

# Dietary differences have contrasting effects on the seed dispersal potential of the titi monkey *Callicebus coimbrai* in north-eastern Brazil

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**Abstract:** Gut transit times and dispersal distances of seeds ingested by *Callicebus coimbrai* at two localities were estimated by tracing seeds found in faeces to feeding sites. Feeding events and faecal samples were recorded/collected and mapped by GPS between April and July, 2012. Junco group fed almost exclusively on fruit, whereas Trapsa group fed on fruit and leaves/flowers in similar proportions. A much higher proportion of faecal samples from Junco contained seeds (47.9%,  $n = 244$ , vs. 33.6%,  $n = 177$ ), and contained more seeds, on average ( $3.0 \pm 2.8$  vs.  $2.1 \pm 2.1$ ) than those from Trapsa. However, gut transit times were absolutely longer at Trapsa (mean =  $4.87 \pm 1.48$  h,  $n = 6$ , vs.  $2.85 \pm 0.53$  h,  $n = 13$  daytime events), and dispersal distances were significantly longer ( $200 \pm 81.0$  m vs.  $126 \pm 53.4$  m). The evidence indicates that, while the more folivorous diet at Trapsa was reflected in a much lower faecal seed count, it was also associated with longer gut transit times, and significantly longer dispersal distances, i.e. while dispersing approximately half the seeds dispersed by Junco group, Trapsa group dispersed these seeds over almost twice the distance.

**Key Words:** Brazil, *Callicebus coimbrai*, diet, faeces, feeding ecology, gut transit times, seed dispersal

## INTRODUCTION

Frugivorous primates play an important role as seed dispersers in tropical forests (Terborgh *et al.* 2002), and a growing number of studies provide data on the potential of primates for the dispersal of seeds (Russo & Chapman 2011). Primates vary considerably in body size and ranging behaviour, influencing the types of fruit and the size of seeds ingested, as well as their potential for dispersal. In general, larger-bodied species tend to ingest larger seeds and disperse them over greater distances, although a number of other factors, such as ranging patterns, diet and gut transit times, may determine the effective contribution of the primate to the dispersal process.

Gut transit times determine the dispersal potential of a species, given that the distance travelled from the source of the seeds will be related primarily – but not exclusively – to the time the seeds are retained in the gut. Given this, the identification of the factors that determine or influence gut transit time may provide

important insights into the dispersal potential of a species, as well as the variation in this potential in relation to different ecological contexts. The available data indicate that, while body size is a primary determinant of gut transit times (Caton *et al.* 1996), it may not necessarily be a good predictor of transit times, considering the anatomical, physiological and dietary variation among taxa (Clauss *et al.* 2008, 2013; Lambert 1998).

Estimates of gut transit times are available for a number of platyrrhine species, based on the monitoring of both captive (Milton 1984, Norconk *et al.* 2002, Price 1993) and free-ranging animals (Dew 2001, Garber 1986, Julliot 1996, Oliveira & Ferrari 2000, Russo 2003, Stevenson 2000, Wehnke *et al.* 2003, 2004). While data on feeding behaviour and faecal samples may be relatively easy to obtain, it can be difficult to estimate gut transit times reliably, given the difficulty of tracing faecal residues (primarily seeds and insect fragments) to specific feeding sites, especially where the animals feed sequentially at a large number of food patches.

The present study provides data on the gut transit times and dispersal distances of seeds in free-ranging groups of the titi monkey *Callicebus coimbrai* resident at two sites

