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# Gum feeder as environmental enrichment for zoo marmosets and tamarins

Barbara Regaioli<sup>1</sup> Chiara Angelosante<sup>2</sup> Giovanna Marliani<sup>2</sup> Pier Attilio Accorsi<sup>2</sup> Stefano Vaglio<sup>1,3,4</sup> Caterina Spiezio<sup>1</sup>

<sup>1</sup>Department of Research and Conservation, Parco Natura Viva - Garda Zoological Park, Bussolengo, Italy

<sup>2</sup>Dipartimento di Scienze Mediche Veterinarie, Università di Bologna, Bologna, Italy

<sup>3</sup>Department of Biology, Chemistry and Forensic Science, University of Wolverhampton, Wolverhampton, UK

<sup>4</sup>Department of Anthropology and Behaviour, Ecology and Evolution Research (BEER) Centre, Durham University, Durham, UK

Correspondence

Stefano Vaglio, Department of Research and Conservation, Parco Natura Viva - Garda Zoological Park, Loc. Figara 40, 37012 Bussolengo, Italy.

Email: S.Vaglio@wlv.ac.uk

## Abstract

Tamarins and marmosets are small-bodied social callitrichines. Wild callitrichines feed on exudates, such as sap and gum; particularly, marmosets are mainly gummivores, while tamarins consume gums only occasionally and opportunistically. Zoo marmosets and tamarins are usually provided with gum arabic as an alternative to the exudates normally found in the wild. The aim of this study was to evaluate the effects of a gum feeder on the behavior and well-being of four zoo-managed callitrichines. We studied four cotton-top tamarins (*Saguinus oedipus*), four red-handed tamarins (*S. midas*), two pygmy marmosets (*Cebuella pygmaea*), and three Geoffroy's marmosets (*Callithrix geoffroyi*) housed at Parco Natura Viva (Italy). We conducted the study over two different periods, a baseline (control, without the gum feeder) and then a gum feeder (when the gum feeder was provided) period. We used continuous focal animal sampling to collect behavioral data, including durations of social and individual behaviors. We collected 240 min of observations per period per study subject, with a total of 3,120 min for all the subjects in the same period and of 6,240 min in both periods. We analyzed data by using nonparametric statistical tests. First, we found that the gum feeder promoted species-specific behaviors, such as exploration, and diminished self-directed behaviors, suggesting an enriching effect on tamarin and marmoset behavior. Moreover, in red-handed tamarins, the provision of the gum feeder reduced the performance of self-directed and abnormal behavior, specifically coprophagy. These results confirm that gum feeders are effective foraging enrichment tools for zoo marmosets and tamarins.

## KEYWORDS

callitrichines, gum arabic, zoo primate welfare

## 1 | INTRODUCTION

Tamarins and marmosets are small-bodied New-World monkeys belonging to the subfamily of Callitrichinae (Groves, 2001). They live in geographical areas ranging from Costa Rica to South Brazil, Bolivia, and Paraguay, with the greatest variety of species found in the Amazonian region (Buckner, Lynch Alfaro, Rylands, & Alfaro, 2015; Emmons, 1990). They are cooperative breeders and may form

familial groups made up of a breeding pair, several siblings and other members helping with parental care of the offspring. The breeding pair is dominant over other group members (Emmons, 1990; Smuts, Cheney, Seyfarth, & Wrangham, 1986).

The diet of wild tamarins and marmosets is affected by seasonality and availability of food resources; they mainly feed on fruit, insects, small vertebrates, leaves, and nectar (Bairrão Ruivo, 2010; Garber, 1993; Rosenberger, 1992). In addition, their natural

diet includes plant exudates, such as gum and sap, which are rich in carbohydrates and minerals (Bairrão Ruivo, 2010; Power, 2010). Many plant gum exudates consist of  $\beta$ -linked complex polysaccharides which often also contain glycoproteins and proteoglycans (Gashua, Williams, Yadav, & Baldwin, 2015) from which energy, water, and minerals, particularly calcium, can be obtained after fermentation. Callitrichines require a high intake of calcium from their diet, as these species generally give birth to twins and plenty of milk is required during the nursing process (Garber, 1993; Heymann & Smith, 1999; Kelly, 1993; Pack, Henry, & Sabatier, 1999; Passamani & Rylands, 2000; A. B. Taylor & Vinyard, 2004). The benefits of gum feeding have been widely investigated in the wild. Therefore, supplementing the diet of zoo nonhuman primate species with plant gum exudates might improve the diet and general well-being of these primate species in captive environments (Garber, 1993; Heymann & Smith, 1999; Kelly, 1993; Pack et al., 1999; Passamani & Rylands, 2000; A. B. Taylor & Vinyard, 2004).

Plant gum exudates are an essential component of the marmoset diet, whilst it is less important for other callitrichines (Bairrão Ruivo, 2010; Power, 2010; Power & Oftedal, 1996). For this reason, marmosets show behavioral, morphological and metabolic adaptations to gum feeding. In particular, their dental adaptations allow them to gouge trees and thereby stimulate gum exudate production as part of the plants' response to wounding (Burrows & Nash, 2010; Eng, Ward, Vinyard, & Taylor, 2009; Vinyard et al., 2004; Vinyard, Wall, Williams, & Hylander, 2003); while modifications of the gastrointestinal tract permit the digestion of gums and other plant exudates (Bairrão Ruivo, 2010; Coimbra-Filha & Mittermeier, 1977; Heymann & Smith, 1999). Tamarins tend to feed on gum and sap only opportunistically, when this food is available in trees wounded by other animals, with seasonal variation in terms of time investment for gum feeding (Garber, 1993; Power, 2010; Power & Oftedal, 1996).

Zoo tamarins and marmosets are generally provided with commercially available gum arabic, as a replacement for the various plant gum exudates that they consume in the wild (Goodrum, Patel, Leykam, & Kieliszewski, 2000). Furthermore, these plant gum exudates may be crucial biochemical digestive challenges for the normal functioning of their digestive tract (Bairrão Ruivo, 2010). Wild tamarins show more frequent gum feeding during the afternoon, as gum digestion is time consuming and would, therefore, be easier during the night sleeping (Bairrão Ruivo, 2010; Heymann & Smith, 1999; Kelly, 1993). On the contrary, gummivore marmosets are known to eat gum frequently throughout the daylight hours as their gastrointestinal system is well-adapted to gum digestion (Bairrão Ruivo, 2010; Heymann & Smith, 1999; Kelly, 1993). Tamarins and marmosets are usually attracted to novel objects, and vigilant and aware of what happens in their surrounding environment (Menzel & Menzel, 1979). Promoting natural gum feeding behavior with specific devices might be important to enhance the feeding strategy and husbandry of zoo-managed callitrichines to improve their physical and mental well-being.

