

Influences on gum feeding in primates

Andrew C Smith⁰

Animal and Environmental Research Group, Department of Life Sciences, Anglia Ruskin University, East Road, Cambridge CB1 1PT U.K.

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Abstract This chapter reviews the factors that may affect patterns of gum feeding by primates. These are then examined for mixed-species troops of saddleback (*S. fuscicollis*) and mustached (*S. mystax*) tamarins. An important distinction is made between gums produced by tree trunks and branches as a result of damage and those produced by seed pods as part of a dispersal strategy as these may be expected to differ in their biochemistry. Feeding on fruit and *Parkia* seed pod exudates was more prevalent in the morning whereas other exudates were eaten in the afternoon. This itinerary may represent a deliberate strategy to retain trunk gums in the gut overnight, thus maximising the potential for microbial fermentation of their β -linked oligosaccharides. Both types of exudates were eaten more in the dry than the wet season. Consumption was linked to seasonal changes in resource availability and not the tamarins' reproductive status providing no support for the suggestion that gums are eaten as a primary calcium source in the later stages of gestation and lactation. The role of availability in determining patterns of consumption is further supported by the finding that dietary overlap for the trunk gums eaten was greater between species within mixed-species troops within years than it was within species between years. These data and those for pygmy marmosets (*Cebuella pygmaea*) suggest that patterns of primate gummivory may reflect the interaction of preference and availability for both those able to stimulate gum production and those not.

Introduction

Animals often eat different foods at different times, with feeding patterns varying over the course of a day as well as seasonally. Physiological requirements, availability, accessibility, and competition may all serve to shape what is eaten, how much is eaten, and when it is eaten. This chapter examines the patterns of exudativory within two associating species of tamarins (*Saguinus* spp.), with the aim of understanding what influences their gum feeding.

When considering patterns of gummivory, it is important to note exactly what type of gum is being eaten as chemical composition and availability may vary not only between exudate species but also with the site of production. This may be particularly true when considering exudates produced at trunks and branches as a result of damage and those produced by some plants around seeds in bean-like pods as part of their seed dispersal strategy, hereafter referred to as trunk and pod gums respectively. In the latter case, the exudates function as a reward to encourage their consumption by primates and other dispersers which then spread the seeds away from the parent tree when they defecate, a strategy referred to as endozoochory (Hopkins, 1983; Peres 2000).

Exudates may provide primates with a potentially significant source of carbohydrates, protein and certain minerals, notably calcium (Bearder and Martin 1980; Garber 1984; Nash and Whitten 1989; Heymann and Smith 1999). However, they are typically composed of β -linked oligosaccharides which are not digestible by mammalian enzymes; microbial fermentation is required to unlock their energy (Soest, 1994; Power and Oftedal 1996). The nutritional composition of pod gums which have evolved to attract vertebrate consumers may be expected to differ from those produced from trunks and branches as a result of damage, with

the former having a greater proportion of more easily digested simple sugars. Primates may therefore show a difference in feeding patterns between these two categories of gum.

Sugar content is not the only factor of gum biochemistry that may influence feeding, toxic and beneficial secondary compounds and elements may all play a role. Although compounds with hypolipidemic, antibiotic and detoxifying effects may be found in some gums (Johns et al. 2000), the high calcium content of gums relative to fruits has been used to explain their inclusion in the diet of both Old and New World primates (e.g. Bearder and Martin 1980; Garber 1984). Consequently gum consumption may be expected to alter according to calcium requirements; with females showing an increase in the later stages of gestation and lactation (Garber 1984). More specifically gummivory has been linked to insectivory in primates, with gums suggested to provide a year-round source of calcium to balance the functionally high phosphorus of the arthropod component of the diet of insectivorous primates (the majority of an insect's calcium being bound in chitin [Uvarov, 1966], inaccessible to the majority of anthropoid primates which lack chitinase [Garber 1984]). However, it is now known that tropical figs (*Ficus* spp.) can contain higher concentrations of calcium than exudates, and as such they may represent the main dietary source of this mineral (O'Brien et al. 1998; Smith 2000).