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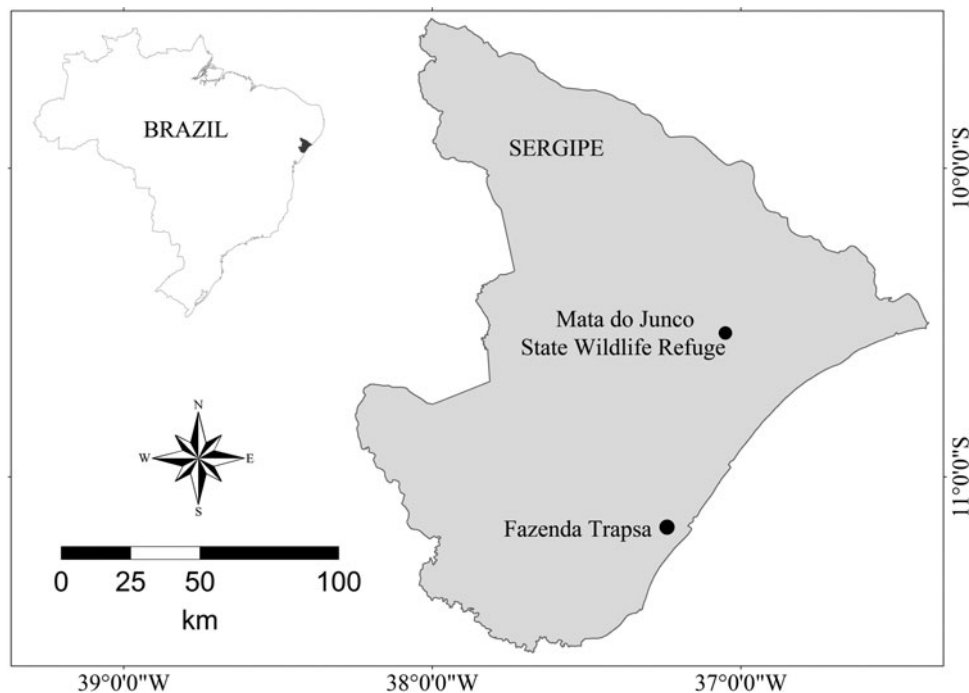


Fig. 1. Location of the *Callicebus coimbrai* study sites in the north-eastern Brazilian state of Sergipe.

in north-eastern Brazil, the first data of their kind for this small-bodied platyrrhine monkey (adult body weight in *C. coimbrai* = 1.03–1.30 kg; Kobayashi & Langguth 1999). Based on the data available for other primates (Edwards & Ullrey 1999, Remis 2000, Remis & Dierenfeld 2004), this study tested the hypothesis that differences in the feeding ecology of the species at the two study sites are reflected in significant differences in gut transit times and the potential for seed dispersal.

## METHODS

### Study sites and groups

Free-ranging groups of *C. coimbrai* were monitored at two sites in the north-eastern Brazilian state of Sergipe – the Fazenda Trapsa (11°12'S, 37°14'W) in the municipality of Itaporanga D'Ajuda, and the Mata do Junco State Wildlife Refuge (10°32'S, 37°03'W) in Capela (Figure 1). The Trapsa group inhabits an isolated 14-ha fragment of Atlantic Forest within a complex of larger fragments of up to 120 ha, while the Junco group occupies the northernmost extreme of a 516 ha fragment surrounded mostly by sugarcane plantations. The two groups nevertheless occupy home ranges of similar size, approximately 10.9 ha for the Trapsa group, and 9.1 ha for the Junco group (Baião 2013).

Mean annual precipitation and temperatures are similar at the two sites, with mean rainfall of  $1422 \pm 87.3$

mm at Fazenda Trapsa (2000–2010), and  $1347 \pm 75.7$  mm at Mata do Junco (2003–2011), and mean monthly temperatures of 22 °C–26 °C at both sites. The rainy season, when the vast majority (> 80%) of precipitation occurs normally coincides with the austral autumn and winter (April–September), but in contrast with most, but not all tropical rain forests, fruit availability tends to be higher during the late dry season (Souza-Alves 2013), even though fruit feeding was highest during the rainy season.

Both groups had been habituated to the presence of human observers in previous studies (Santana 2012, Souza-Alves *et al.* 2011). During the period of the present study, between April and July, 2012, the Trapsa group initially contained five individuals (two adult males, one adult female, one sub-adult female and one juvenile male), but the adult female disappeared in June, leaving only four individuals in the last month of the study period. The Junco group contained six individuals – an adult breeding pair, one subadult, two juveniles and an infant – throughout the study period.