Giving zoo animals the opportunity to perform their species-specific behaviors represents one of the primary goals of modern zoological gardens. In addition, ethological parameters have been

proven to be a valuable tool in assessing zoo animal welfare (Fontani et al., 2014; Hill & Broom, 2009). The occurrence of natural species-specific behaviors, such as exploratory behaviors, is considered an indicator of good welfare status and enriched environment (Mellor & Beausoleil, 2015; Mench, 1994), while abnormal behaviors, such as excessive inactivity, stereotypies, and self-injurious behaviors, may indicate poor welfare or stressful scenarios (Manteca, Amat, Salas, & Temple, 2016; Renner, Feiner, Orr, & Delaney, 2000). Moreover, self-directed behaviors, such as self-grooming and scratching, are usually benign activities that occur commonly in nonhuman primates (Maestripieri, Schino, Aureli, & Troisi, 1992). However, in certain situations such as social tension and conflicting or frustrating contexts, self-directed behaviors can be associated with uncertainty and anxiety and have been considered as displacement activities (Lutz, 2014; Spiezio, Vaglio, Scala, & Regaiolli, 2017; Troisi, 2002; Troisi & Schino, 1987). Thus, a decrease in self-directed behaviors might be considered as a positive welfare indicator, although these activities are normally included and well-represented in the species-specific behavioral repertoire of primate species (Leeds & Lukas, 2018; Spiezio et al., 2017). Similarly, coprophagy occurs in both captive and wild nonhuman primates and may have an adaptive value in these species; however, in controlled environment, this behavior has been related to factors such as nutritional deficiency and medical problems but also boredom and social stress (Krief, Jamart, & Hladik, 2004; Prates & Bicca-Marques, 2005). Therefore, coprophagy has been classified as abnormal behavior and has been identified as a possible indicator of poor well-being (i.e., Lutz, 2018; Prates & Bicca-Marques, 2005).

Environmental enrichment is a widespread practice among modern zoos and has been found to promote the performance of species-specific behavioral repertoire and to address as well as prevent abnormal behavior (Hosey, Melfi, & Pankhurst, 2013). Though some callitrichines may not require gum to reach their nutritional needs in zoo settings, gum feeding may represent a behavioral necessity and could improve the diversity of the behavioral repertoire as well as the welfare status of the zoo marmosets and tamarins (Bairrão Ruivo, 2010). In the current study, zoo tamarins and marmosets were provided with wooden drilled logs as gum feeders. Previous research investigating the effects of a similar gum feeder on zoo marmosets and tamarins suggested that this environmental enrichment could promote species-specific behaviors, reduce abnormal behaviors, such as stereotypies and coprophagy, and decrease inactivity (Huber & Lewis, 2011; McGraw, Brennan, & Russell, 1986; Roberts, Roytburd, & Newman, 1999; T. D. Taylor, 2002). In particular, the provision of hanging feeder baskets and sticks smeared with Acacia gum promoted feeding and foraging while decreasing stereotypic behavior, specifically excessive coprophagy, in red-handed tamarins in a zoo (T. D. Taylor, 2002). Similarly, common marmosets (*Callithrix jacchus*) in different social housing conditions have been found to benefit from foraging enrichments, specifically gum feeders, promoting natural behaviors and leading to a reduction in the time spent performing stereotypic behavior such as pacing (McGraw et al., 1986; Roberts et al., 1999). In general, providing zoo callitrichines with gum arabic in feeders that

require specific feeding abilities has been found to promote naturalistic behaviors and feeding strategies described in the wild. In particular, artificial gum feeders are cheap and easy to build and can be helpful in enhancing the physical and mental well-being of these species, which are well-disposed to work for gum, enhancing also the educative value of zoo exhibit (Huber & Lewis, 2011; McGraw et al., 1986).

The aims of this study were to:

- Assess the effects of the gum feeder on the behavior of two tamarin species (*Saguinus oedipus* and *S. midas*) and two marmoset species (*C. geoffroyi* and *Cebuella pygmaea*) which were scarcely investigated in the past. On the basis of prior work by other authors revealing that gum feeding represents a behavioral need and a digestive challenge for the digestive system of marmosets and, to a lesser extent, tamarins (Bairrão Ruivo, 2010; Heymann & Smith, 1999; Hosey et al., 2013; Roberts et al., 1999; T. D. Taylor, 2002), we predicted that the gum feeder would increase the performance of species-specific behaviors, such as explorative and feeding behaviors and reduce inactivity and abnormal behavior.
- Compare the duration of gum arabic feeding between tamarins and marmosets, particularly the time spent feeding on gum between the morning and the afternoon within the two groups, to identify the optimal time for gum provision. Since gum digestion is time consuming and would, therefore, be easier during night sleeping, tamarins show gum feeding more during the afternoon (Bairrão Ruivo, 2010; Heymann & Smith, 1999). Thus, we expect that marmosets would perform gum feeding more than tamarins and during day time, while tamarins would eat gum during afternoon hours rather than in the morning.

## 2 | MATERIALS AND METHODS 2.1 |

### Study subjects and area

We studied eight tamarins, specifically four cotton-top tamarins and four red-handed tamarins; and five marmosets, three Geoffroy's marmosets, and a pair of pygmy marmosets. The study subjects belonged to two different age-groups: juveniles, including individuals aged <2 years (approximate age of sexual maturity; Abbott, Barnett, Colman, Yamamoto, & Schultz-Darken, 2003; Tardif, 1984; Tardif, Mansfield, Ratnam, Ross, & Ziegler, 2011; Ziegler, Savage, Scheffler, & Snowdon, 1987) and adults, including individuals aged >2 years (Abbott et al., 2003; Tardif et al., 2008, 2011; Table 1).

All groups were housed at Parco Natura Viva-Garda Zoological Park (Bussolengo, Italy) in separated enclosures in the Tropical Green House. Although enclosures were not adjacent to each other, Geoffroy's marmosets, cotton-top tamarins, and red-handed tamarins were in acoustic contact. Their enclosures were made of an outdoor and an indoor area and each area was approximately 30 m<sup>2</sup> and contained trees, branches and logs, ropes, wooden boxes, sheds, and shelves; the indoor areas were heated and provided with UV lamps. The pygmy marmoset enclosure was an 18 m<sup>2</sup> aviary.

