

Review

Exploiting a readily available but hard to digest resource: A review of exudativorous mammals identified thus far and how they cope in captivity

*Francis Cabana^{1,2}, francis.cabana@wrs.com.sg

Ellen S. Dierenfeld³, edierenfeld@aol.com

Wirdateti⁴, teti_mzb@yahoo.com

Giuseppe Donati², gdonati@brookes.ac.uk

K.A.I. Nekaris², anekaris@brookes.ac.uk

1- Wildlife Nutrition Centre, Wildlife Reserves Singapore, 80 Mandai Lake Road, 729826

2- Nocturnal Primate Research Group, Oxford Brookes University, Headington Campus, Gypsy Lane, Oxford, OX3 0BP, United Kingdom

3-Ellen S. Dierenfeld, LLC, St. Louis, Missouri USA

4- Zoological Division, Indonesian Institute of Science, Cibinong, Indonesia

*Contact info: Francis Cabana, Wildlife Reserves Singapore, 80 Mandai Lake Road, Singapore, 729826 Phone: +65 63608652 E-mail: francis.cabana@wrs.com.sg

ABSTRACT

Gum is a widely available carbohydrate, composed mainly of non-digestible structural carbohydrates. No mammalian enzymes can digest gum, therefore a mammal ingesting gum must rely on microbial fermentation in order to access the energy it possesses. Gums are known as relatively nutrient poor. Despite this, some mammals have evolved to exploit this food resource. We aim to review the literature for all mammal species which have been recorded to ingest gum, whether quantified or not and discuss this in context of their evolutionary adaptations. We also investigated the recommended

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/1749-4877.212264](#).

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captive diets for these species to look at if gum is recommended. We conducted a literature search on ISI Web of Knowledge to tabulate all mammal species observed ingesting gum and classify them as obligate, facultative or opportunistic feeders. We encountered 94 mammal species which eat gum in the wild (26 obligate feeders, 35 facultative feeders and 33 opportunistic feeders). Obligate feeders have entirely evolved to exploit this resource but were found to not be given gum in captivity, which may explain why they are failing to thrive, as opposed to facultative feeders which have fewer issues. Gum may be necessary for the health of obligate feeders in captivity. Future research should focus on the physiological effects that gum ingestion poses on different digestive systems.

KEY WORDS: feeding ecology, gum, husbandry, marsupial, primate

INTRODUCTION

The use of gum as a resource by mammals, especially in terms of nutrient uptake, remains largely unstudied despite field studies increasingly revealing the vital nature of this resource to mammals as a obligate or fallback food. In this review, we examine the published literature on the use of this food, how mammals adapted to consume it, and the nutrition it contains. Although reviews of exudativorous primates have been done in the past (Nash 1986; Burrows & Nash 2010; Smith 2010), we will open up our scope to mammals in general and include up to date additions since 2010. Additionally, we will use this information to discuss the current nutritional management of these species in a zoological setting and discuss the importance of gum in their diets.

The very nature of what gum is can be confusing based on definitions available in the literature. All gums are exudates, but not all exudates are gums. The term exudate includes gums, resins and latexes. We use the definition of gum from Nussinovitch (2009): a fluid that is produced by some plant through gummosis, following the creation of an injury that hardens upon exposure to air. Contrary to some usage, sap is not an exudate as it is simply leaking phloem liquid. Sap and gum also both have very different chemical compositions with sap being mostly soluble carbohydrates and water while gum is mostly non-digestible soluble polysaccharides (Ushida *et al.* 2006). In order to exploit this food item fully, a mammal must support a synergistic microbial population capable of fermenting the beta-linked polysaccharides of which gum comprises into short chain fatty acids for assimilation (Ushida *et al.* 2006). Except as a source of difficult-to-obtain energy, gums are not a particularly worthwhile source of macronutrients. Micronutrients, however, may present a different situation. Minerals such as calcium, magnesium, potassium and iron can be found in appreciable quantities in gums relative to other food sources (Hladik 1979). For example, by ingesting only 30 g of gum, a chimpanzee (*Pan troglodytes*) can meet its daily needs for calcium, manganese, magnesium and potassium (Ushida *et al.* 2006). Exudates can transit undigested through the small intestine of mammals (Power & Oftedal 1996); if the species ingesting gum does not have fermentation/digestive capacity within the hindgut, potential micronutrients may not be available for assimilation. Gums also often contain secondary plant secondary metabolites (PSM) such as phenolics and tannins, which may limit the amount of

gum a particular mammal, can ingest (Heymann & Smith, 1999 but also see Wrangham & Waterman 1981).

Even with the documented low nutritional quality of exudates, several mammal species are commonly acknowledged as using gum. The majority of mammal taxa commonly used as examples are heavily biased in Primata and the petaurid marsupials groups. Some taxa use it as an obligate food source (*Nycticebus spp.*: Cabana & Nekaris 2015b, Starr & Nekaris 2012, Wiens *et al.* 2006, Das *et al.* 2014; *Cebuella*: Coimbra-Filho and Mittermier 1977, *Petaurus breviceps*: Smith 1982), some seasonally as a fallback food (*Saimiri*: Stone 2007, *Saguinus spp.*: Egler 1992), and some only opportunistically (*Pan*: Ushida *et al.* 2006). We expect each of these groupings to possess different morphological and physiological feeding adaptations that may allow some mammals to exploit gum food sources more than others (Bearder and Martin 1980). Year-long food availability, competition, seasonal effects on plant phenology, and varying insect abundances should also impact how beneficial or necessary gum is to a particular species and/or population (Garber 1984).