### Data collection

Each study group was monitored on 5 d mo<sup>-1</sup> (except for 1 d in May at Mata do Junco) for the collection of quantitative data on foraging behaviour through the identification and mapping of fruit feeding sites and defecation events. All trees or lianas at which group

members were observed feeding on fruit were marked and identified, the position of the feeding patch was tagged using a handheld GPS model Garmin 60CSx, and the time of the visit was recorded (other data on feeding behaviour were collected, but are not presented here). All defecation events were also recorded and whenever possible, the faeces were collected in standard 50-ml plastic pots, which were kept under refrigeration until analysis in the laboratory. The samples were processed in Petri dishes in a 70% ethanol medium and examined under a Wild M3Z stereoscopic microscope, whenever necessary. All the seeds found within the faecal material were separated for identification through comparisons with material collected directly from the sources in the field, and a representative sample (5–10 seeds, when available) measured (maximum dimension) in order to provide data on seed size. The geographic coordinates of defecation sites were also recorded by GPS.

The composition of the diet was estimated simultaneously by Souza-Alves (2013) using continuous scan sampling, with a 1-min scan being conducted at 5-min intervals throughout the daily activity period of each study group, with the item being recorded for each feeding record. Data collection was non-invasive and satisfied the legal requirements of the Brazilian Environment Institute (IBAMA) for the study of non-human primates.

### Data analysis

Gut transit times – the first appearance of a marker (seed) in the faeces – were estimated by identifying the probable source of seeds found in the faecal samples. The seeds were first identified by comparison with samples of the fruits collected from the feeding sites, and the probable source of the seeds in a given faecal sample was identified by tracing back to the feeding events recorded during the preceding hours. As individuals in both groups defecated as many as six or seven times during a given day (Baião 2013), it was assumed that, in most cases – except for the earliest events of the day – that the source of the seeds found in the faecal samples was visited on the same day, although an arbitrary minimum passage time of 1 h was established a priori for the evaluation of the records. In practice, however, no faecal samples were linked to fruit sources visited within the preceding hour.

Gut transit times were estimated by subtracting the recorded time of the presumed feeding bout from that of the defecation event. When more than one possible source of the seeds in the faecal samples was identified, i.e. when two or more fruit patches of the same species were visited (or a patch was revisited) during the preceding 24 h, the event was not included in the analysis. All plant samples were identified and deposited at the Lauro Pires Xavier

**Table 1.** Composition of the diet of the *Callicebus coimbrai* study groups at the Fazenda Trapsa and RVS Mata do Junco, Sergipe, based on the proportion of feeding records collected in scan samples between April and July, 2012. Data obtained from Souza-Alves (2013: Tables 3.9 and 3.10, pp. 143–144).

Group	Percentage of feeding records identified as:				Number of feeding records
	Fruit	Seed	Leaf	Flower	
Trapsa	47.0	5.4	32.0	15.6	353
Junco	89.2	0.6	9.2	0.8	877

herbarium at the Federal University of Paraíba in João Pessoa.

Dispersal distances were estimated by mapping the coordinates of feeding trees and the corresponding defecation sites in ArcGis 9.3 and calculating the straight-line distance between the pairs of points corresponding to the source and end location of dispersal events. Given the non-parametric characteristics of the data (and the small sample size in the case of dispersal distances), between-group differences in the size and number of the seeds found in the faecal samples and dispersal distances were assessed using Mann–Whitney *U*-tests, run in BioEstat 5.0, considering  $\alpha = 0.05$ .