T A B L E 1 Tamarins and marmosets involved in the study

Species	Name	Sex	Age
Cotton-top tamarin ( <i>Saguinus oedipus</i> ) N = 4	Mum	F	Adult
	Franca	F	Juv
	Rubik	F	Juv
	Dad	M	Adult
Midas tamarin ( <i>S. midas</i> ) N = 4	CS	F	Adult
	OB	F	Adult
	Norman	M	Adult
	CC	M	Adult
Geoffroy's marmoset ( <i>Callithrix geoffroyi</i> ) N = 3	Mum	F	Adult
	Dad	M	Adult
	Sbiru	M	Juv
Pygmy marmoset ( <i>Cebuella pygmaea</i> ) N = 2	Peace	F	Adult
	Love	M	Adult

Note: For each species the table reports the subject name, sex and age class (adult: >2 years of age; Juv: <2 years of age).

Abbreviations: F, female; Juv, juvenile; M, male.

During the study, the gum feeders were placed in the outdoor area of the enclosures. Tamarins and marmosets were fed two times a day with fruits, multi cereal pap, mealworms, gum arabic, and occasionally meat and eggs. Freshwater was available ad libitum. Manipulative, sensory or food-related devices were provided daily as environmental enrichment. The study, which did not involve any invasive or stressful techniques, was conducted in accordance with the EU Directive 2010/63/EU and the Italian legislative decree 26/2014 for Animal Research.

## 2.2 Procedure and data collection

The study was made of two different periods, the baseline and the gum-feeder period. During the baseline, gum arabic was provided in bowls at the time of the afternoon meal following the daily routine husbandry. In the gum-feeder period, gum arabic was provided, using the new gum feeders, at the usual feeding times over the morning and the afternoon. The gum feeder consisted of a wooden drilled disc, with 10–15 holes each, on both sides of the disc (Figure 1). The discs were hung with ropes on the enclosure trees and branches, ~1.5 m above the ground. The daily amount of gum arabic was put in the holes of the feeder. In particular, the amount of gum arabic per subject was prepared using ~8 g of powder and 5 g of water. The entire study consisted of 6,240 min (104 hr) of observation divided in the baseline (52 hr) and in the gum-feeder period (52 hr) for all the subjects. Per period and per subject, a total of 240 min of behavioral observations were carried out and two sessions per day per monkey were run (one in the morning and one in the afternoon). The duration of the data collection sessions per monkey differed between species based on the sample size. In particular, per period, data on each cotton-top tamarin (N = 4) and on each red-handed tamarin (N = 4) were collected during eight 30-min sessions. For the marmosets, per



**FIGURE 1** The gum feeder provided to marmosets and tamarins. In the gum-feeder period, tamarins and marmosets were provided with wooden drilled discs, hanged in the outdoor enclosure and filled with arabic gum. The picture shows one of the study Geoffroy's marmoset interacting with the feeder

period and per monkey, data were collected during six 40-min sessions for Geoffroy's marmosets (N = 3) and four 60-min sessions for pygmy marmosets (N = 2) for an overall of 240 min of observation for each subject within each period. Monkeys were observed in a prescribed sequence following a specific design to avoid time-of-day bias in data collection. Feeding and enrichment times were the same over the study period, one in the morning and one in the afternoon.

A continuous focal animal sampling method (Altman, 1974) was used to collect durations of normal and abnormal individual and social behaviors (Table 2). The time spent out-of-sight, here defined as "not observed," was also recorded. The red-handed tamarins were the only subjects to perform abnormal behavior, specifically coprophagy, which was reported in three out of four monkeys, although for a very low percentage of the total observation time (ranging from 0.13% to 1.67%). To assess the effect of the feeder on the behavior of the red-handed tamarins, we created the category stress-related behaviors (SRB), including coprophagy and self-directed behaviors. Although these behaviors are found in wild animals and maybe adaptive, they both have been related to stressful and conflict situations within controlled environments (Lutz, 2014; Lutz, 2018; Prates & Bicca-Marques, 2005; Spiezio et al., 2017; Troisi, 2002; Troisi & Schino, 1987). The gum-eating behavior was included in the category "feeding/foraging" as in the first-period gum arabic

**TABLE 2** Study ethogram

<b>Individual behaviors</b>	
Abnormal behavior	Coprophagy
Alert	Being watchful
Exploration/play	Exploring the environment, hunting, manipulating enrichment devices, leaves, twigs and other objects found in the enclosure by sniffing, biting, chewing, gouging, handling, pouncing on, and grappling with
Feeding/foraging	Eating food found in the enclosure, either in bowls or foraging on trees, ground and other substrates
Gum feeder*	Eating gum from the gum feeders
Locomotion	Moving around in the enclosure, walking, running, or jumping along with trees or walls of the enclosure
Maintenance	Peeing, defecating, and drinking
Scent marking	Marking branches, shelves, ropes, and other substrates with anogenital, supra-pubic, or sternal glands
Self-directed b.	Cleaning or licking the own hair or other parts of the body, scratching with the hands or with the legs
Visual exploration	Looking around quietly
<b>Social behavior</b>	
Affiliative b.	Allo-grooming (using the hands and/or mouth to clean the partner fur or other parts of the body), being in contact with conspecifics, nuzzling [rubbing or pushing gently with the nose and mouth], anogenital inspection (orienting the face against or toward anogenital region of partner or use hands or mouth to investigate anogenital region of partner), stealing food/objects from the hands or from the mouth
Agonistic b.	Fighting (biting, clawing, and wrestling), attacking (lunging at or pouncing on partner aggressively), cuffing, chasing, threatening (staring with lower eyebrows, furl brow, and tongue flicking), mounting between same-sex individuals
Interspecific b.	Interacting with or directing attention toward individuals of different species, such as humans (visitors and zookeepers) or Azara's agoutis (only in the Geoffroy's marmoset enclosure)
<b>Not visible</b>	
Not observed	The individual is not visible to the observer or it is not possible to identify the behavior being performed

Note: Individual and social behaviors collected in the study periods.

Abbreviation: b, behavior.

\*This behavioral category was recorded only in the second period when gum arabic was put in the gum feeder and it was possible to detect clearly that the subjects were feeding on that food item.

was provided in bowls with other food; however, to compare the time spent feeding on gum between marmosets and tamarins, the duration of gum feeding from the new feeder was also collected (Table 2).

## 2.3 | Data analysis

Data were analyzed using nonparametric statistical tests and the significance level was set at  $p < .05$  (Siegel & Castellan, 1992). In particular, the Wilcoxon test was used to compare the behavior of the study subjects between the two periods (baseline vs. gum feeder), whereas the Mann–Whitney test was used to compare the time spent feeding on gum between the study groups (marmosets vs. tamarins) in the gum-feeder period. StatView version 5.0 (SAS Institute Inc.) was used for all statistical analyses on behavioral data. In addition, single-case analyses were used to test the effect of the gum feeder on the behavior of each individual, comparing the performance of SRBs between different periods within each individual of red-handed tamarins (Fisch, 2001) performing SRB, specifically abnormal behavior and self-directed behavior. For the single-case analyses, Wilcoxon–Mann–Whitney test (Marx, Backes, Meese, Lenhof, & Keller, 2016) was used. For all behavioral categories, medians and interquartile range (IQR) are reported in the manuscript and tables.

