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When to Feed on Gums: Temporal Patterns of Gummivory in Wild Tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Callitrichinae)

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This study examines the temporal patterning of gum feeding in two species of sympatric tamarin monkeys, *Saguinus mystax* and *Saguinus fuscicollis*, during the diurnal activity period. The number and duration of visits to gum sources and number of gum feeding records are used as parameters to analyze the gum feeding itinerary. Both visits to gum sources and gum feeding records show clear peaks in the afternoon, and the duration of visits to gum sources is longer in the afternoon. The observed pattern is interpreted as a behavioral strategy to prolong the time gum remains in the gastrointestinal tract. Only through prolonged gut retention can the b-linked carbohydrates be subjected to microbial fermentation. It is suggested that feeding itineraries receive more attention in primate field studies to provide information that can help to identify optimal strategies of feeding regimens under captive conditions. Zoo Biol 18:459–471, 1999. © 1999 Wiley-Liss, Inc.

Key words: gum feeding; digestion; b-linked carbohydrates; nutritional ecology

INTRODUCTION

Studies on the feeding ecology of primates usually focus on the type, species identity, quantity, and chemical composition of dietary items; on the size and spatial distribution of food patches; and on seasonal or phenological influences on food choice [Clutton-Brock, 1977; Waterman, 1984; Conklin-Brittain et al., 1998]. Temporal patterns of food choice during the activity period (i.e., the day in diurnal primates and the night in nocturnal primates) have received much less attention. However, the type and quality of food and morphological and physiological characteristics of

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the consumer may strongly influence the temporal patterning of food choice and consumption. Understanding this relationship may enhance our comprehension of the nutritional ecology and may provide information that helps to optimize husbandry and nutrition under captive conditions. Chapman and Chapman [1991] reviewed the available information on feeding itineraries and found that leaves are usually consumed before resting periods or sleeping. Such a pattern can be explained as a means to reduce the energy burden of moving around with a stomach full of bulky material, to enhance the digestion of bulky material, to deal with potentially deleterious secondary plant compounds, or to exploit leaves at times when they provide the best nutritional reward [Chapman and Chapman, 1991; Ganzhorn and Wright, 1994].

Most tamarin species studied so far feed regularly on gums exuding from wounds of the bark of trees, palms, and lianas [Hladik and Hladik, 1969; Izawa, 1978; Terborgh, 1983; Garber, 1984, 1988; Soini, 1987; Ramirez, 1989; Egler, 1992; Peres, 1993; Hardie, 1995; Power and Oftedal, 1996], although their proportion in the overall diet is low when compared to specialized gum and sap feeders like marmosets (*Callithrix* sp.) and pygmy marmosets (*Cebuella pygmaea*). Bark gums (for convenience, the word gum throughout the text refers to bark gums) are composed of b- linked carbohydrates that cannot be enzymatically digested by mammals [Soest, 1994]; the energy contained in the carbohydrates can be made available only through microbial fermentation. Specialized gum feeders like fork-tailed lemurs (*Phaner furcifer*), needle-clawed bushbabies (*Euoticus elegantulus*), and marmosets possess an enlarged cecum and colon where digesta can be retained and subjected to microbial fermentation [Vermes and Weidholz, 1930; Chivers and Hladik, 1980; Martin et al., 1985; Power, 1991; Ferrari and Martins, 1992; Ferrari et al., 1993]. Experimental work by Power and Oftedal [1996] suggested that gut retention time plays an important role in gum digestion but cautioned against a simple relationship. They demonstrated that the duration of gut passage increased in *Callithrix jacchus* and *C. pygmaea* when gum arabic was added to the diet but remained unchanged in *Saguinus fuscicollis*, *Saguinus oedipus*, and *Leontopithecus rosalia*. Caton et al. [1996] showed that *C. jacchus* are able to retain selectively fluid phase digesta to make them accessible to microbial fermentation. Tamarins lack morphological adaptations of the gastrointestinal tract that would prolong the retention of digesta. However, a prolonged passage rate can be obtained through the temporal patterning of feeding. Items consumed before retiring for the night will remain in the gut overnight and thus can be subjected to microbial fermentation that is required for gum digestion. This assumption was tested with data on the temporal patterning of gum feeding in two species of sympatric tamarin monkeys, *Saguinus mystax* and *S. fuscicollis*, obtained during several field studies in Peruvian Amazonia.