The lack of research investigating the importance of gum within the diets of mammals is reflected in the captive care procedures of these species. Captive husbandry manuals are often absent in stressing the importance of gum as part of a proposed diet. Diet recommendations either totally omit gum or suggest it only as an enrichment ingredient or feeding-behaviour enhancement technique. For those species which use gum as an obligate food item year round (possibly with some seasonal increases), lack of dietary gum may lead to health issues and in turn impact the breeding and survivability of captive populations (e.g. Cabana & Nekaris 2015). Conversely, reduced gum intake for opportunistic gummivores should result in minimal impact. There is no evidence yet as to how seasonal gum feeders are affected by a lack of gum ingestion.

In this paper, we first review every mammalian taxa reported in the literature to ingest gum, categorized by how important gum is to their feeding ecology either as an obligate, facultative or opportunistic diet ingredient. Secondly, we collate the nutritional information of wild gum samples known to be ingested by these taxa, and lastly interpret why some species depend more on exudates as a food source than others. These results were used to question current husbandry practices for captive

gum eating mammals, with particular importance relative to the importance of gum in their wild diets, to evaluate potential resulting physiologic/psychological effects.

METHODS

We conducted a literature review between January and February 2016 by inputting the following keywords into ISI Web of Knowledge: "gum" OR "exudate" AND "mammal", between 1950 and 2016, inclusively, yielding n=6,304 results. Due to the high number of results, only the first 50 pages were broadly searched. We read the title, abstract and keywords of all English entries and if one of these three had potential, the entire paper was read. Their references were also looked through for potential data. Only if gum eating was explicitly observed by the authors was this data then included in the review. Out of 500 hits, 89 were related to a mammal species ingesting gum. In order to search for grey literature, we repeated the key word search in December 2016 using Google Scholar between 1950 and 2016, however instead of the term "mammal", we searched for every mammal order (Monotremata, Didelphimorphia, Dasyuromorphia, Peramelemorphia, Diprotodontia, Marsupiala, Afrosoricidia, Macroscelidea, Tubulidentata, Hyracoidea, Proboscidea, Sirenia, Lagomorpha, Rodentia, Scnatentia, Dermoptera, Primata, Erinaceomorpha, Soricomorpha, Pholidota, Chirptera, Cetacea, Artiodactyla, Perissodactyla, Carnivora, Cingulata and Pilosa) one after the other. Once we compiled the list of mammal species and the gum(s) they ingested, we performed targeted searches for the chemical composition of each gum species in ISI Web of Knowledge. This search resulted in a total of 145 species from 35 families, with the most numerous being from Fabaceae (62 species), Anacardiaceae (11 species) and Combretaceae (9 species).

In order to categorize these taxa, we define three types of feeding ecologies and we attribute each species to one of them for our analysis. Each mammal was categorized either as: using as obligate feeder, facultative feeder or opportunist feeder. We defined obligate feeding as ingesting gum year round with some, none, or minor seasonal variance. Obligate feeders can be described as exudativores because of the suites of adaptations necessary to subsist on a diet high in gum. Facultative feeding was defined using the definition of Marshall and Wrangham (2007); the consumption of gum must be influenced by the lowered availability of other, usually more nutritious but certainly more preferred,

foods. It can be eaten year round but a seasonal increase is necessary. Only being present in the diet during the lean season is also acceptable. Opportunistic feeding involves species that consume gum as they come across it, not actively seeking it out, in small quantities. There should be no clear seasonal pattern, and ingestion of gum cannot be expected due to season.

For those publications which only described the importance of gum in a mammal's diet qualitatively, we described these as 'Minor', 'Moderate' and 'Major' parts of the diet.

RESULTS

We encountered 94 species of mammals that eat gum in the wild. Of these, 11 are marsupials, 78 are primates, three are rodents, and one each is a perissodactyl and procyonid. All mammals are from equatorial or subtropical climates. For the purpose of this review, we distinguish between the exudativorous obligate -feeding marmosets with the facultative-feeding tamarins within the Callitrichidae. Listed in **Table 1** are species that have been observed feeding on gum as an obligate food (n=27 spp), **Table 2** for facultative feeders (n=34 spp) and **Table 3** for opportunistic feeders (n = 33 spp).

DISCUSSION

Gum Feeders and their Adaptations

Mammals which feed on gum as an obligate food source (26 species) are represented by primates (*Nycticebus*, *Cebuella*, *Phaner*, *Cheirogaleus*, *Callithrix*) and Australian possums (*Petaurus*); all but one genera are nocturnal. Being an obligate feeder requires a unique set of evolutionary adaptations, not only for surviving on this low quality diet (metabolic), but also for harvesting and processing it (anatomical, behavioural). For this reason, mammals of this group can also be considered exudativores/gummivores or gum specialists.

Obligate Gum Feeders

Obligate feeders must have the capability of inducing the production of gum, such as a well-developed dentition adapted to damage a tree or liana severely enough for it to produce gum, a process called gouging. All exudativores have evolved specialised dentition to gouge and harvest gum (Burrows *et al.* 2016; Coimbra-Filho & Mittermeier 1977; Ravosa *et al.* 2010). The upper first

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premolars are used as an anchor for the teeth on the upper mandible to scrape the cambium away, stimulating gummosis (Nussinovitch 2009). The possums and gliders also have this adaptation (Smith 1982). The lower canines of exudativorous primates are incisiform and form a toothcomb with the incisors such as seen in *Nycticebus spp.* (Nekaris 2014). The same specialisations are clear in marmosets and have arisen through convergent evolution (Burrows *et al.* 2016).

In terms of extremities, we also see some elaborate adaptations for reducing the energetic strain congruent with the arboreal lifestyle of obligate gum feeders. Marmoset species and *Phaner* all have keeled nails, which allow them to negotiate climbing and clinging to tree trunks for long periods, reducing the energy necessary during gouging (Hladik 1979). *Nycticebus* do not have keeled nails, instead a special set of blood vessels in their limbs called *retia-mirabilia* (Nekaris 2014). This allows them to contract their hands and feet into vice-like grips, yet only use small proportions of energy.