## RESULTS

### Feeding behaviour

On average, the Junco group visited  $11.4 \pm 5.1$  fruit feeding patches (trees and some lianas)  $d^{-1}$  during the study period ( $n = 228$ ), whereas the Trapsa group visited only  $2.5 \pm 2.1$  patches  $d^{-1}$  ( $n = 58$ ). In both groups, the diet was complemented primarily by leaves (Table 1), although in the case of the Trapsa group, a considerable number of flowers were also consumed. Overall, then, while just under half the diet of the Trapsa group was composed of potentially high-fibre items, these items contributed only 11% of the feeding records for the Junco group.

Considerable differences between sites were also found in the plant species exploited for fruit (Appendix 1). While roughly similar numbers of species (13 at Trapsa and 18 at Junco) were used during the study period at the two sites, only two – *Tapirira guianensis* and *Inga* sp. – were consumed at both sites (Jaccard similarity index = 0.069). While most fruits were small drupes and berries, which were normally ingested whole, only the pulp of some relatively large fruits (e.g. *Genipa americana*, *Passiflora* sp. and *Inga* sp.) was consumed. In some cases – *Protium*, *Manilkara* – the seeds were often spat out, although they were found in the faecal samples, indicating that at least some seeds were ingested together with the pulp.

**Table 2.** Details of the defecation events observed and faecal samples collected during the present study of *Callicebus coimbrai* at two sites in the Brazilian state of Sergipe, between April and July, 2012.

Group	Total number of defecation events observed (mean $\pm$ SD number of events per day)	Number (% of total observed) of faecal samples collected	Number (%) of faecal samples containing seeds
Trapsa	177 (8.9 $\pm$ 4.9)	113 (63.8%)	38 (33.6%)
Junco	244 (12.8 $\pm$ 7.9)	146 (59.8%)	70 (47.9%)

Slightly larger seeds, on average, were found in the faecal samples collected from the Junco group (mean maximum dimension of seed morphotypes =  $6.5 \pm 3.2$  mm) in comparison with the Trapsa group (mean =  $5.3 \pm 2.9$  mm), although the difference was not significant ( $U = 67.5$ ,  $P = 0.383$ ). Similarly, while slightly more seeds were found in the Junco samples, on average (mean number of seeds per faecal sample =  $3.0 \pm 2.8$ , maximum = 14) in comparison with the Trapsa group (mean number =  $2.1 \pm 2.1$ , maximum = 12), the difference was again not significant ( $U = 952$ ,  $P = 0.0636$ ). In addition to consuming a larger proportion of fruit in comparison with the Trapsa group, then, the faeces produced by the members of the Junco group contained larger numbers of relatively larger seeds, on average, in comparison with the Trapsa group.

### Gut transit times

We observed a total of 421 defecation events in the two study groups over the 39 d of monitoring, a mean of  $10.8 \pm 6.8$  events per observation day, with 38.4% more records being collected for the Junco group, which was expected according to its larger size (Table 2). There was considerable variation among days, however, with between four and 23 events being observed on a given day in the Trapsa group, and 1–30 in the Junco group. As the number of events we recorded on some days was lower than the number of group members, it seems likely that the total number of events was underestimated on most, if not all days, and this was reflected in the results, including the relatively small number of events for which transit times could be estimated reliably. This conclusion is reinforced by the fact that individual group members were observed defecating as many as six (Junco) or seven (Trapsa) times during a single day, and in 2013, one member of the Junco group was observed defecating 15 times during a single day (FABC, pers. obs.). In many cases, however, events were closely spaced and probably represented the residues of the same feeding event.

Faecal sample collection followed a very similar pattern in the two groups, with faecal samples being collected from approximately 60% of the observed events in both cases. However, a much larger proportion of the samples

**Table 3.** Gut transit times (h:m) and dispersal distances (m) estimated for the two *Callicebus coimbrai* study groups monitored between April and July, 2012, in north-eastern Brazil.

