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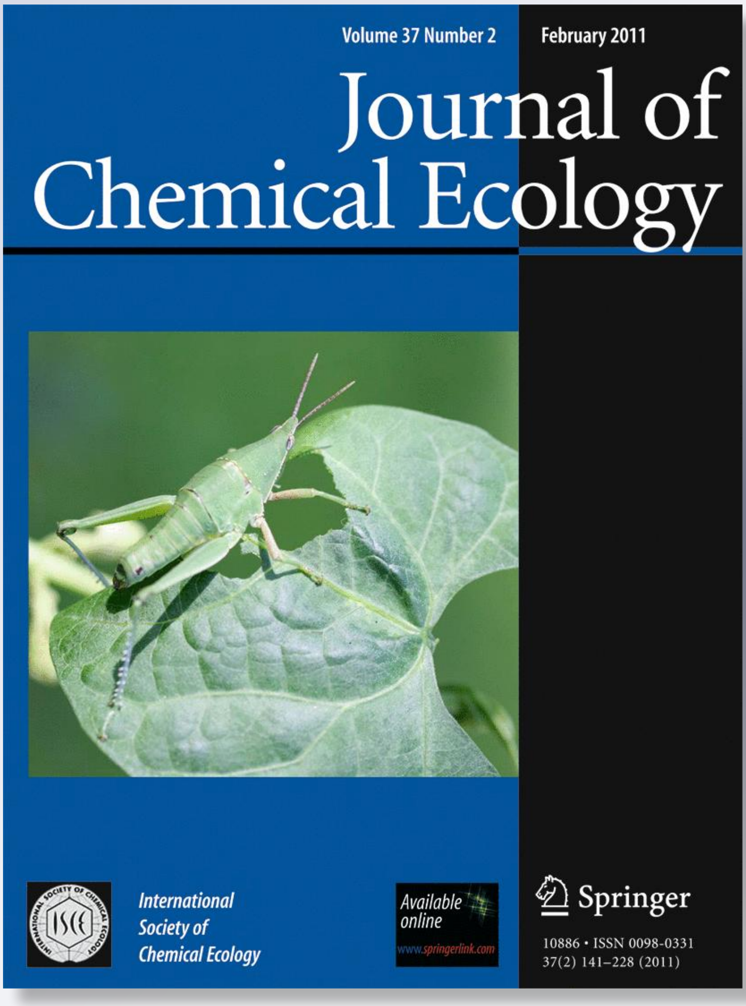
Journal of Chemical Ecology

ISSN 0098-0331
Volume 37
Number 2

J Chem Ecol (2011) 37:145-149
DOI 10.1007/s10886-011-9911-x



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Why Feed on Fungi? The Nutritional Content of Sporocarps Consumed by Buffy-Headed Marmosets, *Callithrix flaviceps* (Primates: Callitrichidae), in Southeastern Brazil

Renato R. Hilário · Stephen Francis Ferrari

Received: 7 July 2010 / Revised: 12 January 2011 / Accepted: 16 January 2011 / Published online: 27 January 2011

Abstract The typical diet of *Callithrix* marmosets is based on gums, although fungi are the dietary staple of a single group of *Callithrix flaviceps* studied in the Augusto Ruschi Biological Reserve, in southeastern Brazil. Here, we present the nutritional composition of two species of *Mycocitrus* fungi consumed by *C. flaviceps*, and discuss possible determinants of the preference of the marmosets for fungi over gums. The fungi were high in sugar/fiber and poor in proteins, and were similar in composition to the gums exploited by other marmosets and to the fungi consumed by *Callimico goeldii*. The reduced protein content of the fungi may be offset by the arthropod component of the diet of the *Callithrix flaviceps* study group. The low relative metabolic rate and enlarged cecum of *Callithrix* enable these marmosets to exploit foods with a high fiber content. In addition, the greater digestibility of chitin in comparison with plant fiber may make fungi a nutritionally more valuable resource to marmosets than gums. Marmosets, thus, may prefer to feed on fungi when an adequate supply of this resource is available in the environment.