METHODS

Study Site, Study Periods, and Subjects

Our studies were conducted at the Estación Biológica Quebrada Blanco (EBQB). The EBQB is located at 4°21'S 73°09'W on the right bank of Quebrada Blanco, a tributary of the Río Tahuayo in northeastern Peruvian Amazonia. (For further details of the study site, see Heymann [1995].) Observations on habituated tamarins were conducted between July 1985 and May 1986 (415 hours), June and September 1990 (345 hours), and in August 1995 (160 hours) (E.W.H.) and between November 1994 and November 1995 (1,440 hours) (A.C.S.). Studies by E.W.H. focused on moustached tamarins, *S. mystax*, whereas A.C.S. also included saddle-back tamarins, *S. fuscicollis*, in his study. Information on the size and composition of the study groups is provided in Heymann [1995] and Smith [1997].

Data Collection

Tamarin groups were usually observed for entire days, i.e., from leaving a sleeping site in the early morning until retiring to a sleeping site in the course of the afternoon. Activities of all visible group members and the location of the group within the home-range area were recorded with an instantaneous scan sampling method [Martin and Bateson, 1993] at 5- (1985/86, 1990) or 10-minute intervals (1994/95). Furthermore, for all visits to a feeding site, time of entering by the first tamarin and time of leaving by the last tamarin were recorded (this parameter was not available for the 1985/86 study period).

Data Analysis

We distinguished two parameters to analyze the temporal distribution of gum feeding: 1) gum feeding records: all individual activity records from the instantaneous scan sampling when a tamarin was feeding on gum and 2) visits to gum source: all visits to a gum source by one, several, or all group members, independent of the number of animals visiting the gum source, but at least one animal must have been seen feeding on gum during the visit. The duration of visits to gum sources was determined as the time that elapsed between the first tamarin entering and the last tamarin leaving a gum source. We used visits to gums sources in addition to feeding records because with the 10-minute sampling intervals much gum feeding would have gone unrecorded because visits were on average much shorter than 10 minutes. For the analyses, data collected by A.C.S. between November 1994 and November 1995 and by E.W.H. in August 1995 were combined because they concerned the same group and thus were not independent. In the first step, we calculated the number of gum feeding records and the number of visits to gum sources for each hour of the day during which the tamarins were active. The frequency (per hour) of gum feeding records and of visits to gum sources was calculated for each hour of the day. The respective profiles are provided as a description of the temporal pattering of gum feeding. This profile was compared with the respective profile of feeding on gums surrounding seeds in pods of *Parkia* sp. (Mimosaceae), hereafter called pod gums. We used pod gums for comparison because these are often lumped together with other gums [Ramirez, 1989], although there are reasons to assume different qualities (see Discussion section). We then calculated the number of gum feeding records and the number of visits to gum sources before and after 1200 hours and compared these values to expected values that were calculated under the assumption that gum feeding is evenly distributed over the day. Observed and expected values were compared with the *G*-test. Mean duration of visits to gum sources before and after 1200 hours were compared with the Mann-Whitney *U*-test of the non-parametric module of STATISTICA® 5.0. The 1200-hour criterion was used because tamarins retire to a sleeping site on average at approximately 1600 hours [Smith, 1997; Heymann, unpublished data], and according to Castro [1991], gums found in fecal samples are changed in color and consistency after >4 hours of gut passage. The α-level was set at 0.05 for all analyses.