## 3 | RESULTS

### 3.1 | Baseline versus gum-feeder period

We investigated the effects of the gum feeder on the behavior of the study subjects comparing the time spent in individual and social behaviors as well as “not observed” between the two periods (Figure 2; Table 3).

When considering each individual behavior, Wilcoxon tests revealed that feeding/foraging, maintenance, and self-directed were performed

significantly more during the baseline than during the gum-feeder period, whereas the opposite pattern was found for visual exploration. No other significant differences were found (see Figure 2 and Table 3 for median, IQR, and statistical values). On the other hand, within social behaviors, interspecific behavior was performed more during the baseline than during the gum-feeder period, whereas no other differences were found (see Table 3 for median, IQR, and statistical values). Finally, Wilcoxon test revealed that “not observed” was performed significantly more during the baseline than during the gum-feeder period ( $z = -2.481$ ,  $p = .013$ ; Table 3).

### 3.2 | Effect of the gum feeder on tamarins

After evaluating the effects of the gum feeder on all subjects, we focused on tamarins and marmosets separately. Regarding tamarins, within individual behaviors, feeding/foraging, and maintenance were performed significantly more during the baseline than during the gum-feeder period, whereas no significant differences were found in any other behavioral category (see Table 3 for median, IQR, and statistical values).

### 3.3 | Effects of the gum feeder on marmosets

Regarding marmosets, “not observed” was performed significantly more during baseline than during the gum-feeder period ( $z = -2.023$ ,  $p = .043$ ), while no other significant differences were found between the two periods (see Table 3 for median, IQR, and statistical values).

### 3.4 | Effects of the gum feeder on SRBs in the red-handed tamarins

Three red-handed tamarins (CS, OB, and Normann) showed the abnormal behavior “coprophagy.” To test whether the gum

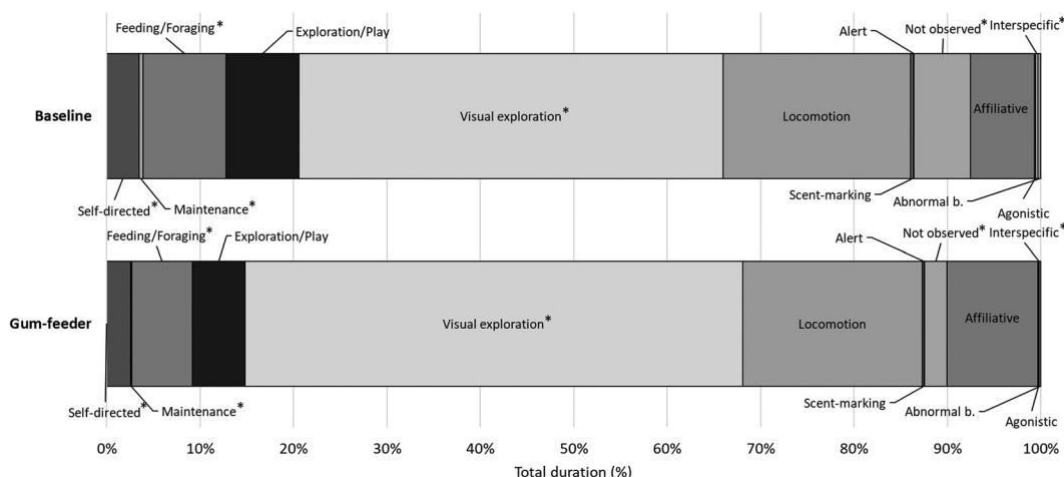


FIGURE 2 Behaviors of the study marmosets and tamarins. The bars report the % total duration in seconds of individual and social behaviors as well as “not observed” in the baseline and in the gum feeder. Asterisks indicate categories that differed significantly between periods (Wilcoxon test:  $p < .05$ )

T A B L E 3 Individual behaviors, social behaviors, and “not observed” in the baseline and in the gum-feeder period

	All			Tamarins			Marmosets		
	Baseline	GF	z and p value	Baseline	GF	z and p value	Baseline	GF	z and p value
Individual behavior									
Abnormal	0 (0)	0 (9)	#	0 (60.8)	0 (79.5)	#	0 (0)	0 (0)	#
Alert	7 (17.5)	0 (4.5)	z = -1.868, p = .062	8 (15.8)	4 (9.5)	z = -1.016, p = .310	5 (18.5)	0 (0)	z = -1.826, p = .068
Expl/play	869 (1,307.5)	663 (612)	z = -1.922, p = .055	974.5 (1,569.5)	857.5 (1,308.5)	z = -1.400, p = .161	321 (1,509)	494 (723.5)	z = -1.214, p = .225
Feeding/foraging	1,219 (590.5)	826 (665.5)	z = -2.481, p = .031*	1,312.5 (635.3)	1,233.5 (864.5)	z = -2.100, p = .036*	1,081 (653.5)	763 (485.5)	z = -1.483, p = .138
Locomotion	2,920 (980.5)	2,859 (1,572.5)	z = -0.384, p = .701	2,958.5 (890.3)	3,340.5 (1,155.8)	z = -2.260, p = .208	2,920 (1,199.5)	1,622 (1,432)	z = -1.483, p = .138
Maintenance	57 (70)	10 (32)	z = -3.111, p = .002*	83 (42.8)	13 (30.5)	z = -2.521, p = .012*	19 (11.5)	0 (22.5)	z = -1.761, p = .078
Scent marking	38 (36.5)	22 (28.5)	z = -1.049, p = .294	27.5 (36)	28 (32.8)	z = -0.491, p = .624	49 (55.5)	19 (37)	z = -0.944, p = .345
Self-directed	420 (240.5)	392 (337)	z = -2.201, p = .028*	464 (257.3)	437.5 (183.3)	z = -1.260, p = .208	384 (250.5)	208 (354)	z = -1.753, p = .080
Visual expl	6,891 (2,946.5)	8,097 (1,760)	z = -2.201, p = .028*	6,578 (3,024.8)	7,860.5 (2,860.3)	z = -1.680, p = .093	7,080 (2,402.5)	8,119 (2,034)	z = -1.483, p = .138
Social behavior									
Affiliative	764 (632.5)	1,331 (1,180.5)	z = -1.712, p = .087	704.5 (753.5)	776.5 (798.8)	z = -0.560, p = .575	1,110 (964)	1,797 (1,269.5)	z = -1.753, p = .080
Agonistic	0 (34.5)	8 (28.5)	z = -0.533, p = .594	9.5 (43.3)	7 (20.8)	z = -0.280, p = .779	0 (21.5)	8 (54.5)	z = -1.604, p = .110
Interspecific	0 (69)	0 (0)	z = -2.023, p = .043*	0 (59.3)	0 (0)	z = -1.342, p = .180	38 (94)	0 (0)	z = -1.604, p = .110
Not observed	956 (881.5)	207 (553.5)	z = -2.481, p = .013*	724.5 (846.5)	172 (633)	z = -1.540, p = .124	1,117 (740)	303 (615)	z = -2.023, p = .043*