R. R. Hilário (✉)
Department of Systematics and Ecology,
Universidade Federal da Paraíba, Cidade Universitária,
58.059-900, João Pessoa, PB, Brazil
e-mail: renatohilario@gmail.com

R. R. Hilário
Department of General Biology,
Universidade Federal de Minas Gerais,
Belo Horizonte, Brazil

S. F. Ferrari
Department of Biology, Universidade Federal de Sergipe,
São Cristóvão, Brazil

Key Words Mycophagy · Atlantic forest · *Mycocitrus* · Diet · Feeding choices · Primate · Callitrichidae

Introduction

Primates exploit a wide range of resources, including reproductive and non-reproductive plant parts and animal prey (Chapman et al., 2002). Despite this, fungi constitute an unusual resource for primates, and mycophagy has been recorded only to date in 23 of the more than 400 recognized species (Hanson et al., 2006; Hilário and Ferrari, 2010). In most cases, fungi are an occasional food used to complement the diet as and when available, although for some species, such as the black snub-nosed monkey (*Rhinopithecus bieti*) and Goeldi's monkey (*Callimico goeldii*), fungi are a dietary staple (Kirkpatrick et al., 1998; Porter, 2001).

Food quality is an important factor influencing foraging decisions (Chapman and Fedigan, 1990). In addition to nutrients such as carbohydrates, proteins, and lipids, which provide essential substances for bodily functions (Maynard and Loosli, 1974), fiber is an important digestive aid (NRC, 2003). While they vary considerably in their composition, fungi tend to be a relatively rich source of carbohydrates, although much of this component may be present in the form of fiber, which requires specializations for efficient digestion (Claridge and Cork, 1994; Claridge et al., 1999).

Atlantic Forest marmosets (genus *Callithrix*) are small-bodied monkeys specialized for the dietary exploitation of plant exudates (gums), which are relatively rich in polysaccharides and minerals such as calcium. Their primary feeding specializations are their chisel-like lower incisors, which allow them to gouge the bark of gum-producing plants to provoke the flow of exudates (Rosenberger, 1978), and an enlarged cecum, in which the gums are probably fermented for digestion (Coimbra-Filho et al., 1980).

Two cases of mycophagy are known in *Callithrix*, in populations that inhabit montane coastal forests in southeastern Brazil (Corrêa, 1995; Hilário and Ferrari, 2010). In the case of buffy-headed marmosets, *Callithrix flaviceps*, which is reported here, fungi were a staple food, and largely have substituted both gum and fruit in the group's diet. In this research, samples of sporocarps consumed by these marmosets were analyzed to establish their nutritional content for comparisons with other fungi consumed by mammals, and with gums exploited by *Callithrix* marmosets, in an attempt to evaluate the factors that determine the preference for fungi over gum in the *C. flaviceps* study group.

Methods and Materials

Study Site and Group Ecological data were collected at the Augusto Ruschi Biological Reserve (RBAR—19°52′ S, 40°33′W), a 3589 ha fragment of montane Atlantic Forest, located in the Brazilian state of Espírito Santo. The vegetation within the study group's home range varied from primary to early successional forest, with dense stands of *Merostachys* bamboo in many areas. The composition of the diet of a free-ranging group of *C. flaviceps* was estimated by using scan sampling records (Altmann, 1974) collected between January and December, 2008. Data were collected on 6 to 9 days per month, with a 1-min scan being conducted at 5-min intervals throughout the daily activity period on a total of 91 days (Hilário and Ferrari, 2010).