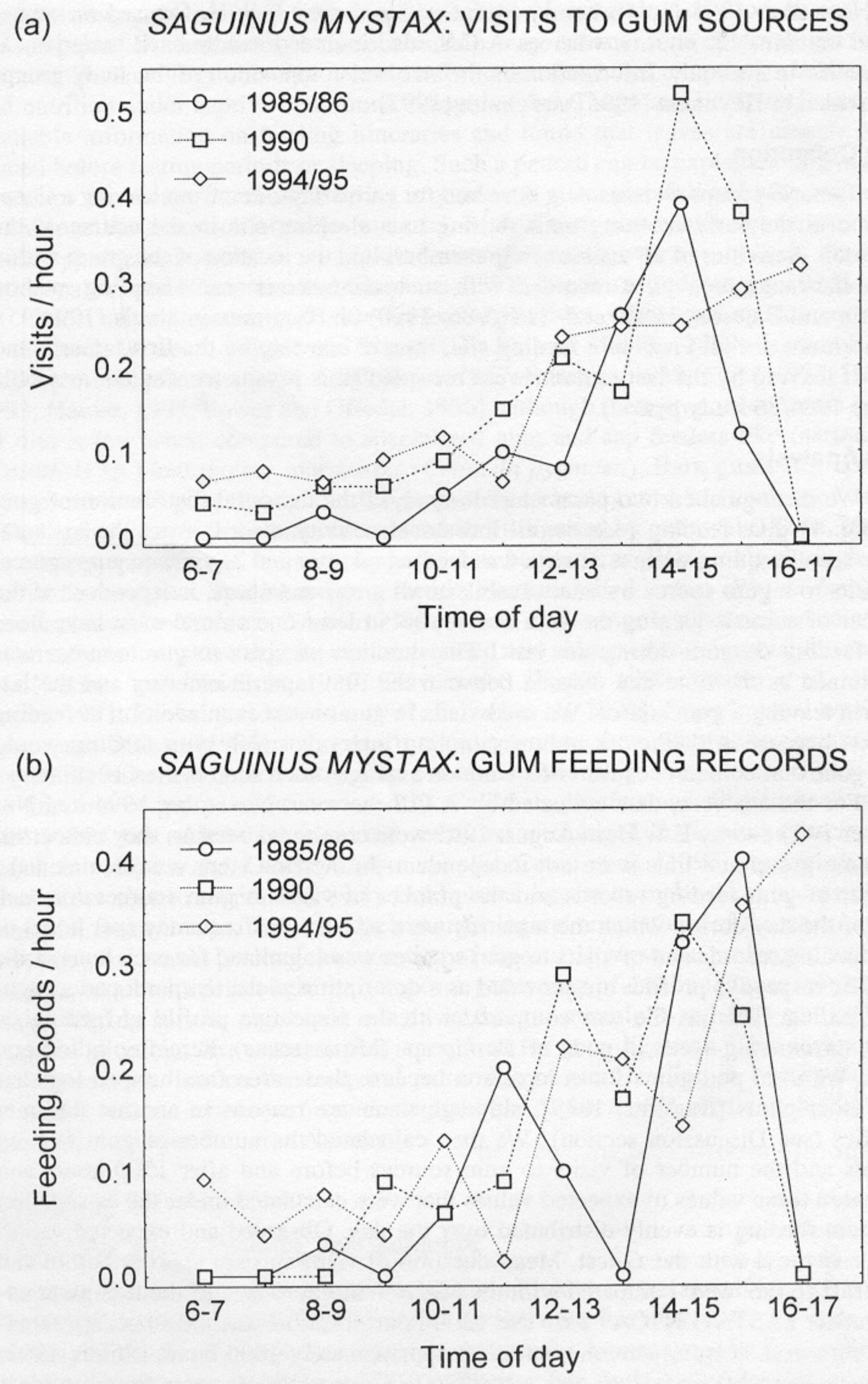

Fig. 1. Temporal distribution of visits to gum sources and gum feeding records in *Saguinus mystax* (**a, b**) and *Saguinus fuscicollis* (**c**).