Lastly, gum is composed mainly of soluble structural carbohydrates/polysaccharides that require a host of digestive adaptations. Fermentation, rather than intrinsic enzymatic digestive processes, is necessary to fully digest gum (Anderson and Bell 1974; Power 2010). All obligate gum feeders possess some gut fermentation capabilities. This process is accomplished either by possessing an expanded caecum and large intestine or a complex hindgut (Dierenfeld *et al.* 2006). Within these chambers, some established microbes hold the capability of cleaving the β -bonds (Hladik 1979).

Although many arboreal possums ingest gum, the only species that are obligate feeders, *P. breviceps* and *P. leadbeateri*, have the largest caecum in relation to body size among marsupials (Smith 1984).

Gliders also display a relatively long food mean retention time, of about 29 hours, which allows time for gum to ferment (Dawson 1979). All of these exudativores share similar traits that enable efficient harvest, processing and digestion of gum as an obligate food source. The patas monkey (*Erythrocebus patas*) is not described as an exudativore in the literature, yet it uses gum as an obligate food source (Isbell 1998). Although lacking other adaptations, their hindgut must be able to ferment a portion of the ingested gum for them to intake sufficient energy.

The species that are the most exudativorous may also have a modified metabolism that can assist in coping with the diet. Using *N. coucang* as a model, Muller (1979) showed that they have a basal

metabolic rate (BMR) which is 60% that of a similar sized primate. The *Cheirogaleus*, *Petaurus* (in addition to the lower BMR of most marsupials), and some Galago can enter daily torpor in order to reduce overall metabolic costs (Schmid *et al.* 2000, but see Mzilikazi *et al.* 2006). Whether this evolved concomitantly with their feeding ecology or not, it has allowed exudativores to be able to thrive on gums and insects.

Facultative Gum Feeders

Seasonal facultative gum feeders identified in Table 2 (35 species) may possibly have some, or none of the necessary adaptations for exudativory, with an example being the many *Saguinus* spp.

Tamarins do not possess the specialised dentition necessary to gouge tree bark (Soini 1987). Rather, they harvest gum from pre-occurring tree wounds (Soini 1987). The mean retention times (MRT) of tamarins are heavily dependent upon the structure of food ingested (Power & Oftedal 1996). When large indigestible particles are present, such as seeds, the MRT deviates from normal and becomes shorter in order to void this nutritionally inaccessible item, leaving space for more digestible foods. When gum was added to experimental diets, tamarin MRT values did not significantly differ, unlike the marmoset MRT which increased by 40 to 60 minutes, most likely to maximise fermentation opportunities (Power & Oftedal 1996). While facultative feeders may digest and assimilate some nutrient content of gum, they exploit other seasonal food sources such as fruit, where fermentation is a helpful, yet less essential adaptation (Heymann & Smith 1999). Forest guenons are described as frugivores, yet contain a complex hindgut with active fermentation (Cords 1986, Chapman *et al.* 2002). When the fibrous fruits are not in season, this adaptation would be necessary to extract nutrients and energy from gum (Homewood 1978).

Opportunistic Gum Feeders

The opportunistic gum feeders are almost as numerous as the obligate feeders (31 species). This group appears to have no targeted adaptations for dealing with this foodstuff. Some species may possess the necessary fermentation chambers to digest the carbohydrates within gum such as black-striped wallabies (*Macropus dorsalis*) and langurs (*Semnopithecus entellus* and *Trachypithecus pileatus*)

which possess foregut microbial fermentation (Newton 1992, Irbeck & Hume 2003). Remaining opportunistic gum feeders must rely on varying levels of hindgut fermentation. Any adaptations an opportunistic feeder may possess to harness or process gum is the product of some other selection pressures. Clearly gums are not considered a major dietary component for these species, which is why for the remainder of the discussion; we shall focus on obligate and facultative feeders.

Gum Composition

We identified that the 94 mammal taxa in this study consume gums from 144 species of plants, belonging to 78 genera in 35 families. Chemical compositions were found for gums from 32 plant species (Table 4). From a plant's perspective, a primary function of exudates is to seal off wounds from the outside environment to prevent entry of pathogens, as well as to minimize desiccation (Nussinovitch 2009). A high PSM load should theoretically deter predators. In a study of fallback feeding behaviours of vervet monkeys (*Chlorocebus pygerythrus*) on two different *Acacia* species, Wrangham and Waterman (1981) documented that the monkeys preferentially ingested *A. xanthophloea* rather than *A. tortilis*, attributing this to its lower PSM concentrations (0.23-0.31% versus 27.99-70.96% DM basis). Exudativorous species may have further physiologic mechanisms for coping with high dietary PSM loads, including detoxification of compounds through gut microbes or specialised saliva (Rode-Margonno & Nekaris 2015). Conversely, seasonal or opportunistic feeders may behaviorally ingest gums with less concentrated PSM. Animals that feed on exudates seem to be very sensitive to different PSM compounds and sometimes seem to select a gum for its particular PSM (Wrangham & Waterman 1981).

Gum exudates have been generally described as being virtually devoid of lipids, low in protein, and relatively high in trace minerals (Garber 1984, Nash & Whitten 1989, Power 2010); the summary data in **Table 4** supports this description. Indeed, crude protein of tree gum can range between 1.10-11.3% (DM basis), although high values are exceptional and most gums tend to have a protein concentration nearer to the low end of this range. Pod gum protein concentrations (*Parkia spp.*) are generally higher, from 2.2 to 13.9% (DM basis). Both trunk and pod gums are abundant in minerals and have a high calcium to phosphorous ratio (Ca:P). It has been shown repeatedly that a positive dietary Ca:P ratio is

necessary for proper nutrition in all life stages, and especially important during gestation, lactation and juvenile growth (Dierenfeld *et al.*2006). Gums also contain minerals that are considered limiting in a tropical context such as sodium, copper and iron (Rode-Margono *et al.*2014).