Variable	Trapsa group	Junco group
Daytime events		
Transit time (mean $\pm$ SD) (h)	4.87 $\pm$ 1.48	2.85 $\pm$ 0.53
Range of values	3.85–7.83	1.85–3.52
Dispersal distance (mean $\pm$ SD) (m)	200 $\pm$ 81.0	126 $\pm$ 53.4
Range of values	87.9–305	37.3–207
Number of samples collected	6	13
Overnight events		
Transit time (mean $\pm$ SD) (h)	–	15.6 $\pm$ 1.88
Range of values	–	13.6–16.1
Dispersal distance (mean $\pm$ SD) (m)	–	90.7 $\pm$ 29.5
Range of values	–	54.9–132
Number of samples collected	–	6

from the Junco group contained seeds (Table 2). This is consistent with the difference in the diet of the two groups (Table 1), but less than might have been expected according to the overall difference in fruit feeding. This is probably at least partly related to the fact that during the consumption of larger fruits – which were more typical of Junco – only the pulp was ingested. Combining this index (percentage of faeces containing seeds) with the mean number of seeds found per sample, an average of 1.44 seeds was dispersed per defecation event, overall, in the Junco group, while the value was only 0.71 in the Trapsa group.

Gut transit times could only be estimated reliably for a small portion of the samples containing seeds (Table 3), but they provide a clear measure of the difference between groups, with the minimum value recorded for the Trapsa group being 0.33 h longer than the maximum value recorded for the Junco group. Even if the outlier (7.83 h) is omitted from the Trapsa data, the mean would be  $4.27 \pm 0.35$  h, still almost 1.83 h (or 49.7%) longer than the mean value for the Junco group.

This difference is reflected in the mean dispersal distances recorded at each site (Table 3), with the mean distance recorded at Trapsa being 58.8% longer than that at Junco. Despite the significant difference found between sites ( $U = 13$ ,  $z = 2.24$ ,  $P = 0.0251$ ), there was only a weak relationship between gut transit times and dispersal distances, with the outlier transit time (7.83 h) returning only the fourth longest dispersal distance (188 m).

It was possible to trace a further six events in the Junco group back to fruit sources visited during the preceding day. These events returned a mean gut transit time of  $15.6 \pm 1.88$  h, more than five times longer than the mean recorded for daytime events. As the group typically spent more than 12 h in the nightly roost each day during the study period, however, this value equates to little more than 3 h of activity time, and the mean dispersal distance recorded for these events ( $90.7 \pm 29.5$  m,  $n = 6$ ) was considerably shorter than the mean for daytime events in the Junco group (Table 3), which may reflect differences in ranging patterns at the beginning and end of the day.

## DISCUSSION

While seed dispersal has received increasing attention in recent years (Russo & Chapman 2011, Seidler & Plotkin 2006, Shivanna & Tandon, 2014), reliable estimates of gut transit times in the wild are still unavailable for most primate species or even genera, including *Callicebus*, and the present study provides the first data for the titi monkey. In general, the daytime transit times recorded here were similar to those reported for most other platyrrhines, ranging from the small-bodied callitrichids (Garber 1986, Oliveira & Ferrari 2000, Price 1993) to the large frugivores, such as *Ateles* and *Lagothrix* (Dew 2001, Russo 2003, Stevenson 2000, Zhang & Wang 1995), although retention times may vary considerably in these species (Caton *et al.* 1996). Only the folivorous howlers (*Alouatta* spp.) present longer transit times (Julliot 1996, Milton 1984, Pavelka & Knopff 2004, Souza 1999, Zhang & Wang 1995), which appear to be related to the high-fibre diet of these monkeys (Clauss *et al.* 2008).