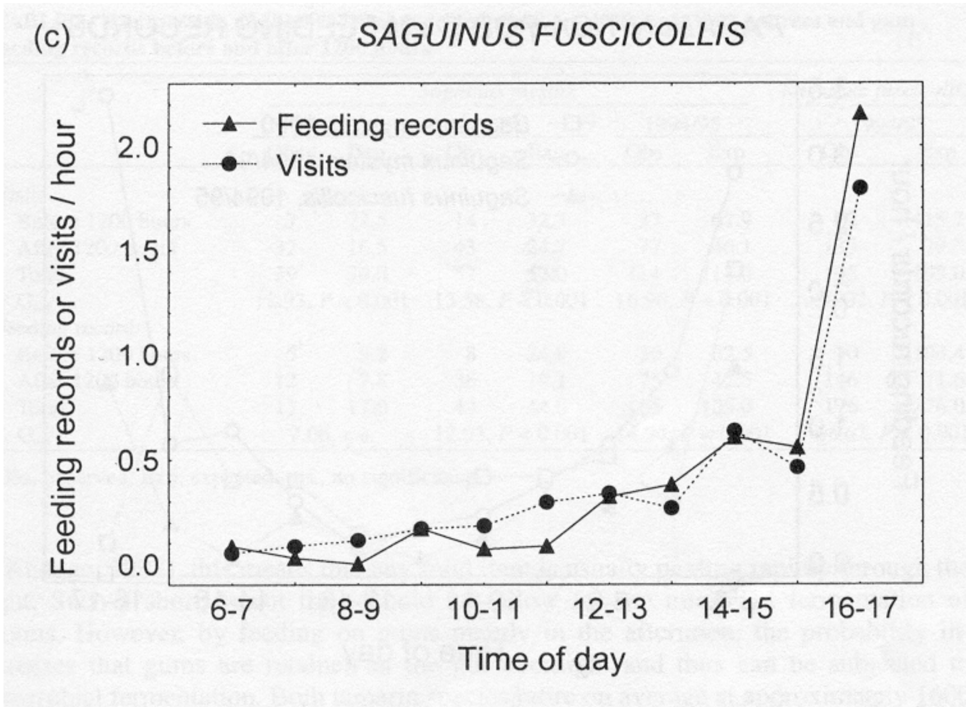

Figure 1c.

RESULTS

Sources of Gum

Feeding on gums accounted for 3.8% (1985/86), 5.5% (1990), and 2.3% (1994/ 95) of plant-based food in *S. mystax*, and for 7.3% in *S. fuscicollis*. *S. mystax* and *S. fuscicollis* exploited the gums of more than 20 identified and approximately the same number of unidentified plant species (see Appendix). The most important species during all study periods both in terms of number of feeding records and number of visits was *P. igneiflora*. Other species, e.g., *Jessenia* (= *Oenocarpus*) *bataua*, were used consistently during all study periods but less frequently. Many other species were exploited only during one or two study periods, either intensively like *Acacia* sp. or only sporadically.

Temporal Patterns of Gum Feeding

Gum feeding is not evenly or randomly distributed over the activity period of the tamarins. Rather, both visits to gum sources and gum feeding records show peaks in the afternoon in both *S. mystax* and *S. fuscicollis* (Fig. 1). This is in marked contrast to the temporal distribution of feeding on *P. nitida* pod gums in both species (Fig. 2).

Observed and expected number of visits and of feeding records differ significantly before and after 1200 hours (Table 1). Furthermore, the duration of visits to gum sources differs significantly before and after 1200 hours for *S. mystax* in 1990 and for *S. fuscicollis* in 1994/95 (Fig. 3).

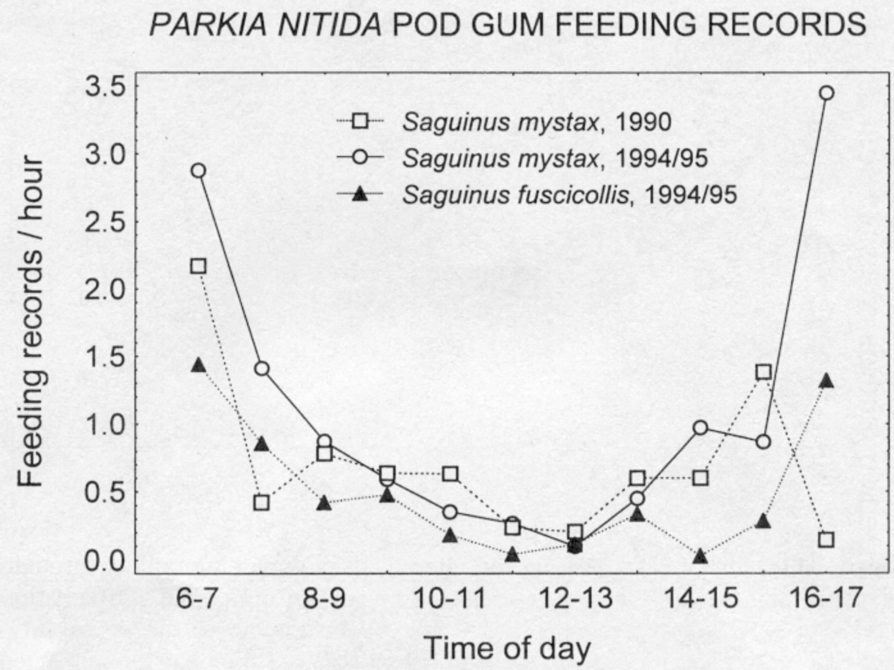

Fig. 2. Temporal distribution of feeding records on *Parkia* pod gum in *Saguinus mystax* and *Saguinus fuscicollis*.