The majority of primates lack the dental adaptations that allow marmosets (*Callithrix* spp.) and a few other species to stimulate gum flow through gouging. As such, their patterns of exudate consumption may be principally determined by the availability and accessibility of exudates. The exudates that non-gouging primates could consume are trunk gums produced in response to a pathological condition, insect or other mechanical damage, or the unhealthy state of the plant due to other environmental factors (Glicksman, 1969; Meer, 1980; Adrian

and Assoumani, 1983) or pod gums produced as part of a dispersal strategy. The species and quantities of the exudates eaten will be a product of the somewhat random process of their generation and any preferences or nutritional requirements of the primates consuming them. Consequently greater variation may be expected between groups or between years in the exudate proportion of the diet when compared to other more reliable resources such as fruit or animal prey.

This chapter has two main aims. The first is to investigate patterns of gummivory, both at day and seasonal scales, taking into account trunk gums and endozoochorous pod gums. The second is to examine overlap in gum species exploited, both at a local scale for sympatric primates within and between years. These are achieved using data from field studies of associating saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*).

Methods

Three mixed-species troops of saddleback and mustached tamarins were observed at the Estación Biológica Quebrada Blanco (EBQB) (4°21'S 73°09'W). The site is located approximately 1 km northwest from the right bank of the Quebrada Blanco in north-eastern Peru. The Quebrada Blanco is a white water tributary of the Río Tahuayo which is, in turn, primarily a black water tributary of the Río Amazonas (for details see Heymann & Hartmann 1991). The annual rainfall at EBQB is 2740 ± 454 mm (n=5 years). The climate at EBQB can be divided into wet and dry seasons. The wet season, characterized by higher rainfall, runs from February until May and the dry season from June to January (see Smith et al. 2004).

Troop 1 was observed between November 1994 and December 1995 for 141 full days and initially was comprised of five saddleback (three males, two females) and five mustached

tamarins (two males, three females). Troop 2 was observed between January and December 2000 for 112 full days and was initially comprised of four saddleback (two males, two females) and five mustached tamarins (three males and two females). Troop 3 was observed between July and December 2000 for 36 full days and initially comprised eight saddleback (four males, four females) and eight mustached tamarins (five males and three females). See Smith et al (2002; 2007) for details of changes in group composition over the study period. Although comprising totally different individuals, Troops 1 and 2 occupied almost the same home range approximately five years apart. Troop 3's home range was adjacent to that of Troop 2's. Troop 1 was observed for approximately 14 days each month with each species being the focus of observations for half the time. Troop 2 was similarly observed until July 2000. From July 2000 observations were split between Troops 2 and 3 with each troop being observed for eight days. As for Troop 1, each species was the focal for half of the time. The tamarins were followed from when they left their sleep tree in the morning until they entered their next sleep tree in the afternoon. Continuous recording was used to collect data on all observed instances of feeding on plant parts, with the number of tamarins feeding and the length of time for which they fed being noted. Feeding was defined as actively ingesting or manipulating food and bouts were measured to the nearest minute.

Data Analysis

For each feeding bout the number of tamarin feeding minutes was calculated by multiplying the number of tamarins feeding by the number of minutes they fed for; one "tamarin feeding minute" equals one tamarin feeding for one minute. Differences in group size were accounted for by dividing this value by the number of tamarins present to give the number of

tamarin feeding minutes per group member. This was summed for the two halves of each day, 0500 – 1100 hr and 1100 – 1700 hr, to give a daily total time spent feeding per group member. The amount time spent feeding on each of the three plant parts in the two halves of the day were compared using paired t-tests, with data restricted to days when the part in question was consumed. Data points were normally distributed, and were considered independent as there is no reason to suspect that temporal feeding itineraries would be correlated between days. The effects of troop and species on the mean time spent feeding on each of the three plant parts per day was examined using ANOVAs. Here the unit of analysis was the month to avoid problems with repeated sampling and autocorrelation. For these analyses data were restricted to July to December when all three groups were observed. The effect of season was analysed using unequal variance t-tests to account for the unequal number of wet and dry season months. The unit of analysis was the month, with mean daily feeding times calculated for each month. Troop 3 was excluded from this analysis as it was only observed during the dry season. It was also excluded from calculations of dietary composition for the same reason. The number of feeding bouts in the first and second half of each day was analysed using χ^2 with Yates' correction. Dietary overlap was examined via Schoener's (1968) index of niche overlap (O_{ij}). This index takes into account the relative proportions of each item in the diet and varies between between 0.00 (no overlap) to 1.00 (complete overlap). It was calculated from the formula:

$$O_{ij} = 1 - 0.5 \sum |p_i - p_j|$$

Where:

p_i = proportion of i's feeding records for each of a set of resources

p_j = proportion of j's feeding records for each of a set of resources

Results

Tamarin Exudate Feeding

The tamarins ate exudates from 29 plant species, with 28 being exploited by the saddlebacks and 13 by the mustached tamarins. Trunk and branch gums accounted for $6.3 \pm 1.8\%$ ($n=2$ groups) of the plant-based diet of the saddlebacks and $1.3 \pm 0.1\%$ of the mustached tamarins, and pod-gums accounted for $14.5 \pm 1.5\%$ of the plant-based diet of the saddlebacks and $15.7 \pm 0.3\%$ of the mustached tamarins (group 1, 16.0%; group 2, 15.4%) for the two troops that were studied year-round. Schoener's index of overlap for non-pod exudates was greater between species for a given troop (Troop 1 $O_{fm}=0.70$; Troop 2 $O_{fm}=0.98$) than it was within species between troops (Saddleback $O_{T1T2}=0.58$; Mustached 2 $O_{T1T2}=0.47$).

The mean time each tamarin spent feeding on fruit and *Parkia* pod exudates each day was not different between groups (Fruit $F_{35}=1.8$ $p>0.05$; Pods $F_{35}=2.5$ $p>0.05$) and tamarin species (Fruit $F_{35}=1.9$ $p>0.05$; Pods $F_{35}=0.1$ $p>0.05$) but the time feeding on exudates from other sources was significantly different between groups ($F_{35}=10.7$ $p<0.05$) and tamarin species ($F_{35}=10.3$ $p<0.05$) (Figure 1). The time spent feeding on each of the three categories of plant parts showed different temporal patterns (Figure 2). Fruits (Saddleback $t=3.6$ 160 d.f. $p<0.05$; Mustached $t=4.5$ 149 d.f. $p<0.05$) and exudates from *Parkia* pods (Saddleback $t=4.2$ 71 d.f. $p<0.05$; Mustached $t=4.6$ 69 d.f. $p<0.05$) showed a bias for consumption in the morning and exudates from other sources predominately in the afternoon (Saddleback $t=-8.4$ 101 d.f. $p<0.05$; Mustached $t=-4.7$ 60 d.f. $p<0.05$). Season had no effect on the time spent feeding on fruits (Saddleback $t=-1.6$ 21.9 d.f. $p>0.05$; Mustached $t=-2.1$ 18.4 d.f. $p>0.05$) but significantly more time was spent feeding on *Parkia* pod exudates during the dry season (Saddleback $t=2.7$ 18.2 d.f. $p<0.05$; Mustached $t=2.6$ 21.0 d.f. $p<0.05$). The same was true of

exudates from other sources for saddleback but not mustached tamarins (Saddleback $t=2.3$ 22.0 d.f. $p<0.05$; Mustached $t=-0.3$ 12.0 d.f. $p>0.05$) (Figure 3).