Gums comprise complex linkages of monosaccharides and typically have no sweet taste (Power and Oftedal 1996). Numerous sugars have been identified from gums (see **Table 4**), these compounds are misleading in understanding the nutrition of exudativores. They are the end product of laboratory hydrolysis and not primary substrates available for digestion (Hall 2007). The declared sugar content of gums depends on plant species and perhaps analytical methodology. These complex links of sugar are very different in digestibility compared to simple sugars found in saps, nectars and domestic fruit, which are generally completely digested. The fermentable fibres in gum are not interchangeable with sugars. Gum fermentation typically does not result in the same end products as sugar, and fermentation can be inhibited by a drop in pH (and accompanying change in gut microbiome) that may occur when high soluble sugar (i.e. domestic fruit) diets are fed, and may lead to negative health consequences (Topping *et al.* 1988). Development and maintenance of appropriate microfloral populations in the digestive tract of the all gum feeders, but especially the obligate feeders, are critical for animals' ability to obtain energetic benefits from gums.

Obligate Feeder's Diets Revolve Around Gum

For obligate feeders, the nutrients found in gum are integrated into their daily metabolism and are used in conjunction with other diet components to reach nutrient targets. Simply looking at the nutrient concentrations found in their selected food types can be an indication on the role gum plays in their diet. *Nycticebus*, *Phaner* and some *Cheirogaleus* have diets comprising insects, nectar, perhaps sap, and other plant parts (Schulke 2003, Genin 2008, Starr & Nekaris 2013). Fruit is not a main component of their diets, nor is it for possums and gliders (Smith 1980). This removes a major seasonal variability from their feeding ecology because, except for some blossoms and perhaps overall abundance of some insects, most of their diet is available year round. Marmosets have more food diversity than other obligate feeders, and do exploit fruit seasonally (Garber 1984). As explained by Gaulin (1974), the Jarman-Bell Principle allows small mammals to subsist on insects and gums

because they do not have large total nutrient requirements. They theoretically should be able to meet nutrient targets by balancing gum, insects and plant matter intake. This is not feasible for larger mammals with greater nutritional needs (Gaulin 1974). *Erythrocebus patas* has a relatively low fruit diet and ingests mostly insects and gum (Isbell *et al.* 2013). Insects are known to be a concentrated source of animal-based nutrients, high in protein, often fat, some vitamins and some minerals as well as dietary fibre in the form of chitin (Finke 2015). They also have typically inadequate calcium to phosphorous ratio which renders an insect-only diet inappropriate for long periods of maintenance, and anytime during growth or reproduction (Garber 1984, Finke 2015). The trends observed in this review (Table 4) corroborate Garber's (1984) hypothesis that insects and gums appear to provide nutritional complementarity contributing to a balanced diet. With insects and gum available throughout most of the year, this feeding strategy is relatively stable and requires little dietary divergence. Isbell and associates (2013) showed how *E. patas* are able to reach their nutrient targets with a diet of insects, gum and some plant matter, as well as gestate and lactate on this diet. This approach is limited by inhabiting a location where gum trees and insect are abundant, and competition for the gum resource isn't too severe. Isbell (1998) found that *E. patas* is indeed an exception to the Jarman-Bell rule, being a medium-sized primate that subsists on insects, gum and little other plant matter.

The Seasonal Gum Intake of Facultative Feeders

One main characteristic that unifies the facultative feeders is their highly seasonal diet due to their preference for fruit (29 of the 33 species listed in Table 2). Not possessing one of the aforementioned adaptations may rendered the energy gained from gum not worth the energy spent harvesting it when fruit is present. The Australian marsupials in this category each have their unique niches that include honey, ants, nectar and fruits (Jackson 2001, Rawlins & Handasyde 2002). Severe nutritional stress periods are common when fruits are seasonal and appear in patches. Correa *et al.* (2000) discusses the inverse relationship that exists between the consumption of fruits and exudates. *Leontopithecus chrysopygus* increase their gum consumption as the fruiting period ends (Albernaz 1997). Different species may target fruits at different phenological stages - small or large unripe or ripe or even by

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fruits' chemical composition (Porter 2001). The fruits selected by *Cheirogaleus major* were high in fibre, low in fat and protein, with moderate sugar content (Lahann 2007). This proportion of nutrients is reflective of most fruits consumed by wild animals which are generally low in calcium and have a low Ca:P ratio. Both gum and fruit are low in protein, high in fibre (albeit different fibre types: soluble versus insoluble), and can contain PSM (Power & Oftedal 1996). Fruit can be abundant seasonally, as well as distributed in patches, which allows for a much higher energetic yield during fruiting season(s). When gum becomes more important in the diet, the overall energy intake will be lower since sugars are more difficult to extract, which may lead to a lean season with an overall decrease in body mass (Stone 2007). The lean season also occurs simultaneously with the breeding season of some species, correlated with a diet higher in minerals, particularly essential nutrients during gestation and lactation (Garber 1984). *Saguinus bicolor*, for example selects gum between June to December with birthing season between May and November (Egler 1992). For such species, the intake of gum during this period is essential to provide suitable nutrients to offspring, as well as to slow fat catabolism.