DISCUSSION

In this study, a clear pattern emerged with regard to the temporal patterning of gum feeding in *S. mystax* and *S. fuscicollis*: gum feeding is most pronounced, both in terms of number of visits to gum sources and number of feeding records, in the afternoon. Furthermore, there is also a trend for visits to gum sources to be longer in the afternoon than during the morning. Only Ramirez [1991] provided comparative data for *S. mystax*. In contrast to our results, she found a maximum of number of visits to gum sources in the morning. However, the duration of visits was longer in the afternoon, and Ramirez [1991] concluded that moustached tamarins spent more time gum feeding in the afternoon. No information is available on the gum feeding itinerary for other tamarin species.

A simple explanation for this feeding itinerary might be that plants produce more gums in the afternoon. The botanical literature does not provide pertinent information. However, given the function of gums in wound sealing and protection of the plant from infection [Smith and Montgomery, 1959; Kozlowski et al., 1991; Guariguata and Gilbert, 1996], diurnal variation in gum production is unlikely. Furthermore, the tamarins do not only feed on single droplets of gum but also on bulks of gum accumulated over several days that they could readily exploit at any time of the day.

We offer an alternative hypothesis for the feeding itinerary that relates to the digestive physiology of tamarins. *S. mystax* and *S. fuscicollis* have a short transit time through the gastrointestinal tract. The mean transit time of swallowed seeds voided the same day is 2.5 hours in *S. mystax* and 2.2 hours in *S. fuscicollis* [Knogge, 1998]. Because seeds are found in 95% and 96%, respectively, of fecal samples

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TABLE 1. Comparison of observed and expected numbers of visits to gum sources and gum feeding records before and after 1200 hours

	Saguinus mystax						*Saguinus fuscicollis*	
	1985/86		1990		1994/95		1994/95	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Visits								
Before 1200 hours	7	22.5	14	32.3	37	67.9	62	115.7
After 1200 hours	32	16.5	43	24.7	77	46.1	133	79.3
Total	39	39.0	57	57.0	114	114.0	195	195.0
G_{adj}	12.93, $P < 0.001$		13.58, $P < 0.001$		16.96, $P < 0.001$		30.02, $P < 0.001$	
Feeding records								
Before 1200 hours	5	9.2	8	24.9	30	62.5	30	104.4
After 1200 hours	12	7.8	36	19.1	75	42.5	146	71.6
Total	17	17.0	44	44.0	105	105.0	176	176.0
G_{adj}	2.06, n.s.		12.03, $P < 0.001$		14.94, $P < 0.001$		66.62, $P < 0.001$	

Obs, observed; Exp, expected; n.s., no significance.

[Knogge, 1998], this means that any food item is usually passing rapidly through the gut. Such a short transit time would not allow for the microbial fermentation of gums. However, by feeding on gums mainly in the afternoon, the probability increases that gums are retained in the gut overnight and thus can be subjected to microbial fermentation. Both tamarin species retire on average at approximately 1600 hours (range, approximately 1400–1730 hours [Smith, 1997; Heymann, unpublished data]). Seeds not voided with the feces the same day they were ingested are retained in the gut on average for 16.5 hours [Knogge, 1998]. Gums consumed in the afternoon and not voided with the feces before retirement thus have a similar retention time that would allow for microbial fermentation. Castro [1991] observed that gum droplets in fecal samples appear unaltered if gut passage was less than 2 hours but had changed in color and consistency after >4 hours of gut passage. Tamarins do not defecate during the night [Power, 1991] and thus would not already void gums with their feces after a short transit time.

Prolonged retention of gums in the gut would be meaningless if most time were spent in the rectum where fermentation products (volatile fatty acids) cannot be absorbed. This is, however, highly unlikely. The rectum empties as a reflex to distention [Schmidt and Thews, 1990], and rapid filling would cause defecation during the night, which, as mentioned previously, tamarins do not do. There may also be thermoregulatory savings in consuming gums before retiring for the night. The microbial fermentation of the complex structural carbohydrates contained in gums produces heat that is usually eliminated as a waste product [Power, 1991]. However, this heat may be important to small-bodied animals like tamarins, especially during the night when their body core temperature is reduced [Hampton, 1973; Petry, 1991].