Note: For each behavioral category, the table reports the median (interquartile range) duration in seconds calculated in the baseline and in the gum-feeder period (GF), as well as the z and p values of the Wilcoxon test performed to compare the two periods. All: Data collected on different species pulled together; Tamarins: Analysis performed within the tamarin group (N = 8) (*Saguinus oedipus* and *S. midas*); Marmosets: Analysis performed within the marmoset group (N = 5; *Callithrix geoffroyi* and *Cebuella pygmaea*).

\*Significant difference between the two periods (p < .05).



feeder positively affected the behavior as a measure of welfare of these individuals, a single-case analysis was done to compare the performance of SRBs between different periods within each individual. For CS, the median duration of SRB was 113.5 (50) s in the baseline and 74.5 (51.25) s in the gum-feeder period; for OB, the median duration of SRB was 90 (70.25) s in the baseline and 52 (72.75) s in the gum-feeder period; for Normann, the median duration of SRB was 101 (99.75) s in the baseline and 60 (70) s in the gum-feeder period. Wilcoxon–Mann–Whitney tests revealed that SRBs were performed significantly more during the baseline than the gum-feeder period in CS ( $p = .037$ ) but no significant differences were found for OB and Normann ( $p > .05$ ).

### 3.5 | Gum feeding in marmosets and tamarins

Finally, we focused on the time spent feeding on gum arabic- by the study subjects. The median time spent feeding on gum arabic was 42.5 (90.8) s for tamarins and 235 (255.5) s for marmosets. Marmosets tended to spend more time eating gum arabic than tamarins ( $U = 7, p = .056$ ). When considering gum feeding during the day within each group, the median time spent feeding on gum arabic by tamarins was 31.5 (91.8) s in the morning and 0 (20) s in the afternoon. In the case of marmosets, the median time spent feeding on gum arabic was 116 (207) s in the morning and 114 (281) s in the afternoon. Wilcoxon tests revealed no significant differences between morning and afternoon in both tamarins ( $Z = -1.572, p = .116$ ) and marmosets ( $Z = -0.365, p = .715$ ; Figure 3).

## 4 | DISCUSSION

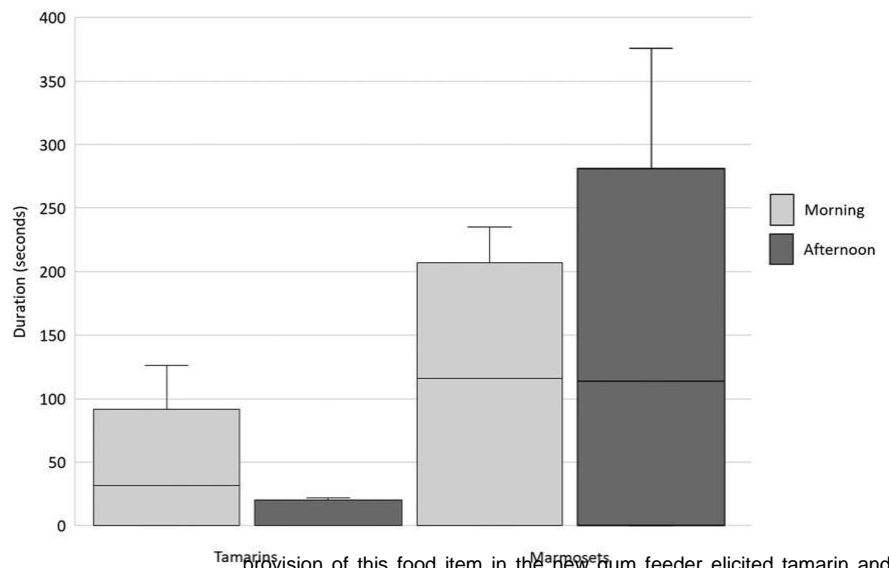
This study aimed to investigate the effects of a gum feeder, a wooden disc drilled with holes, on the behavior of zoo tamarins and marmosets, to assess their welfare. Moreover, the study aimed to compare the

time spent feeding on gum arabic between these species. First, each species interacted with the gum feeders performing a new behavior to obtain gum arabic, confirming the enriching role on the animal daily routine and feeding strategies of this device (Huber & Lewis, 2011; McGraw et al., 1986; Roberts et al., 1999). All the study monkeys interacted with the gum feeder and showed the behavior of eating arabic gum from the holes. In particular, marmosets and tamarins had to cling on to the wooden disc holding with one or both hands and then retrieve gum directly with the mouth or grasping it with one hand. When retrieving the gum, marmosets gouged and scraped the disc moving the head and mouth similarly as in the tree-gouging behavior reported in the wild, indeed, the jaws were widely open around the gum in the hole, the upper jaw anchored on the wooden disc, whereas the lower jaws indented the area around the hole, favoring both gouging and scraping movements (Burrows & Nash, 2010; Rylands, 1984; Thompson et al., 2014; Vinyard et al., 2003, 2004). This movement was less pronounced in tamarins as they simply retrieved the superficial gum coming out the holes and consumed it.

First, we found that subjects were out-of-sight (“not observed”) more during the baseline than during the gum-feeder period. This result seems to suggest that the gum feeder could enhance the welfare of the study subjects, engaging them in the performance of species-specific behaviors and increasing the time they were visible to the public. This finding is consistent with previous research on gum-feeder provision in marmosets, reporting increased animal visibility (Kelly, 1993).