Gum Eating Mammals in Captivity

Understanding the nature of gum consumption by mammals has great implications for maintaining these species in captivity. Indeed, 71% of the species listed in Tables 1, 2 and 3 are found in captive settings, either as part of a managed breeding program in accredited zoological institutions worldwide or in rescue centres being rehabilitated and reintroduced. Wild diets are often the first step when formulating a diet, as well as using domestic or laboratory animal models to determine specific nutrient requirements (Cabana and Nekaris 2015). Many accrediting zoo bodies now produce their own husbandry/best practice guidelines for holders, or endorse studies or guides put together by outside organizations. Exudativores, with *Nycticebus* in particular, have been fed diets that contain little to no actual exudates (Fitch-Snyder *et al.* 2001). Association of Zoos and Aquaria's (AZA) recommendations mention how gum can be used as enrichment but do not actually include them in their diet formulation recommendations.

Since they include obligate or facultative feeders, husbandry recommendations for the Callitrichidae and Lorisidae should include gum in their diets. Cabana and Nekaris (2015) provided evidence that diets high in fruit and low in gum contribute to the dental diseases in *Nycticebus*. The free ranging diet of *N. javanicus* significantly differs between rehabilitated and released individuals versus wild individuals (Rode-Margonno *et al.* 2014). Callitrichids should receive gum two to three times per week as enrichment (Ruivo 2010). These primate groups contain a high proportion of endangered species (56% for marmosets and 50% for tamarins), placing importance on their respective breeding programs. Marmosets and tamarins have been plagued in captivity with a wasting syndrome since the 1970s, and it is still present in captive populations today (Gozalo *et al.* 2008). Although no causal link has yet been established, all underlying hypotheses (apart from stress) appear to be of a nutritional basis. Similar to slow lorises, many captive callitrichid diets are high in fruit and generally low in exudates (Nash 1986; Ruivo 2010). Although no case is identical, Jarcho and associates (2013) report a common instigator linked with intestinal inflammation which causes malabsorption, and leads to the observed clinical symptoms. Studies now focus on the underlying cause of the initial inflammation, with a lack of fibre being one of the current hypotheses (Pham & Barr 1996). The species most affected are the most gummivorous of the tamarins: *S. bicolor* and *S. oedipus*, as well as *C. jacchus*, *C. geoffroyi* and *Calimico goeldii* (Gozalo *et al.* 2008). The lack of gum in diets has been suggested as one of the factors linked with marmoset wasting syndrome (Nash 1986).

The Australian exudativorous marsupials may also not receive adequate amounts of gum in their captive diets. The species most commonly kept in captivity include *Dactylopsila trivirgata*, *Peturus australis*, *P. breviceps*, *P. gracilis* and *P. norfolensis*, none of which have gum listed in common diet recommendations of high protein mixes, nectar replacers and fruits (Dierenfeld *et al.* 2006). Similarly to *Nycticebus*, the most studied species of gliders *Petaurus breviceps*, also suffers from several health ailments in captivity (Dierenfeld *et al.* 2006), including tetany and osteodystrophy, both of which can be related to inappropriate, imbalanced high fruit diets. As described in Table 4, gum is a source of calcium, which is also found in the natural diet of sugar gliders. A reduction of fruit, and increase in gum, could impact the health of these captive animals, specifically reducing calcium based illnesses

(assuming vitamin D intake was sufficient). Reported dental issues, diarrhoea and kidney issues may also benefit from the gum's lower sugar, higher fibre and low protein levels, respectfully.

Additionally, gut health and overall microbiome may be improved (Dierenfeld *et al.* 2006). Many other species, which would be interesting case studies, are either not maintained in captivity (e.g. *Phaner*) or do not yet have a husbandry manual. Due to the adaptable behaviours seen in the feeding ecology of fall-back and opportunistic feeders, primary health issues related to lack of gum in captive diets are less anticipated (or reported).

Much remains to be learned about exudate consumption in mammals. We suspect that upon further study, many other taxa will be categorized as opportunistic consumers. Clearly gum consumption has evolved in multiple mammal lineages, with a variety of morphological adaptations to cope with the exploitation, processing and digestion of this readily available, yet difficult to digest food source. The evident evolutionary adaptations to this resource mean that an understanding and certain mimicry of their natural feeding ecologies is essential to their proper management in captivity. Future research should focus on the physiological effects that gum ingestion poses on different digestive systems. This would enable us to assess other potential evolutionary driving sources related to exudativity.

ACKNOWLEDGEMENTS

We would like to thank Longleat Safari and Adventure Park, Whitley Wildlife Conservation Trust, Primate Society of Great Britain, and International Primatological Society Captive Care Working party, Nacey Maggioncalda Foundation, University's Federation for Animal Welfare, National Geographic (GEFNE101-13), People's Trust for Endangered Species, Disney Worldwide Conservation Fund, Columbus Zoo, Phoenix Zoo, Cleveland Zoo and Zoo Society, Shaldon Wildlife Trust, Shepreth Wildlife Park, Sophie Danforth Foundation, Conservation International Primate Action Fund, and Mazuri Zoo Feeds for their funding support with various elements of this ongoing research. We are also thankful to Dr J.G. Lee and to three anonymous reviewers for improving the quality of the manuscript.

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TABLES

Table 1 Mammal species which have been identified to be obligate gum feeders, where gum is a major part of their feeding ecology.