In the opportunistically gum feeding *Coua cristata* (Cuculidae), a diurnal frugivorous-insectivorous bird of Madagascar, 83% of visits to gum sources (*Terminalia* sp., Combretaceae) were observed in the afternoon after 1300 hours [Charles-Dominique, 1976]. Hanuman langurs, *Presbytis entellus*, show peaks of gum feeding between 0830 and 0930 hours and between 1430 and 1530 hours, but remain active until 1900 to 2000 hours [Winkler, 1988]. As folivorous primates, they possess a

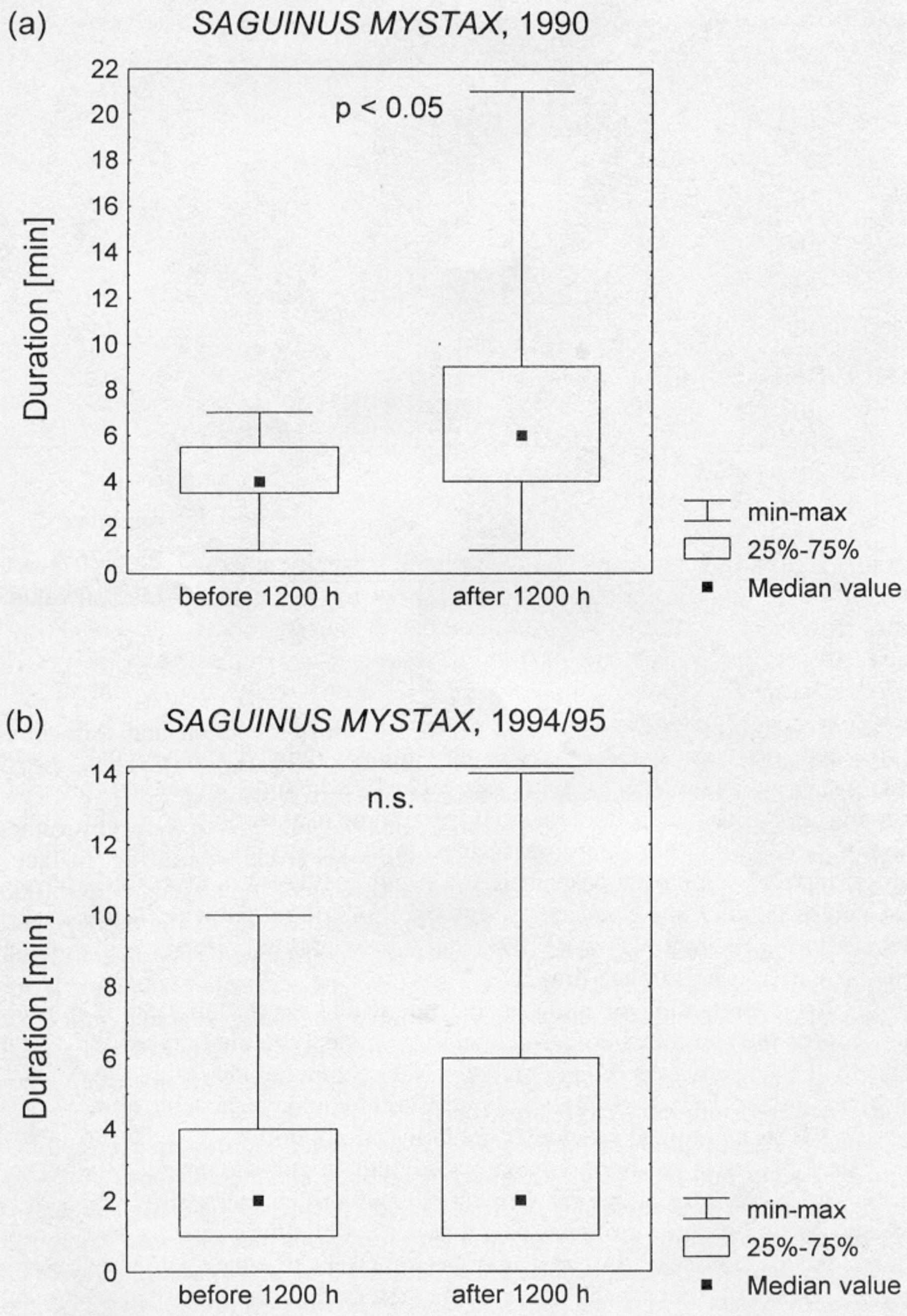

Fig. 3. Duration of group visits to gum sources before and after 1200 hours. **a:** *Saguinus mystax*, 1990 study period (U = 123.000, $Z_{adj} = -2.139$, $N_1 = 12$, $N_2 = 35$); **b:** *Saguinus mystax*, 1994/95 study period (U = 1,085.000, $Z_{adj} = -0.641$, $N_1 = 34$, $N_2 = 69$); **c:** *Saguinus fuscicollis*, 1994/95 study period (U = 2,956.500, $Z_{adj} = -3.261$, $N_1 = 62$, $N_2 = 133$).

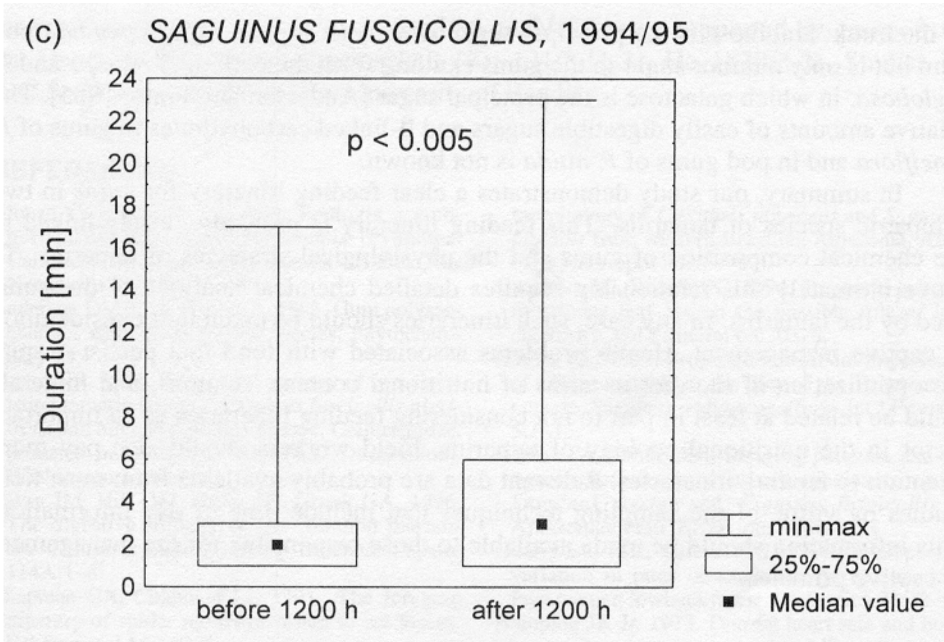

Fig. 3 (continued).

specialized gastrointestinal tract that allows prolonged retention and fermentative degradation of digesta [Chivers and Hladik, 1980; Chivers, 1994]. Thus, they are less obliged to position gum feeding temporarily before retiring.

Specialized gummivores with morphological adaptations of their gastrointestinal tract are not expected to increase gum consumption before retiring. In fact, *C. pygmaea* shows a peak in gum feeding at the beginning of the activity period (0600– 0700 hours) while bark gouging was concentrated at the end of the activity period (1700–1800 hours) [Ramirez et al., 1977]. *C. jacchus* shows peaks of gum feeding and gouging between 0600 and 0700 hours and between 1600 and 1700 hours [Alonso and Langguth, 1989], but this study did not differentiate between actual gum feeding and gouging. The nocturnal *P. furcifer* shows a peak in the number of visits to gum sources between 1800 and 1830 hours, i.e., at the beginning of its nocturnal activity period [Charles-Dominique and Petter, 1980].