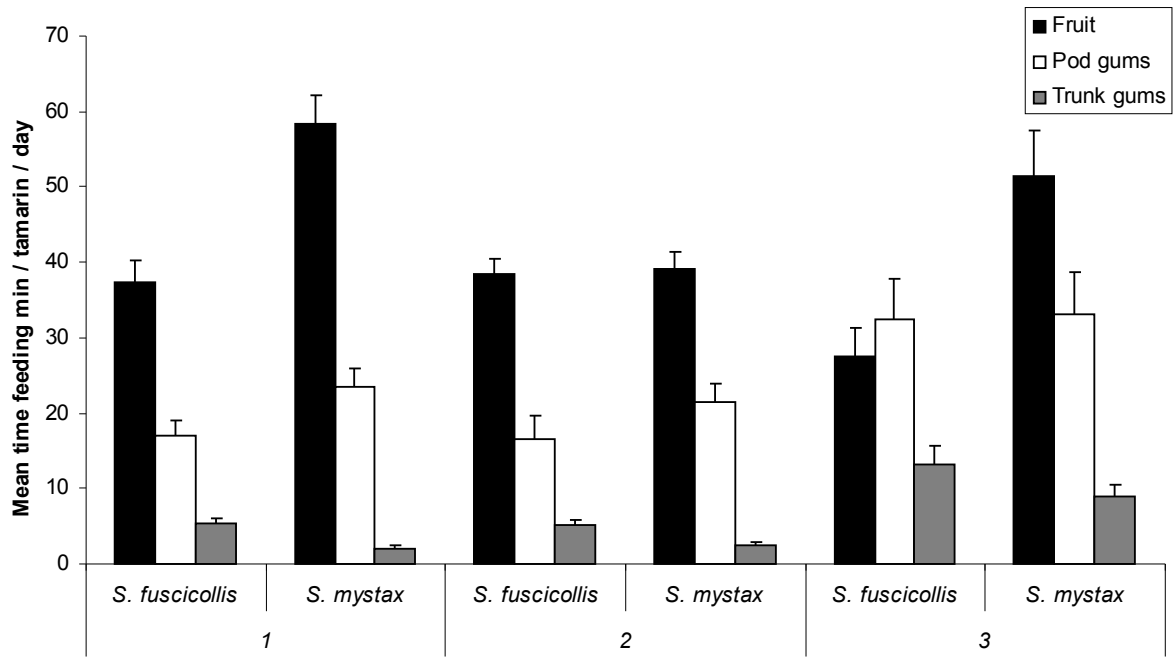


Figure 1: Mean time spent feeding on fruit, pod gums and trunk gums by three mixed-species troops of saddleback and mustached tamarins (error bars indicate SEM).