Common Name	Scientific name	% of foraging	References
Marsupials			
Striped Possum	<i>Dactylopsila trivirgata</i>	26	Rawlins & Handasyde 2002
Leadbeater's possum	<i>Gymnobelideus leadbeateri</i>	29-77	Irlbeck & Hume 2003, Smith 1984
Yellow-Bellied Glider	<i>Petaurus australis</i>	59-91	Henry 1985, Quin et al 1996
Sugar Glider	<i>Petaurus breviceps</i>	29-55	Smith 1982, Quin 1995, Henry 1985
Squirrel glider	<i>Petaurus norfolcensis</i>	59	Irlbeck & Hume 2003, Quin 1995, Sharpe & Goldingay 1998, Menkhorst et al. 1988
Primates			
<i>Strepsirhines</i>			
Madame Berth's Mouse Lemur	<i>Microcebus berthae</i>	49	Hammhahn & Kappeler 2010
Reddish-Gray Mouse Lemur	<i>Microcebus griseorufus</i>	78	Genin 2008
Golden-brown Mouse Lemur	<i>Microcebus ravelobensis</i>	50	Radespiel et al. 2006
Hairy-eared dwarf lemurs	<i>Allocebus trichotis</i>	19†	Biebow 2009
Masoala Fork-marked lemur	<i>Phaner furcifer</i>	65-85	Schulke 2003
Pale Fork-marked Lemur	<i>Phaner pallescens</i>		Charles-Dominique 1977
Bengal slow loris	<i>Nycticebus bengalensis</i>	76.5-85.3	Das et al. 2014
Sunda slow loris	<i>Nycticebus coucang</i>	43	Wiens et al. 2006
Javan Slow Loris	<i>Nycticebus javanicus</i>	54	Rode-Margonno et al. 2014
Pygmy Slow Loris	<i>Nycticebus pygmaeus</i>	51	Starr and Nekaris 2013
Southern Needle-clawed Bushbaby	<i>Euoticus elegantulus</i>	75	Charles-Dominique 1974
Lesser bushbaby	<i>Galago moholi</i>	Major	Bearder and Martin 1980
Thick-tailed Greater Galago	<i>Otolemur crassicaudatus</i>	5-90	Bearder & Martin 1980, Crompton 1983, 1984, Harcourt 1986, Clark 1978
<i>Platyrrhines</i>			
Pygmy Marmoset	<i>Cebuella pygmaea</i>	67	Soini 1982, Moynian 1976, Castro and Soini 1977
Silvery Marmoset	<i>Mico argentatus</i>	59	Veracini 1997
Common marmoset	<i>Callithrix jacchus</i>	30-70	Thompson et al. 2013, Alonso & Langguth 1989, Stevenson & Rylands 1988, Cunha et al. 2006, Alonso 1984, Castro 2003

Black-tufted Marmoset	<i>Callithrix penicillata</i>	25-70	Muskin 1984, Rylands 1984, de Fonesca and Lacher 1984
Geoffroy's Marmoset	<i>Callithrix geoffroyi</i>	14-69.7	Passamani & Rylands 2000, Passamani 1998, Garber 1984, Dawson 1979
Buffy-tufted marmoset	<i>Callithrix aurita</i>	12.9-50.5	Muskin 1984, Rylands 1984, Correa <i>et al.</i> 2000, Correa 1995, Martins & Setz 2000, Coutinho & Correa 1995, Ferrari <i>et al.</i> 1996
Buffy-headed marmoset	<i>Callithrix flaviceps</i>	65.7-87	Correa <i>et al.</i> 2000, Ferrari 1991
<i>Catarhines</i>			
Patas monkey	<i>Erythrocebus patas</i>	0.1-36.9	Isbell 1998
Grivet Monkey	<i>Chlorocebus aethiops</i>	Moderate	Isbell 1998

† % of total activity

Minor, moderate and major were used when the reference described the importance of gum in the diet qualitatively, and not numerically.

Table 2 Mammal species identified as exploiting gums as a facultative food where the gum may or may not be in the diet all year long, it will seasonally become more important when another more preferred food resource becomes less available.

Common Name	Scientific name	% of foraging	References
Marsupials			
Tasmanian bettong	<i>Bettongia gaimardi</i>	Minor	Irbeck & Hume 2003, Taylor 1992
Primates			
<i>Strepsirhine</i>			
Geoffroy's Dwarf Lemur	<i>Cheirogaleus major</i>	1	Lahann 2007
Grey Mouse Lemur	<i>Microcebus murinus</i>	4-69	Dammhahn & Kappeler 2008, Radespiel <i>et al.</i> 2006, Lahann 2007, Joly & Zimmermann 2007
Giant Mouse Lemur	<i>Mirza coquereli</i>	0-20	Hladik & Hladik 1969, Pages 1980
Potto	<i>Perodicticus potto</i>	20-21†	Oates 1984, Charles-Dominique 1977
Senegal Bushbaby	<i>Galago senegalensis</i>	15-60	Harcourt 1986
Kenyan galago	<i>Galago senegalensis braccatus</i>	Major	Nash & Whitten 1989
Prince Demidoff's Bushbaby	<i>Galagoides demidovii</i>	0-10	Charles-Dominique 1977, 1974
<i>Platyrrhine</i>			
Snethlage's Marmoset	<i>Mico emiliae</i>	Minor	Lopes & Ferrari 1994
Hershkovitz's Marmoset	<i>Mico intermedius</i>	15.5	Rylands 1982
Santarem Marmoset	<i>Mico humeralifer</i>	5†	Rylands 1984, Stevenson & Rylands 1988
Black-tailed Marmoset	<i>Mico melanurus</i>	Minor	Rylands 1984
Wied's marmosets	<i>Callithrix kuhlii</i>	7-28.4†	Raboy & Dietz 2004, Rylands 1989, Raboy <i>et al.</i> 2008
Goeldi's monkey	<i>Callimico goeldii</i>	1-14	Porter 2001, Porter <i>et al.</i> 2007
Pied Tamarin	<i>Saguinus bicolor</i>	0-17	Egler 1992
Emperor Tamarin	<i>Saguinus imperator</i>	Minor	Terborgh 1983
Brown-Mantled Tamarin	<i>Saguinus fuscicollis</i>	12-14.4	Peres 1993, Haymann & Smith 1999, Porter 2001
Illiger's Saddle-back Tamarin	<i>Saguinus fuscicollis illigeri</i>	3.4-42	Terborgh 1983, Soini 1987, Garber 1988
White-Lipped Tamarin	<i>Saguinus labiatus</i>	8	Porter 2001
Golden-handed Tamarin	<i>Saguinus midas</i>	Minor	Smith 2010
Moustached Tamarin	<i>Saguinus mystax</i>	10.4	Peres 1993, Haymann & Smith 1999, Castro & Soini 1977
Black-handed Tamarin	<i>Saguinus niger</i>	3.1	Oliveira & Ferrari 2000
Black-Mantled Tamarin	<i>Saguinus nigricollis</i>	Minor	Izawa 1978
Cotton-Topped Tamarin	<i>Saguinus oedipus</i>	5-14.4	Neyman 1977, Power & Oftedal 1996, Hladik & Hladik 1969, Garber 1980, Garber 1984
Black-faced Lion Tamarin	<i>Leontopithecus caissara</i>	Minor	
Golden-rumped Lion Tamarin	<i>Leontopithecus chrysopygus</i>	12.5-15.2‡	Albernaz 1997, Passos 1999, Valldares-Padua 1993
Golden lion headed tamarin	<i>Leontopithecus chrysomelas</i>	Mar-55	Raboy & Dietz 2004, Rylands 1989, 1993
<i>Catarrhine</i>			
Squirrel Monkey	<i>Saimiri sciureus</i>	11.5	Stone 2007
Yellow-Breasted Capuchin	<i>Sapajus Xanthosternos</i>	2-9	Canale <i>et al.</i> in press
Red-tailed Monkey	<i>Cercopithecus ascanius</i>	Minor	Chapman <i>et al.</i> 2002