Nutritional Analysis The marmosets consumed two species of *Mycocitrus* (Ascomycetes) fungi, *Mycocitrus* sp. 1 and *Mycocitrus* sp. 2 (Fig. 1), the sporocarps of which were invariably attached to the stems of bamboos of the genus *Merosthachys*. Samples of sporocarps were collected between July and December, 2008. Approximately 200 g of sporocarps of *Mycocitrus* sp. 1 and 130 g of *Mycocitrus* sp. 2 were collected for analysis. Samples initially were dried in a plant specimen drier under an incandescent lamp, triturated in a Wiley mill, sieved through a size 42 mesh, and then stored in tightly-sealed glass flasks at room temperature until processing. The sporocarps were triturated together to produce a single homogeneous sample for each species. Three sub-samples were analyzed for each species, and the results are presented as simple means, given the negligible variation among them. During processing, the samples were first dried in a laboratory oven at 100–105°C, following Cuniff (1995), to determine the humidity level by weighing the material before and after drying. The ash content was determined by heating the material, initially over a Bunsen burner, and then in a muffle furnace at 550°C, until it had turned into lightly-colored ash.

Nitrogen content was determined using the Kjeldahl method and multiplied by a Nitrogen/protein factor of 6.25, following the procedure recommended by Cuniff (1995). Lipid content was determined through hot extraction in ethyl ether, by the Soxhlet method, using QUIMIS-Q-308 G26 as the extractor. An attempt was made to determine the gross fiber content of the sample by acid digestion with citric, acetic, and trichloroacetic acids, as recommended by Diemair (1963), but during processing, the material became gelatinized, possibly due to the presence of complex carbohydrates. As this can compromise the digestion and filtering process, and affect the reliability of the results, we opted to estimate the fiber and sugar content as a single value, by subtracting the weight of the other substances (protein, lipid, and ash) from that of the sample. Caloric value of the fungi, per gram, was calculated by multiplying the proportion of protein by 4.80, carbohydrates by 4.10, and lipids by 9.45, according to Paine (1971).

Results

Diet of the C. flaviceps Study Group During the 12 months of the study period, a total of 2278 records of feeding behavior were collected, and in 1673 of these, the item being ingested was identified. Hilário and Ferrari (2010) proposed that most of the unidentified records probably

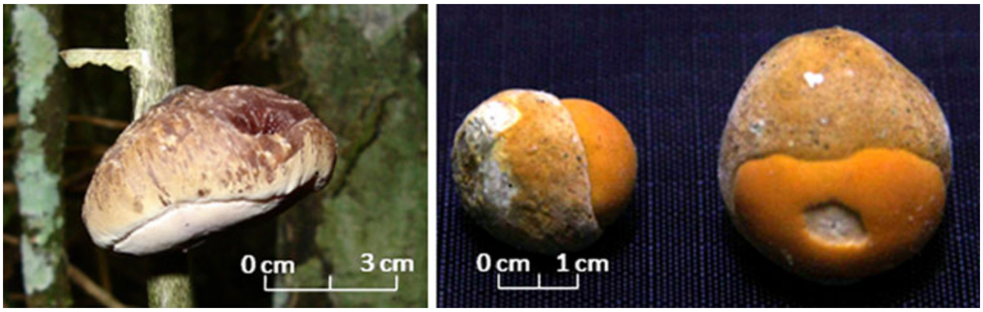

Fig. 1 The two *Mycocitrus* morphospecies exploited by the *Callithrix flaviceps* group in the RBAR, Espírito Santo, Brazil. Photographs: Frederico Pereira. Reproduced with permission from Hilário and Ferrari, 2010

were related to the ingestion of fungi, in which case, the contribution of this item to the diet would have been underestimated. Even so, fungi contributed 64.6% of feeding records for identified items on average over the study period, and never contributed less than 54.0% in any 1 month. In addition to being the most mycophagous diet recorded for any platyrrhine species, including *Callimico goeldii* (Porter, 2001; Porter et al., 2007), the animals appeared to ignore other plant resources (fruit and exudates). In other words, they fed preferentially on fungi, even when the resources typically exploited by other marmosets were available in the environment.

The role of fungi as a dietary staple throughout the year for the *C. flaviceps* study group is comparable to that of plant exudates in the diets of other *Callithrix* marmosets. This includes a second *C. flaviceps* group studied at a site where edible fungi were apparently rare (Ferrari, 1991; Guimarães, 1998).