Regarding individual behaviors, when data on tamarins and marmosets were pooled together, we found that feeding/foraging behaviors, as well as maintenance behaviors, were performed significantly less during the gum-feeder period than during the baseline. Within each group (tamarins and marmosets), we found the same patterns and significant differences for these categories in tamarins, while they did not differ significantly in marmosets. Gum arabic is a high-energy food source, rich in carbohydrates and minerals, requiring a longer time to be digested than other food items (Bairrão Ruivo, 2010; Kelly, 1993; Power, 2010). It is possible that the

**FIGURE 3** Time spent feeding on arabic gum in the gum feeders in the morning and in the afternoon by tamarins and marmosets. Box and whisker plot of the time spent feeding on gum in the morning (light gray) and in the afternoon (dark gray) by tamarins and marmosets. The horizontal lines within the box indicate the medians, boundaries of the box indicate the first and third quartile. The whiskers extend up from the top of the box to the largest data element that is  $\leq 1.5$  times the interquartile range (IQR) and down from the bottom of the box to the smallest data element that is  $> 1.5$  times the IQR



provision of this food item in the new gum feeder elicited tamarin and marmoset interest, inducing them to eat gum arabic before the rest of the food. Given the nutritional properties of the gum (Power, 2010; Power &

Oftedal, 1996), we speculate that a small amount of this food could be sufficient for these small primates, leading to the reduction in the overall time spent feeding and foraging in the second period. Also, it is possible that the interest toward the gum feeder as a novel device might supply the callitrichines with the need of looking for food elsewhere in the enclosure (e.g., bowls, usual feeding points). In other words, the study monkeys may have spent less time feeding and foraging in the second period because they consumed gum arabic first, and the same could extend to the decrease in maintenance behavior during the second period. However, the presence of the gum feeder increased visual exploration, which was performed significantly more during the gum-feeder period than during the baseline. This behavior is particularly relevant in callitrichines as they are curious, attracted to novel objects and aware of their surroundings (Menzel & Menzel, 1979). Such features of these small-bodied primates have been related to improved vigilance and antipredator behaviors (Caine, 1984). Therefore, the gum feeder seemed to encourage the performance of species-specific behaviors that are particularly important for the survival of the species in the wild (Caine, 1984).

The presence of the gum feeder also led to a significant decrease in self-directed behaviors, which have been described as potential behavioral indicators of stress and anxiety in nonhuman primates, at least in some situations (Leeds & Lukas, 2018; Maestriepieri et al., 1992). As our results underlined a decrease in the performance of these behaviors, the presence of the gum feeder seems to positively impact the behavior of the study monkeys (Leeds & Lukas, 2018; Spiezio et al., 2017). However, the study monkeys spent a relatively low amount of time performing self-directed behaviors in both the baseline and the gum-feeder periods (4% and 3% of the total observation time, respectively) suggesting that this statistically significant change may not necessarily be biologically important.

Regarding social behaviors, during the second period, a significant decrease in interspecific behaviors, including interacting with or directing attention to humans was also reported. As visitors may be distressing for the study subjects, this finding seems to highlight that the gum feeder might help tamarins and marmosets to better cope with humans, promoting the performance of species-specific social behaviors and discouraging possibly deleterious human-animal interactions. Together with the decrease in the time spent out-of-sight in the presence of the feeder, this result highlights a possible positive effect of gum-feeding devices on callitrichines' well-being in zoo environments.

Except for the decrease in feeding/foraging and maintenance behavior reported in the gum-feeder period, no significant differences between periods were found in tamarins. The decrease in feeding/foraging behaviors within tamarins seems consistent with the same result obtained when data from both species were pooled together. Indeed, tamarins do not have as many adaptations for gum feeding and digestion as marmosets (Bairrão Ruivo, 2010; Heymann & Smith, 1999; Hosey et al., 2013; Roberts et al., 1999; T. D. Taylor, 2002); therefore, consuming the gum before other food items due to the new

presentation modality might have reduced the tamarin appetite and the performance of other food-related behavior, but had no effect on gummivore marmosets. However, the lack of significant differences in marmosets might be due to the small sample size and thus further research is needed to better investigate this aspect.

On the other hand, marmosets were out-of-sight ("not observed") significantly more during the baseline than the gum-feeder period, suggesting that for these species the presence of the drilled wooden discs might help to increase the visibility of these species to zoo visitors. Inactive behaviors, such as sleeping, were rather uncommon in the study subjects, as tamarins and marmosets tend to be very active during the day. However, the study subjects had rested in the wooden nest boxes in the highest part of the enclosure where the observer was not able to see them. Therefore, the behavioral category "not observed" also included resting, which was otherwise not recorded in the study periods. For this reason, it is possible, by decreasing the time spent out-of-sight, the presence of the gum feeder also reduced the inactive behavior of the study subjects, especially within marmosets. This is consistent with findings by other authors on common marmosets (*C. jacchus*; Roberts et al., 1999).

When analyzing the behavior of each study subject during the two periods, we found that in three red-handed tamarins, the gum feeder had a positive effect as reduced SRBs, such as self-directed behaviors and coprophagy. In addition, red-handed tamarins performed auto-coprophagy, which has been previously related to physical or psychological stress in nonhuman primates (Anderson, Combette, & Roeder, 1991; Krief et al., 2004; Prates & Bicca-Marques, 2005). One of the main effects of the gum feeder was the reduction of SRBs, including coprophagy. This was reported in other studies on gum feeders in the red-handed tamarin, suggesting that gum-related enrichment might be particularly relevant to prevent coprophagy in this species (T. D. Taylor, 2002), and on laboratory common marmosets, where similar gum-feeding devices decreased stereotypies (Roberts et al., 1999).

Based on data collected during the second period, this study aimed at verifying the presence of differences in gum feeding between tamarins and marmosets and investigate whether the time spent feeding on gum arabic differed between morning and afternoon within each group. First, although no statistically significant difference was found, marmosets tended to feed on gum more than tamarins. This finding agrees with previous work on these species, as gummivore marmosets spend a large amount of time feeding on gum, based on the importance of this food in their diet, whereas tamarins rely more on fruit and invertebrates and cannot easily obtain and digest plant exudate (Bairrão Ruivo, 2010; Heymann & Smith, 1999; Kelly, 1993). However, it could not be excluded that the greater interaction of the marmosets with the feeder was due to species differences in approaching the new enrichment devices, as previously suggested (Renner et al., 2000).

Similarly, no differences in time spent feeding on gum arabic were found between mornings and afternoons, neither within marmosets nor within tamarins. In the wild, marmosets feed on exudates frequently throughout the daylight hours, as their gastrointestinal system is well-adapted to gum digestion (Bairrão Ruivo, 2010; Heymann & Smith,

1999; Kelly, 1993). Therefore, the gum-feeding behavior of the study Geoffroy's and pygmy marmosets resembles that reported in the wild, as the study subjects ate gum arabic to the same extent in both the morning and the afternoon. In the case of tamarins, these species are known to eat exudates mainly during the afternoon, so that they can digest this food item overnight (Bairrão Ruivo, 2010; Heymann & Smith, 1999; Kelly, 1993). However, we collected data on the time spent eating gum but not the amount of gum that was eaten. Again, providing gum in the new gum feeders might have incentivized the consumption of this food item regardless of the time of the day.