Blue Monkey	<i>Cercopithecus mitis</i>	1.9-2.8	Cords 1986
Vervet monkey	<i>Chlorocebus pygerythrus</i>	30	Wrangham & Waterman 1981
Yellow Baboon	<i>Papio cynocephalus</i>	8-15	Altmann <i>et al.</i> 1977, Post 1982
Human	<i>Homo sapiens</i>	Minor	Sugiyama & Koman 1992

† % of total activity

‡ Estimated % of diet

Minor, moderate and major were used when the reference described the importance of gum in the diet qualitatively, and not numerically.

Table 3 Mammal species identified as only opportunistically ingesting gum and not being a necessarily important part of the mammal's feeding ecology.

Common Name	Scientific name	% of total foraging	References
Marsupial			
Rufous rat-kangaroo	<i>Aepyprymnus rufescens</i>	Minor	Irlbeck & Hume 2003
Brush-tailed bettong	<i>Bettongia penicillata</i>	Minor	Irbeck & Hume 2003
Black-striped wallaby	<i>Macropus dorsalis</i>	Minor	Irbeck & Hume 2003
White-eared Opossum	<i>Didelphis albiventris</i>	Minor	Alessio <i>et al.</i> 2005
mahogany glider	<i>Petaurus gracilis</i>	Minor	Irbeck & Hume 2003, Jackson 2001
Primates			
<i>Strepsirhine</i>			
Fat-tailed Dwarf Lemur	<i>Cheirogaleus medius</i>	2	Lahann 2007, Martin 1972
Brown mouse lemur	<i>Microcebus rufus</i>	2	Atsalis 1999
Aye Aye	<i>Daubentonia madagascariensis</i>	Minor	Petter 1977
Ring-tailed Lemur	<i>Lemur catta</i>	Minor	Sussman <i>et al.</i> 2003
Brown Lemur	<i>Eulemur fulvus</i>	Minor	Smith 2010
Black Lemur	<i>Eulemur macaco</i>	0-2	Simmen <i>et al.</i> 2007
Black-and-white-Ruffed Lemur	<i>Varecia variegata</i>	Minor	Ratsimbazafy <i>et al.</i> 2002
Mysore Slender Loris	<i>Loris lydekkerianus</i>	3	Nekaris & Rasmussen 2003
<i>Platyrrhine</i>			
Golden Lion Tamarin	<i>Leontopithecus rosalia</i>	1.6	Dietz <i>et al.</i> 1997
Tufted Capuchin	<i>Sapajus apella</i>	Minor	Peres 1993, 1994a, b
Northern Night Monkey	<i>Aotus trivirgatus</i>	Minor	Hladik & Hladik 1969
Peruvian Red Uakaris	<i>Cacajao calvus</i>	Minor	Bowler & Bodmer 2011
White-footed Saki Monkey	<i>Pithecia albicans</i>	Minor	Peres 1993, 1994a, 1994b
Red-handed Howler Monkey	<i>Alouatta belzebul</i>	Minor	Bonvicino 1989
Mantled Howler Monkey	<i>Alouatta palliata</i>	Minor	Hladik & Hladik 1969
Guianan Red Howler Monkey	<i>Alouatta seniculus</i>	Minor	Izawa 1975
Red-faced Spider Monkey	<i>Ateles p paniscus</i>	1	Van Roosmalen 1985
Woolly monkey	<i>Lagothrix lagotricha</i>	6.9	Peres 1994b
<i>Catarhine</i>			
Putty-nosed Monkey	<i>Cercopithecus nictitans</i>	Minor	Gautier-Hion <i>et al.</i> 1980
Tana River Crested Mangabey	<i>Cercocebus galeritus</i>	0-6	Gautier-Hion <i>et al.</i> 1980, Homewood 1978
Hanuman langur	<i>Semnopithecus entellus</i>	1	Newton 1992
Capped Langur	<i>Trachypithecus pileatus</i>	Minor	Solanki <i>et al.</i> 2008
Chimpanzee	<i>Pan troglodytes</i>	Minor	Ushida <i>et al.</i> 2006
Rodentia			
Black Agouti	<i>Dasyprocia fuliginosa</i>	Minor	Peres 1993, 1994a, b
Silky Desert Mouse	<i>Pseudomys apodemoides</i>	Minor	Cockburn 1981
Bush Squirrel	<i>Paraxerus cepapi</i>	Minor	Viljoen 1977
Procyonidae			
Ring-tailed Coati	<i>Nasua Nasua</i>	Minor	Peres 1993, 1994a, b
Perissodactylae			
Lowland Tapir	<i>Tapirus terrestris</i>	Minor	Peres 1993a, 1994a, b