However, the only data available for the sakis (*Pithecia*), which not only represent the genus closest to *Callicebus* in phylogenetic terms (Silva *et al.* 2013), but also the most similar in body size and ecology (Norconk & Setz 2013), indicate much longer gut transit times, of 20 h for *Pithecia monachus* (Milton 1984) and 15 h for *Pithecia pithecia* (Norconk *et al.* 2002). The latter authors proposed that the relatively long transit times recorded in *Pithecia* may be related to the predation of seeds by the sakis, although Milton (1984) recorded much shorter times (5 h) for captive *Cacajao calvus* and *Chiropotes albinasus*, larger-bodied pitheciines that feed on much higher proportions of seeds in the wild (Barnett *et al.* 2013, Veiga & Ferrari 2013). These times are consistent with those recorded in field studies of the similarly sized capuchins, *Cebus* spp. (Rowell & Mitchell 1991, Wehnke *et al.* 2003, 2004, Zhang & Wang 1995).

Overall, then, while the daytime transit times recorded in the present study for *Callicebus coimbrai* are more consistent with those from other platyrrhine field studies, the overnight times recorded for the Junco group are more

similar to those recorded in captive *Pithecia*. There appear to be a number of reasons for assuming that this is related more to methodological differences among studies rather than absolute contrasts in the digestive tract or physiology of these species, that might reflect distinct dietary adaptations. One is the fact that Ferrari & Lopes (1995) found no pronounced difference in the gut morphology of *Callicebus* and *Pithecia*. In addition, a similar degree of difference has been found between daytime and overnight events in *Lagothrix lagothricha* (Stevenson 2000) and *Callithrix jacchus* (Caton *et al.* 1996). The considerable variation in gut transit times encountered in most studies emphasizes the importance of standardizing procedures, which can be problematic in the field, due to the lack of control on most variables. In the present study, daytime and overnight events were analysed separately to ensure the reliability of comparisons between sites, and this would be a recommendation for future studies.

While it was possible to trace only a small proportion of the observed defecation events to specific feeding trees, differences in estimated gut transit times between sites are considerable – the mean times recorded for the Trapsa group were at least half as long again as those recorded during the daytime for the more frugivorous Junco group. Similar variation has been recorded in other primates (Edwards & Ullrey 1999, Remis 2000, Remis & Dierenfeld 2004). Garber (1986) and Stevenson (2000) also found evidence of the possible contribution of seed size to transit time. In the present study, however, no significant difference was found between groups in the size of the seeds ingested, nor the number of seeds per faecal sample.

The marked differences in gut transit times recorded between sites were also reflected in dispersal distances, with significantly longer distances being recorded in the Trapsa group. While the more folivorous members of this group ingested far fewer seeds than those of the more frugivorous Junco group, then, this difference in their diets may have contributed to the greatly enhanced dispersal distances recorded at Fazenda Trapsa.

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**Appendix 1.** Plant species exploited for fruit by the Trapsa and Junco *Callicebus coimbrai* study groups during the study period (April–July 2012).

Taxon		Fruit exploited (in months) by the:	
		Trapsa group	Junco group
Anacardiaceae	<i>Tapirira guianensis</i>	May	May, June, July
Annonaceae	<i>Xylopia aromatica</i>		April
Burseraceae	<i>Protium heptaphyllum</i>		April–June
Cucurbitaceae	<i>Gurania subumbellata</i>		June, July
Erythroxylaceae	<i>Erythroxylum</i> sp.		April
Fabaceae	<i>Inga</i> sp.	May, June	
Malpighiaceae	<i>Byrsonima sericea</i>		April
Melastomataceae	sp. 1		June, July
Myrtaceae	<i>Eugenia ligustrina</i>	May, June	
	<i>Campomanesia</i> sp.		July
	sp. 1	April, June	
Nyctaginaceae	<i>Guapira</i> sp.		July
Passifloraceae	<i>Passiflora</i> sp.	June	
Rubiaceae	<i>Genipa americana</i>		May, June
	<i>Guettarda viburnoides</i>		May
	<i>Guettarda</i> sp.		May
	<i>Salzmannia nitida</i>		May
Sapotaceae	<i>Manilkara</i> sp.		April, May
Urticaceae	<i>Cecropia</i> sp.	April	
Vitaceae	<i>Cissus</i> sp.	July	
Unidentified	6 spp.	April–July	
	4 spp.		April–July