denticulata* and *C. carbonaria* density estimates varied from 25 to 31 and from 8 to 20 individuals km^{-2}, respectively (Jerozolimski 2005).

To place an important quantitative component of seed dispersal by *C. denticulata* in perspective, we compared estimates of numbers of seeds dispersed by *C. denticulata* to the few available estimates for other dispersal agents in tropical forests. Because of their cryptic behavior and frequent use of dense vegetation, we were unable to record defecation rates from individuals we tracked in the forest. Therefore, we used the mean defecation rate of 1.5 feces $individual^{-1}$ day^{-1} reported by Guzmán and Stevenson (2008) to estimate the total number of seeds dispersed by the *C. denticulata* population at our study site. Considering that the density of *C. denticulata* in the A'Ukre village territory varied from 25 to 31 individuals km^{-2} (Jerozolimski 2005) and the mean number of seeds per feces was 51.89 in the rainy season and 7.13 in the dry season (mean value of 29.51 seeds per feces for the transitional periods between the rainy and the dry seasons), the *C. denticulata* population could disperse from 479,462 to 594,533 seeds km^{-2} $year^{-1}$. Link and Di Fiore (2006) estimated that a spider monkey (*A. belzebuth*) group in Equador, disperse 1,351,200 seeds (>1 mm) km^{-2} $year^{-1}$. Stevenson (2000) estimated that woolly monkeys in Colombia, disperse more than 9 million seeds km^{-2} $year^{-1}$; however, only 17% of these seeds are ≥ 3 mm. Poulsen et al. (2001) estimated that seven primate species (density of 77 individuals km^{-2}) which comprise the diurnal primate community in Cameroon, disperse 412,085 seeds km^{-2} $year^{-1}$: an average of 58,869 seeds km^{-2} $year^{-1}$ dispersed by each primate species. Therefore, forest tortoises appear to play a significant role in seed dispersal in Amazonian forests, although more quantitative data on most dispersal agents, especially on terrestrial dispersers, are needed to further clarify their roles.

In conclusion, this study demonstrates that *C. denticulata* should be highly placed in both qualitative and quantitative categories of seed dispersal in Amazonian forests. First, fruits comprise a high proportion of the diet of this tortoise species, highlighted by an abundance and diversity of seeds found in its feces, including large seeds dispersed by a limited number of animals. Secondly, passage through the digestive tract of *C. denticulata* apparently does not negatively effect seed viability. Thirdly, its long gut passage rates combined with the significant movement capacity of this solitary species, especially during the rainy season, results in the scattered dispersal of ingested seeds relatively far from where they were eaten and, consequently, increases their chance of escaping from pathogens and predators. Additionally, the tortoise predilection for visiting tree fall gaps might be particularly relevant for direct dispersal of light-demanding plant species. Finally, this tortoise species is abundant in many parts of its wide geographic range, increasing its influence on seed distribution. Therefore, if the role of *C. denticulata* in seed dispersal is indeed relevant for Amazon forest dynamics, as suggested in this study, declines in their populations might result in significant impacts on the plant community.

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