Nutrient Content of the Sporocarps Moisture represented 11.49±0.03% of the composition of *Mycocitrus* sp. 1 and 9.78±0.03% for *Mycocitrus* sp. 2. These values are not necessarily comparable with those from other studies, however, due primarily to the fact that the sporocarps were partly dried, rather than fresh.

The two species of fungi analyzed here were relatively poor in protein, in comparison with other fungi and most gums (Table 1), although lipid content was similar to that of other fungi. Fiber/sugar content was relatively high in comparison with other fungi, by contrast, and more compatible with that of the gums. The ash content of *Mycocitrus* also was more similar to that of gums than to other fungi.

The two *Mycocitrus* species also were highly similar in their energy content, with 4.18 kcal per gram for species 1, and 4.12 kcal/g for species 2. These values are slightly higher than those obtained for *Auricularia auricula* (4.10 kcal/g) and *A. delicata* (4.01 kcal/g) by applying Paine's (1971) formula to the proportions of nutrients provided by Hanson et al. (2006)—see Table 1. Practically all these values also are within the range for gums—4.02–4.28 kcal/g—provided by Passamani (1996) and Melo et al. (1997).

There are considerable disparities in some values—in particular, the two analyses of *Acacia paniculata*—which may reflect either methodological differences or real variation in the composition of the samples. Despite this variation, one other clear pattern apparent from the data is the greater similarity of the composition of *Mycocitrus* to that of *Ascopolyporus* and *Auricularia* (the bamboo fungi

Table 1 Nutritional content, in dry matter basis, of fungi consumed by several species of mammals, including *Callithrix flaviceps* in the augusto ruschi biological reserve, and gum, consumed by other *Callithrix* species

Resource/species	Fruiting habitus (fungi only)	Content (% dry matter) of:				Reference
		Ash	Proteins	Lipids	Fiber+sugars	
Sporocarp						
Mycocitrus sp. 1	Epigeous	0.96	2.29	1.85	94.89	This study
Mycocitrus sp. 2	Epigeous	1.57	4.60	1.08	93.86	This study
Ascopolyporus polychrous	Epigeous	2.9–3.2	5.5–9.5	0.0–1.6	69.6–78.5	(Hanson et al., 2006)
Auricularia aurícula	Epigeous	3.1	10.1	1.4	85.0	(Hanson et al., 2006)
Auricularia delicata	Epigeous	4.0	13.4	0.9	80.0	(Hanson et al., 2006)
Boletus edulis	Hypogeous	1.7	37.5	2.2	29.6[a]	(Bozinovic and Muñoz-Pedreros, 1995)
Elaphomyces granulatus	Hypogeous	3.4–5.4	15.4–23.8	–	26.0–44.8[b]	(Cork and Kenagy, 1989)
Mesophellia glauca	Hypogeous	2.9	10.2	–	46.6[a]	(Claridge and Cork, 1994)
Rhizopogon luteolus	Hypogeous	2.0	10.0	–	18.9[a]	(Claridge and Cork, 1994)
Gum						
Acacia karroo	–	2.3–3.4	0.7–1.1	0.1	75.9–77.6	(Bearder and Martin, 1980)
Acacia paniculata	–	0.8–1.7	2.6–3.5	0.3–0.4	94.5–95.9	(Melo et al., 1997)
	–	2.0	11.4	2.5	84.1	(Passamani, 1996)
Paulinia carpopodia	–	2.0	16.3	2.9	78.7	(Passamani, 1996)
Bauhinia angulosa	–	2.0	6.8	3.1	88.1	(Passamani, 1996)
Dyctioloma incanensis	–	2.0	7.6	3.6	86.7	(Passamani, 1996)

[a] Neutral detergent fiber;

[b] Total cell wall constituents

consumed by *Callimico*) in comparison with the hypogeal species, especially in relation to proteins and fibers/sugars.