Our findings seem to highlight positive effects of the gum feeder on the behavior of zoo callitrichines, as previously reported in the species considered in the current study as well as in other species of marmosets and tamarins (Huber & Lewis, 2011; McGraw et al., 1986; Roberts et al., 1999; T. D. Taylor, 2002). However, the small sample size and the relatively small amount of data collected in our study hamper the ability to draw firm conclusions and future research is needed to investigate more deeply the gum-feeding behavior of zoo callitrichines, focusing on larger samples and longer periods of time.

## 5 | CONCLUSION

In conclusion, our findings suggest that providing zoo tamarins and marmosets with gum arabic in a naturalistic and innovative way, such as using a wooden gum feeder, might enhance the welfare of these species by:

- 1) Promoting the performance of species-specific behaviors, such as visual exploration and decreasing self-directed behaviors that can in some cases indicate a stressful situation of the animal.
- 2) Improving the visibility to zoo visitors by decreasing the time spent out-of-sight and in interspecific interactions.
- 3) Reducing the performance of abnormal behaviors, as reported in the study of red-handed tamarins.
- 4) Increasing the consumption of this crucial food item, at least in the first stages of the introduction of the feeder.

Our results add to previous literature on gum-feeding devices in tamarins and marmosets, highlighting that the wooden gum feeders can improve the welfare of these species in controlled environments by stimulating natural behaviors and promoting naturalistic feeding strategies (Huber & Lewis, 2011; McGraw et al., 1986; Roberts et al., 1999; T. D. Taylor, 2002).

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## ORCID

Barbara Regaioli  <http://orcid.org/0000-0003-2844-1775>  
Giovanna Marliani <http://orcid.org/0000-0002-8609-8349>  
Pier Attilio Accorsi <http://orcid.org/0000-0001-8614-7131>  
Stefano Vaglio <http://orcid.org/0000-0003-0885-8573>  
Caterina Spiezio <http://orcid.org/0000-0003-1326-1835>

## REFERENCES

- Abbott, D. H., Barnett, D. K., Colman, R. J., Yamamoto, M. E., & Schultz-Darken, N. J. (2003). Aspects of common marmoset basic biology and life history important for biomedical research. *Comparative Medicine*, 53, 339–350.
- Altman, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–267.
- Anderson, J. R., Combette, C., & Roeder, J. J. (1991). Integration of a tame adult female capuchin monkey (*Cebus apella*) into a captive group. *Primate Report*, 31, 87–94.
- Bairrão Ruivo, E. (2010). EAZA husbandry guidelines for Callitrichidae (2nd edition.). Saint-Aignan, France: Beauval Zoo.
- Buckner, J. C., Lynch Alfaro, J., Rylands, A. B., & Alfaro, M. E. (2015). Biogeography of the marmosets and tamarins (Callitrichidae). *Molecular Phylogenetics and Evolution*, 82, 413–425.
- Burrows, A. M., & Nash, L. T. (2010). The evolution of exudativory in primates, *Developments in primatology: Progress and prospects*. New York, NY: Springer.
- Caine, N. G. (1984). Visual scanning by tamarins: A description of the behavior and tests of two derived hypotheses. *Folia Primatologica*, 43, 59–67.
- Coimbra-Filha, A. F., & Mittermeier, R. A. (1977). Tree-gouging, exudate-eating, and the short-tusked condition in Callitrix and Cebuella. In D. C. Kleiman (Ed.), *The biology and conservation of the Callitrichidae* (pp. 105–115). Washington DC: Smithsonian Institution Press.
- Emmons, L. H., & Feer, F. (1990). Neotropical rainforest mammals: A field guide. Chicago, IL and London, UK: The University of Chicago Press.
- Eng, C. M., Ward, S. R., Vinyard, C. J., & Taylor, A. J. (2009). The morphology of the masticatory apparatus facilitates muscle force production at wide jaw gapes in tree-gouging common marmosets (*Callitrix jacchus*). *Journal of Experimental Biology*, 212(24), 4040–4055.
- Fisch, G. S. (2001). Evaluating data from behavior analysis: Visual inspection or statistical models. *Behavioural Processes*, 54, 137–154.
- Fontani, S., Vaglio, S., Beghelli, V., Mattioli, M., Bacci, S., & Accorsi, P. A. (2014). Fecal concentrations of cortisol, testosterone, and progesterone in cotton-top tamarins housed in different zoological parks: Relationships among physiological data, environmental conditions and behavioral patterns. *Journal of Applied Animal Welfare Science*, 17, 228–252.
- Garber, P. A. (1993). Feeding ecology and behavior of the genus *Saguinus*. In A. B. Rylands (Ed.), *Marmosets and tamarins: Systematic, behavior, and ecology*. Oxford, UK: Oxford University Press.
- Gashua, I. B., Williams, P. A., Yadav, M. P., & Baldwin, T. C. (2015). Characterisation and molecular association of Nigerian and Sudanese Acacia gum exudates. *Food Hydrocolloids*, 51, 405–413.
- Goodrum, L. J., Patel, A., Leykam, J. F., & Kieliszewski, M. J. (2000). Gum arabic glycoprotein contains glycomodules of both extensin and arabinogalactan-glycoproteins. *Phytochemistry*, 54, 99–106.
- Groves, C. (2001). *Primate taxonomy*. Washington DC: Smithsonian Institution Press.