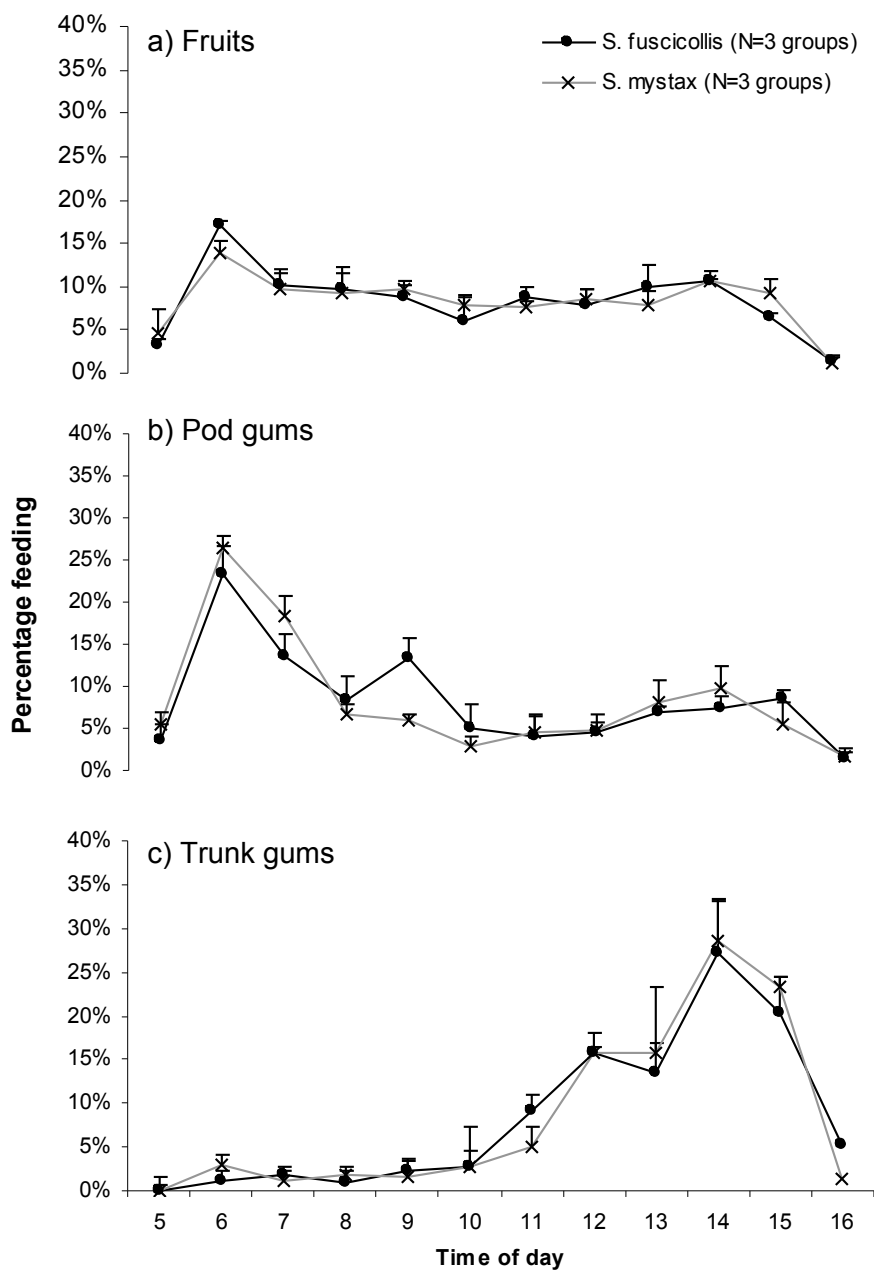


Figure 2: Temporal distribution of feeding records on a) fruits b) *Parkia* pod gums and c) trunk gums (error bars indicate SEM).

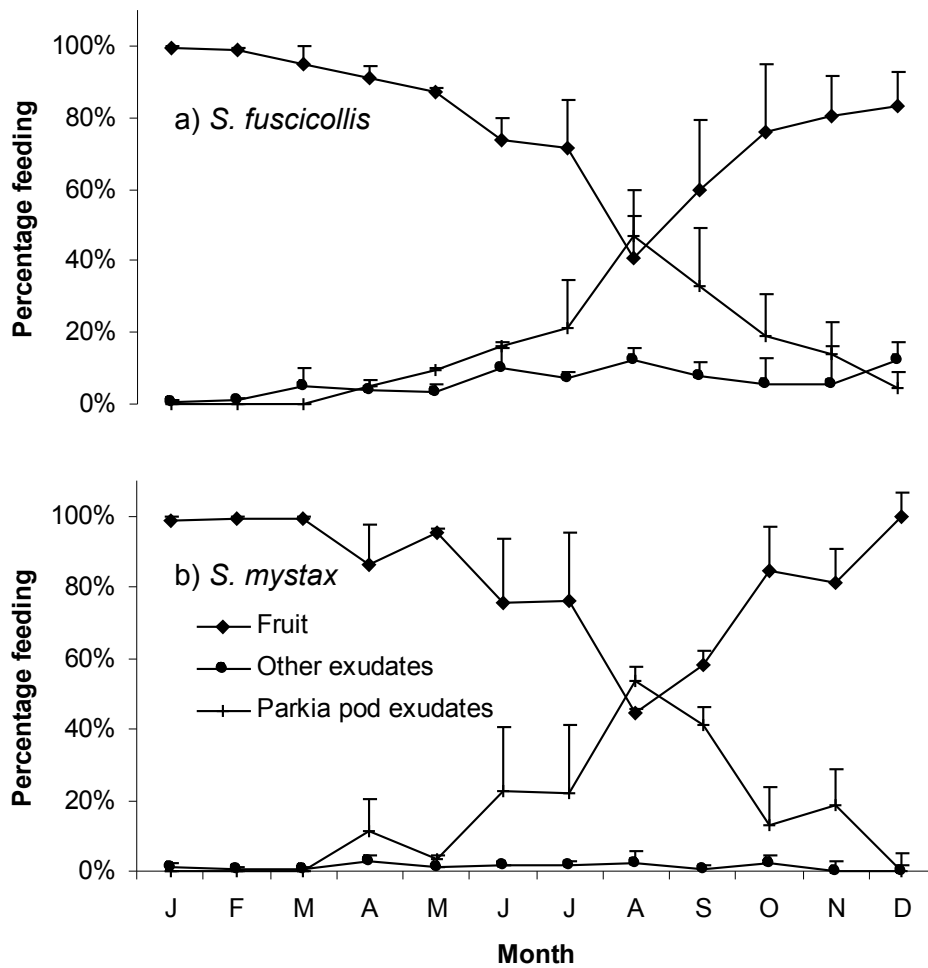


Figure 3: Seasonal variation in percentage feeding records allocated to fruits, *Parkia* pod exudates, and exudates from other sources for a) *S. fuscicollis* and b) *S. mystax* (error bars indicate SEM; n=2 groups Jan - Jun, 3 groups Jul - Dec).

Discussion

The proportion of exudates in the plant diet of saddleback and mustached tamarins at EBQB is similar to that for other tamarins and Amazonian marmosets for which data are available (see Smith this volume). Exudates from *Parkia* pods contributed the majority of feeding records, although 28 other species were also observed to be eaten.