The observed pattern of gum feeding is in marked contrast to the feeding on *Parkia* pod gums and to feeding on fruit pulp, which show peaks both in the early morning and the afternoon before retiring (Fig. 2) [Smith, 1997]. This indicates that the chemical composition of pod gums is different from that of gums. Such differences would be expected considering the different function of these gums. Gums serve to seal wounds and protect the plant from infection (see previously). Pod gums, however, probably function to attract seed dispersers in the absence of fruit pulp [Hopkins, 1983] and might be modified arils [D.J. Chivers, pers. comm. to A.C. Smith, 1997]. In fact, seeds of *Parkia* are swallowed by both species of tamarins and dispersed with their feces, remaining viable after deposition [Knogge, 1998]. One might therefore expect that pod gums should be richer in simple, more readily digestible carbohydrates. There is some evidence that within the genus *Parkia* gums of seed pods have a different composition than those produced in response to damage of the trunk: arabinose is the principal sugar after hydrolysis in *Parkia pendula* pod gum but is only a minor sugar in the gums exuding form the bark of *P. bicolor* and *P. biglobosa,* in which galactose is the principal sugar [Anderson and Pinto, 1985]. The relative amounts of easily digestible sugars and b-linked carbohydrates in gums of *P. igneiflora* and in pod gums of *P. nitida* is not known.

In summary, our study demonstrates a clear feeding itinerary for gums in two sympatric species of tamarins. This feeding itinerary is probably closely linked to the chemical composition of gums and the physiological strategies of tamarins. To prove ultimately this relationship requires detailed chemical analyses of the gums used by the tamarins. In any case, such itineraries should be taken into consideration in captive management. Health problems associated with food that persist despite the optimization of the diet in terms of nutritional content, vitamins, and minerals could be related at least in part to not considering feeding itineraries as an important factor in the nutritional ecology of tamarins. Field workers should also pay more attention to feeding itineraries. Relevant data are probably available from most field studies by virtue of the sampling techniques that include time of day information. This information should be made available to those responsible for the management of captive primates.

CONCLUSIONS

1. Wild moustached (*Saguinus mystax*) and saddle-back tamarins (*Saguinus fuscicollis*) show a gum feeding itinerary: gums are preferably consumed in the afternoon, as measured by the number and duration of visits to gum sources and the number of gum feeding records.
2. The gum feeding itinerary is interpreted as behavioral strategy to prolong the time that the gums are retained in the gastrointestinal tract. Only through prolonged gut retention can b-linked carbohydrates be subjected to microbial fermentation.
3. We suggest that more attention be paid to feeding itineraries in field studies of primates. Such information may help to identify optimal strategies for feeding schedules in captive primates.

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APPENDIX. List of plant species used as gum sources

Family/Species	Study period 1985/86	1990	1994/95
Anacardiaceae			
Tapirira guianensis			m,f
Araceae			
Heteropsis spruceana			f
Arecaceae			
Catoblastus drudei			m
Iriartea (= *Socratea*) *exorrhiza*	m		m,f
Jessenia (= *Oenocarpus*) *bataua*	**m**	m	m,f
Wettinia augusta	**m**		m,f
Boraginaceae			
Cordia nodosa			f
Chrysobalanaceae			
Licania sp.			f
Combretaceae			
Buchenavia guianensis			m,f
Elaeocarpaceae			
Sloanea floribunda			m,**f**
Sloanea sp.			f
Fabaceae			
Acacia sp.			m,**f**
Erythrina glauca			f
Inga sp.			f
Parkia igneiflora	**m**	**m**	**m**,**f**
Parkia nitidia			m,f
Peltogyne altissima			**m**,**f**

(*continued*)

APPENDIX (continued).

Moraceae			
Pourouma cecropiaefolia			f
Ochnaceae			
Cespedezia spathulata			f
Sapotaceae			
Undetermined			f
Violaceae			
Leonia cymosa			m,f
Vitaceae			
Cissus sicyoides			f
Vochysiaceae			
Ruizterania trichanthera			f
Undetermined species			
# 85/141	m		
# 85/780	m		
# 85/807	m		
# 85/825	**m**		
# 85/904	**m**		
# 85/938	m		
# 90/169		**m**	
# 90/192		m	
# 572			m
# 582			f
# 606			f
# 848			m,f
# 853			f
# 903			f
# 914			f
# 998			f
# 1070			f
# 1122			m,f
# 1378			f
# 1667			f

m; used by *Saguinus mystax*; f; used by *Saguinus fuscicollis*; bold m or f indicate that this plant species accounted for > 5% of gum feeding records or visits to gum sources for the respective tamarin species.