- Heymann, E. W., & Smith, A. C. (1999). When to feed on gums: Temporal patterns of gummivory in wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Callitrichinae). *Zoo Biology*, 18, 459–471.
- Hill, S. P., & Broom, D. M. (2009). Measuring zoo animal welfare: Theory and practice. *Zoo Biology*, 28, 531–544.
- Hosey, G., Melfi, V., & Pankhurst, S. (2013). *Zoo animals behavior, management and welfare*. Oxford, UK: Oxford University Press.
- Huber, H. F., & Lewis, K. P. (2011). An assessment of gum-based environmental enrichment for captive gummivorous primates. *Zoo Biology*, 30, 71–78.
- Kelly, K. (1993). Environmental enrichment for captive wildlife through the simulation of gum feeding. *Animal Welfare Information Center Newsletter*, 4(1-2), 5–10.
- Krief, S., Jamart, A., & Hladik, C. M. (2004). On the possible adaptive value of coprophagy in free-ranging chimpanzees. *Primates*, 45, 141–145.
- Leeds, A., & Lukas, K. E. (2018). Experimentally evaluating the function of self-directed behaviour in two adult mandrills (*Mandrillus sphinx*). *Animal Welfare*, 27(1), 81–86.
- Lutz, C. K. (2014). Stereotypic behavior in non-human primates as a model for the human condition. *ILAR Journal*, 55, 284–296.
- Lutz, C. K. (2018). A cross-species comparison of abnormal behavior in three species of singly-housed old world monkeys. *Applied Animal Behavior Science*, 199, 52–58.
- Maestriperieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behaviour*, 44(5), 967–979.
- Manteca, X., Amat, M., Salas, M., & Temple, D. (2016). Animal-based indicators to assess welfare in zoo animals. *CAB Reviews*, 11, 1–10.
- Marx, A., Backes, C., Meese, E., Lenhof, H. P., & Keller, A. (2016). EDISON-MMW: Exact dynamic programming solution of the Wilcoxon-Mann-Whitney Test. *Genomics, Proteomics & Bioinformatics*, 14(1), 55–61.
- McGraw, W. C., Brennan, J. A., & Russell, C. (1986). An artificial gum tree for captive marmosets. *Zoo Biology*, 5, 45–50.
- Mellor, D., & Beausoleil, N. (2015). Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare*, 24, 241–253.
- Mench, J. A. (1994). Environmental enrichment and exploration. *Laboratory Animal*, 38–41.
- Menzel, E. W., & Menzel, C. R. (1979). Cognitive, developmental and social aspects of responsiveness to novel objects in a family group of marmosets (*Saguinus fuscicollis*). *Behaviour*, 70, 251–279.
- Pack, K. S., Henry, O., & Sabatier, D. (1999). The insectivorous-frugivorous diet of the golden-handed tamarin (*Saguinus midas midas*) in French Guiana. *Folia Primologica*, 70, 1–7.
- Passamani, M., & Rylands, A. B. (2000). Feeding behavior of Geoffroy's marmosets (*Callithrix geoffroyi*) in Atlantic forest fragment of south-eastern Brazil. *Primates*, 41, 27–38.
- Power, M. L. (2010). Nutritional and digestive challenges to being a gum feeding Primates. In A. Burrows & L. Nash (Eds.), *The evolution of exudativory in Primates* (pp. 25–44). New York, NY: Springer.
- Power, M. L., & Oftedal, O. T. (1996). Differences among captive callitrichids in the digestive responses to dietary gum. *American Journal of Primatology*, 40, 131–144.
- Prates, H. M., & Bicca-Marques, J. C. (2005). Coprophagy in captive brown capuchin monkeys (*Cebus apella*). *Neotropical Primates*, 13, 18–21.
- Renner, M. J., Feiner, A. J., Orr, M. G., & Delaney, B. A. (2000). Environmental enrichment for new world primates: Introducing food-irrelevant objects and direct and secondary effects. *Journal of Applied Animal Welfare Science*, 3(1), 23–32.
- Roberts, R. L., Roytburd, L. A., & Newman, J. D. (1999). Puzzle feeders and gum-feeders as environmental enrichment for common marmosets. *Contemporary Topics in Laboratories Animal Science*, 38(5), 27–31.
- Rosenberger, A. L. (1992). Evolution of feeding niches in New World Monkeys. *American Journal of Physical Anthropology*, 88, 525–562.
- Rylands, A. B. (1984). Exudate-eating and tree-gouging by marmosets (Callitrichidae, Primates). In A. C. Chadwick & S. L. Sutton (Eds.), *Tropical rain forest: The Leeds symposium* (pp. 155–168). Leeds, UK: Leeds Philosophical and Literary Society.
- Siegel, S., & Castellan, N. J. (1992). *Statistica non parametrica*. Milano, Italy: McGraw-Hill.
- Smuts, B. B., Cheney, D. L., Seyfarth, R. M., & Wrangham, R. W. (1986). *Primate Societies*. Chicago, IL and London, UK: University of Chicago Press.
- Spiezio, C., Vaglio, S., Scala, C., & Regaioli, B. (2017). Does positive reinforcement training affect the behaviour and welfare of zoo animals? The case of the ring-tailed lemur (*Lemur catta*). *Applied Animal Behaviour Science*, 196, 91–99.
- Tardif, S. D. (1984). Social influences on sexual maturation of female *Saguinus oedipus oedipus*. *American Journal of Primatology*, 6(3), 199–209.
- Tardif, S. D., Araujo, A., Arruda, M. F., French, J. A., Sousa, M. B. C., & Yamamoto, M. E. (2008). Reproduction and aging in marmosets and tamarins. In S. Atsalis, S. W. Margulis & P. R. Hof (Eds.), *Primate reproductive aging. interdisciplinary topics in gerontology* (36, pp. 29–48). Basel, Switzerland: Karger Publisher.
- Tardif, S. D., Mansfield, K. G., Ratnam, R., Ross, C. N., & Ziegler, T. E. (2011). The marmoset as a model of aging and age-related diseases. *Institute for Laboratory Animal Research Journal*, 52, 54–65.
- Taylor, A. B., & Vinyard, C. (2004). Comparative analysis of masseter fiber architecture in tree-gouging (*Callithrix jacchus*) and non-gouging (*Saguinus oedipus*) callitrichids. *Journal of Morphology*, 261, 276–284.
- Taylor, T. D. (2002). Feeding enrichment for red-handed tamarins. *The Shape of Enrichment: A Quarterly Source of Ideas for Enrichment*, 11(2), 1–3.
- Thompson, C. L., Valença-Montenegro, M. M., César de Oliveira Melo, L., Maranhão Valle, Y. B., Borstelmann de Oliveira, M. A., Lucas, P. W., & Vinyard, C. J. (2014). Accessing Foods Can Exert Multiple Distinct, and Potentially Competing, Selective Pressures on Feeding in Common Marmoset Monkeys. *Journal of Zoology*, 294, 1–9.
- Troisi, A. (2002). Displacement activities as a behavioral measure of stress in non-human primates and human subjects. *Stress*, 5, 47–54.
- Troisi, A., & Schino, G. (1987). Environmental and social influences on autogrooming behaviour in a captive group of Java monkeys. *Behaviour*, 100, 292–302.
- Vinyard, C. J., Lucas, P. W., Valença-Montenegro, M. M., Melo, L. C. O., Valle, Y. M., & Monteiro da Cruz, M. A. O. (2004). Where the wild things are: Linking lab and field work in studying tree gouging in common marmosets (*Callithrix jacchus*). *American Journal of Physical Anthropology*, 38, 200–201.
- Vinyard, C. J., Wall, C. E., Williams, S. H., & Hylander, W. L. (2003). Comparative functional analysis of skull morphology in tree-gouging primates. *American Journal of Physical Anthropology*, 120, 153–170.
- Ziegler, T. E., Savage, A., Scheffler, G., & Snowdon, C. T. (1987). The endocrinology of puberty and reproductive functioning in female cotton-top tamarins (*Saguinus oedipus*) under varying social conditions. *Biology of Reproduction*, 37(3), 618–627.