Overlap in gums eaten between species and groups

For primates that lack adaptations to stimulate gum production, such as tamarins, the degree of gummivory and which plant species are exploited may be influenced by the abundance of the various sources of gums. This is supported by the finding that the interspecific overlap between the exudate portion of the diet of associating saddleback and mustached tamarins was greater than the intraspecific overlap between years. Interpopulation differences in exudate feeding may also exist in species able to gouge trunks, e.g. pygmy marmosets (*Cebuella pygmaea*) (Yépez et al. 2005). That the extent of exploitation by this species does not seem to correlate with their abundance indicates an active preference based on unknown, though probably nutritional, characteristics. Consequently the pattern of primate gummivory may reflect the interaction of preference and availability for both those able to stimulate gum production and those not.

Seasonal patterns of gummivory

In contrast to the year-round consumption of trunk exudates, feeding on gums from *Parkia* pods was markedly seasonal. Likely due to availability they were fed upon between April and December during which they accounted for up to 32% and 38% of the saddleback and mustached tamarin monthly diets, respectively. The importance of *Parkia* as a keystone resource for a wide variety of species, not just primates, has been highlighted by Peres

(2000). Pod exudates may be more seasonal by their nature than those produced by trunks and branches as a result of damage, though these too may exhibit a degree of seasonality, for example trees may be damaged by high winds more prevalent during certain months.

Seasonal changes in gum feeding have been reported for 21 out of 23 primates (see Smith this volume, Table 2); the majority (19) of which show an increase in gum consumption in the dry season linked to a reduction in fruit availability. However with few exceptions these studies do not differentiate between the two gum types. As such it is not possible to determine if such increases are due to pod gums or whether feeding on trunk gums also increase significantly during this period. Differentiating between them is important because their different functions predict differences in biochemistry directly relevant to consumers such as primates.

Variation in gum consumption over the year was linked to seasonal changes in resource availability and not the tamarins' reproductive status. No support was found for the suggestion that exudates are consumed as a primary source of calcium in the later stages of gestation and lactation (Garber 1984). Reports that female saddleback tamarins (Garber 1993) and grey mouse lemurs (Génin 2003) dominate gum licks may be linked to a more general female feeding priority (see Young et al. 1990; Box 1997; Radespiel and Zimmermann 2001; White and Wood 2007), as opposed to calcium requirements; further Isbell (1998) reports male patas monkeys consume more gums than females. Whilst exudates may supply dietary calcium, some in significant amounts (Bearder and Martin 1980; Garber 1984; Smith 2000), it is unlikely that they play a key role during reproduction. In the only study to examine it to date (Smith 2000), consumption of different sources of exudates was not correlated with calcium content. Moreover, the relative importance of exudates as a

source of calcium has been called into question by the finding that fruits of tropical figs (*Ficus* spp.) are significantly higher in calcium than non fig fruits (O'Brien et al. 1998), and can contain levels greater than those found in exudates (Smith 2000). However, for those primates that do not consume figs, exudates may still have a role to play.

Patterns of gummivory across the day

The pattern of gum feeding observed across the active period corresponds to that found by Heymann and Smith (1999) for saddleback and mustached tamarins and Ramirez (1989) for mustached tamarins, with pod gums consumed more in the mornings and those from trunks consumed more in the afternoon. This almost certainly reflects a deliberate strategy since there is no reason to suspect variation in gum production over the day (Heymann and Smith 1999), and tamarins show movement patterns consistent with mental maps, knowledge of resource availability, and rule-based foraging (Garber 1988; Garber and Dolins 1996; Bicca-Marques 2006). Lacking the dental adaptations for gouging of other gummivores, tamarins are often referred to as opportunistic consumers of exudates. Whilst not being able to stimulate gum flow, tamarins clearly do not eat gums entirely opportunistically; they either pass up opportunities to ingest trunk gums in the morning or actively seek them out in the afternoon. For non-specialists lacking lower intestinal adaptations, consumption later in the day may allow for their retention in the gut over night, thus maximizing the amount of energy that can be assimilated from them via microbial fermentation of β -linked oligosaccharides (see Heymann and Smith 1999).