Minor, moderate and major were used when the reference described the importance of gum in the diet qualitatively, and not numerically.

Table 4 A compilation of published chemical compositions of gums which have been observed being ingested by mammals in the wild, where all nutrients are presented as % concentration on a dry matter basis.

Family	Species eaten	Crude Protein	Sugar [†]	NDF	Galactose	Arabinose	Fructose	Mannose	Xylose	Rhamnose	Glucose	Tannins	Ash	Na	K	Ca	Mg	P	Reference
Anacardiaceae	<i>Anacardium excelsum</i>	1.7												0.02	0.31	0.55	0.02	0.08	Garber 1984
Anacardiaceae	<i>A. occidentale</i>	2.8			61	14		2	2	7	8		1.3	0.03	0.32	0.41	0.06		de Pinto <i>et al.</i> 1995
Anacardiaceae	<i>Lanea coromandelica</i>	1.38			69.5	11	2.5						3.5						Anderson and Hendrie 1970
Anacardiaceae	<i>Spondias mombin</i>				43	30		7		3									de Pinto <i>et al.</i> 2000
Burseraceae	<i>Commiphora arofy</i>	4.4																	Genin <i>et al.</i> 2010
Combretaceae	<i>Terminalia mantalis</i>	2.4																	Genin <i>et al.</i> 2010
Combretaceae	<i>T. manteliopsis</i>	1.4																	Genin <i>et al.</i> 2010
Combretaceae	<i>Terminalia sp.</i>	1.12			20	51		9	4	5			1.8						Anderson & Bell 1974
Combretaceae	<i>Anogeissus latifolia</i>	4.18	76.36		21.97	37.07		1.93	1.28	1.09	0.78		1.14						Kang <i>et al.</i> 2011
Fabaceae	<i>Acacia dealbata</i>	1.6			63	20				10			1.3						Anderson <i>et al.</i> 1973
Fabaceae	<i>A. drepanolobium</i>	3.29		4.99								0-0.49	2.23	0.08 -	0.11 -	0.6- 0.78	0.07- 0.09	negl	Mhinzi <i>et al.</i> 2008
Fabaceae	<i>A. irrorata</i>	9.8			44	30				9			2.7						Anderson <i>et al.</i> 1984
Fabaceae	<i>A. karroo</i>	1.025			50	31				6			3.35	0.02	0.99	0.97 -	107	0.011	Hladik 1979
Fabaceae	<i>A. mearnsii</i>	7.0	95.0		46	43				7	trace								Grein <i>et al.</i> 2013
Fabaceae	<i>A. nitolica</i>	1.265			34.1	44.5				2.7			2.24						Kapoor & Farooqi 1991
Fabaceae	<i>A. obliquinervia</i>	4.4																	Lindenmayer <i>et al.</i> 1994
Fabaceae	<i>A. seyal</i>																		
Fabaceae	<i>A. tortilis</i>	5											49.475						Wrangham & Waterman 1981
Fabaceae	<i>A. xanthophloea</i>	1.79		3.73									0.27		0.13	0.72	0.07	negl	Wrangham & Waterman 1981
Fabaceae	<i>A. auriculiformis</i>	5.75			59	8				5			5.3						Anderson & Gill 1975
Fabaceae	<i>A. terminalis</i>	3.4			82	12				1			1.1						Anderson <i>et al.</i> 1971
Fabaceae	<i>Albizia mainaea</i>	11.3																	
Fabaceae	<i>A. procera</i>	7.34			30.17	44.92	0.02			0.22			4.1	0.02	0.05	0.03	0.23		Pachau <i>et al.</i> 2012
Fabaceae	<i>Albizia sp.</i>	3.18											0.42						Mhinzi 2002
Fabaceae	<i>A. zygia</i>											0.1-1		0.09	0.24	1.19	0.04		Ushida <i>et al.</i> 2006
Fabaceae	<i>Allantsilodendron alluadianum</i>	21																	Genin <i>et al.</i> 2010

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Fabaceae	<i>Delonix decaryi</i>	3.9																	Genin et al 2010
Fabaceae	<i>Enterolobium sp.</i>	1.18	46	19		12	0.2	3.95	0.03	0.46	0.88	0.1							Clamens et al.2000
Fabaceae	<i>Parkia bicolor</i>	5.8	74	9				3											Anderso & de Pinto 1985
Fabaceae	<i>P. nitida</i>	13.9							0.08	0.12	-	0.36	0.1	negl					Anderson et al.1990
Fabaceae	<i>P. pendula</i>	2.575	30	62				1.5				1.07		0.02					Anderso & de Pinto 1985
Sphaerosepalaceae	<i>Rhopalocarpus similis</i>	4.6																	Genin et al.2010

negl=negligible

NDF=neutral detergent fibre

Sugar fractions are % of total sugar, not of total dry matter

†Actual sugar amounts here may not theoretically be all sugar, and may instead be the value for soluble structural carbohydrates.