Discussion

Overall, the nutritional composition of the fungi consumed by *Callithrix flaviceps* is similar to that of both the fungi consumed by *Callimico goeldii* (Hanson et al., 2006) and to the gums exploited by other *Callithrix* species (Melo et al., 1997; Passamani, 1996—see Table 1). As fungi contributed to the diet of the *C. flaviceps* study group in a proportion similar to that of gum in other *Callithrix* studies (see Hilário and Ferrari, 2010), it seems reasonable to conclude that the fungus-rich diet recorded in the present study had a nutritional balance similar to that of other marmosets.

A small, but potentially important difference is the smaller protein content of the *Mycocitrus* fungi in comparison with gums (Table 1). The values for the fungi may even be overestimated given that they were determined via the nitrogen content, which includes the proportion present in the carbohydrate chitin molecules of the fungus. While the protein content of the fungus may be lower than the daily requirement for marmosets (6.6% dry matter for *Callithrix jacchus*: NRC, 2003), this may not be a limiting factor, given that 25.8% of the study group's diet was made up of animal prey, primarily arthropods, which are an excellent source of protein (Sterling et al., 1994; Baker et al., 1998).

Based on the results of Hanson et al. (2006), it seems reasonable to conclude that the carbohydrates in *Mycocitrus* are composed primarily of fiber, which slows the transit time of food through the gut (Power and Oftedal, 1996), and may thus impose ecological constraints on small-bodied animals such as marmosets (adult body weight 300–400 g), given their relatively higher metabolic rates (Milton, 1984). However, marmosets have a lower metabolic rate than predicted by their body weight (Ross, 1992), and an enlarged cecum, which is thought to aid in the digestion of fiber through bacterial fermentation (Coimbra-Filho et al., 1980).

The fiber of fungi is mainly chitin (Martin, 1979), which is also the primary component of the arthropod exoskeleton. Some insectivorous mammals produce chitinase (Jeuniaux, 1961; Cornelius et al., 1975) and, while this has not been confirmed in marmosets, chitin is more easily digested by these primates than plant fiber (Krombach et al., 1984). In this case, fungi may represent a more nutritionally valuable resource for marmosets than gums, in which the fiber content is composed primarily of heteropolysaccharides, with a predominance of arabinose, galactose, rhamnose, and aldobiouronic acids (Bearder and Martin, 1980). The higher nutritional quality of fungi in comparison with exudates could thus account for the preference of fungi over exudates, and explain why these marmosets appeared to ignore fruit during their foraging activities.

Fungi nevertheless pose other challenges. Edible species are rare in most forests and have slow rates of regeneration (Hanson, 2000; Hanson et al., 2003), which may impose a need for relatively large home range, given the need to ensure access to a number of feeding patches sufficient to maintain an adequate diet over the course of the year. The *C. flaviceps* study group occupied a home range approximately four times larger than the next largest recorded to date for any marmoset group (Hilário, 2009). Relatively large home ranges are also characteristic of a second callitrichid, *Callimico goeldii* (Porter et al., 2007), a characteristic which also has been attributed to the importance of mycophagy in the ecology of this species (Porter and Garber, 2010). In the marmosets, this large home range problem may nevertheless be partly offset by other benefits, such as the avoidance of bark gouging, which is necessary to maintain a regular supply of gum exudates (Digby et al., 2011). Given the findings of the present study, the predominance of gum in the diets of other marmosets may be primarily a consequence of the relative lack of edible fungi at most study sites. Future studies should target the understanding of the relationship between the consumption of fungi and their availability within the environment. Systematic analyses of the nutritional content of other marmoset foods will provide more definitive insights into the factors that determine feeding and foraging choices.

Acknowledgments We extend special thanks to Professor José Virgílio Coelho, who dosed the nutrient content of the fungi. We are also grateful to Tatiana Gibertoni and Jadergudson Pereira for identification of the fungi. We thank Eduardo Mignone, director of the Augusto Ruschi Reserve, Flávio Rodrigues, Adriano Chiarello, Kátia Corrêa, Milene Martins, Sérgio Mendes, Ítalo Mourthé, Waldney Martins, and Frederico Pereira. The project was supported by Idea Wild and US Fish and Wildlife Service, RRH by FAPEMIG and CAPES, and SFF by CNPq (process no. 302747/2008-7).

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