Experimental work by Power and Oftedal (1996) suggested that gut retention time does play an important role in gum digestion but cautioned against a simple relationship. The retention of the fluid portion of digesta, containing the complex polysaccharides from gums, has since

been demonstrated in captive common marmosets (Caton et al. 1996), although this ability to retain digesta may be lacking in non-specialist gummivores such as the tamarins, particularly since they often swallow large seeds that may impede retention of any part of the digesta (see Garber 1986, Garber and Kitron 1997; Oliveira and Ferrari 2000; Knogge and Heymann 2003). In addition to benefits from consuming gums later in the day there are also potential costs of consuming them earlier. As Power (1991) noted, they can delay glucose absorption in the small intestine (Blackburn and Johnson 1981; Tsai and Peng 1981; Johnson et al. 1984; Rainbird et al. 1984) and slow both gastric emptying and small intestinal passage (Blackburn and Johnson, 1981; Johnson et al. 1984; Nash 1986; Power and Oftedal 1996). Such effects may be less important during periods of reduced metabolic rate, e.g. the afternoon, when tamarins travel less and rest more, and the night when callitrichids lower their metabolic rate (Hetherington 1978; Thompson 1991; Schnell and Wood 1993; Thompson et al. 1994).

In contrast to the observations of wild tamarins, Heron et al. (2001) reported decreased consumption of gum presented late in the afternoon to eight species of captive callitrichids (*Saguinus bicolor*; *S. oediopus*; *Callithrix geoffroyi*; *Mico argentata*; *Callimico goeldii*; *Leontopithecus rosalia*; *L. chrysomelas*; *L. chrysopygus*). Presentation time may be an important factor in this case as callitrichids are known to enter their sleeping sites from mid afternoon (Smith 2007). Feeding itinerary may not be as important for specialist gummivores with intestinal adaptations; indeed several such species show either a peak of gum feeding at the start of their active period or a bimodal pattern with peaks at the start and end of their active period (e.g. *C. aurita*, Corrêa 1995; *C. geoffroyi*, Passamani 1998; *C. flaviceps*, Ferrari 1988; *C. pygmaea*, Ramirez et al. 1978; Yépez et al. 2005; *P. furcifer*, Charles-Dominique and Petter 1980). Similarly, consuming gum towards the end of the active period may not be

as important for larger species of primates with longer transit times. It is worth noting that transit times may vary by a factor of 10 between species, e.g. 20-26 hours in chimpanzees (*Pan troglodytes*) (Ushida et al. 2006) compared to 2.2-2.5 hours in saddleback and mustached tamarins (for foods voided the same day) (Knogge 1998). Consequently it is smaller species with shorter retention times that would gain most from scheduling feeding to increase the chance that gum is retained overnight.

In contrast to trunk and branch exudates, pod gums are more frequently eaten in the morning. The opposing feeding patterns for these two types gum may be linked to differences in their chemistry, particularly in terms of simple sugars and β -linked oligosaccharides, predicted from their respective endozoochorous and protective functions (Heymann and Smith 1999). However whether pod gums are more readily digested by mammalian enzymes than trunk gums, or whether they are richer in simple sugars, has yet to be investigated. Of the pod gums eaten by primates *Parkia pendula* is the most frequently exploited (Smith, this volume), and the only one for which biochemistry has been investigated. Contrary to what may be expected, its principal post-hydrolysis sugar is arabinose (Anderson and de Pinto, 1985), the natural L-form of which is indigestible in animals and may reduce sucrose digestion (Hizukuri 1999). However, whilst the pod gums of other *Parkia* spp. are produced around the seeds those of *P. pendula* are produced at the pods' sutures when it dehisces (H.C. Hopkins, pers. com. to D. M. W. Anderson, cited in Anderson and de Pinto, 1985); if this corresponds to differences in function or biochemistry is unknown. Further work is required on these keystone resources and their relationship with the many primates that exploit them.

Summary

Exudates may form a year-round dietary staple for primates or their exploitation may vary on a seasonal basis with consumption typically increasing during the dry season when other resources are scarce. The pattern of exudate feeding may also vary across the day to allow increased retention for microbial fermentation. The available data suggest these feeding patterns are not influenced by the gum's calcium content or the reproductive status of the primates consuming them, but instead reflect the interaction of preferences based on other factors. Availability is liable to be key since gum feeding was more similar between associating tamarin species within years than within species between years. Importantly feeding itineraries may be significantly different for the two main types of gum commonly fed upon by primates, namely pod and trunk / branch gums demonstrating a clear need to avoid blindly lumping all exudates together.

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