Review

New sniffing at New World primates: recent advances in the study of platyrrhine olfactory communication

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This paper reviews the advances made in the study of olfactory communication in New World primates (Platyrrhini) made since the last major review in 2006, particularly the findings on scent-marking. Relatively few papers specifically addressed this topic, and some others include pertinent information collected during studies addressing other research questions. The majority of papers stems from research on callitrichids and night monkeys. Results of the latter studies refute my earlier hypothesis on a link between sex-biased scent marking and the relative importance of paternal care, but emphasize the need for using sexual selection as a theoretical framework for analyzing olfactory communication. The only two papers that examined scent marking in the context of territoryality and intergroup relations rejected a territorial function, but this remains a debated issue. I suggest to exploit the quasi-experimental condition created by habitat fragmentation to address this question. Portable Gas Chromatography-Mass Spectrometry (GC-MS) devices have been employed for the first time to examine the chemical composition of scent-gland secretions of wild New World primates. Expanding this technology to examine scent marks in situ and how their chemical profile and thus information content changes after deposition will be a promising approach for the future. Finally, I propose to integrate the theoretical framework developed by Carthey and co-workerson the role of microbes for the mediation of olfactory communication into studies of New World primate scent marking.

KEY WORDS: scent marking, sex differences, sexual selection, territoruality, chemical composition, habitat fragmentation, microbe-mediated communication, portable GC-MS.
INTRODUCTION

There is increasing recognition of the role of olfaction in primate ecology and behavior (e.g., Hoover 2010; Drea 2015; Laska & Hernandez Salazár 2015; Nevo & Heymann 2015). This goes along with an increasing number of studies examining the role of olfaction in finding and selecting food (e.g., Hiramatsu et al. 2009; Rushmore et al. 2012; Nevo et al. 2015; Cunningham et al. 2021) and the evolutionary implications of odors and the sense of smell for primate-plant interactions (e.g., Nevo et al. 2018; Nevo & Valenta 2018). Also, studies on the role of olfaction in primate behavior have extended to research questions that had received little or no consideration before, e.g. the detection of genetic relatedness (Charpentier et al. 2010), and the avoidance of parasitized group mates (Poirotte et al. 2017). Nevertheless, a “classical” topic – namely scent marking, i.e., the active communication via odors emerging from skin gland secretions, urine or other sources – that had already received attention in earlier periods of primate research (e.g., Bolwig 1960; Epple 1976) – remains on the agenda. First, because misconceptions still exist (like e.g., “among anthropoids, only callitrichids have been shown to actively scent mark” (Liebal et al. 2013, p. 74). Second, and more importantly, because we are still far from fully understanding the functions of scent marking behavior in platyrhines and other primates.

In a review of scent-marking strategies in New World primates, I examined three major functional hypotheses: territoriality, regulation of social and reproductive dominance, and mating competition/mate attraction (Heymann 2006). I concluded that existing evidence is consistent with a primary function of scent marking in intra-sexual competition and in mate choice, and made suggestions for future research. It is therefore timely to review the findings that emerged since then, in order to examine whether my previous conclusions can be upheld or rejected, but also to examine methodological progress and to provide new ideas and hypotheses.

METHODS

I searched in Web of Science with the terms “(scent mark* or scent-mark*)” and (Saguinus or Leontocebus or Leontopithecus or Callimico or Callithrix or Mico or Cebuella or Cebus or Sapajus or Saimiri or Aotus or Alouatta or Ateles or Lagothrix or Brachyteles or Callicebus or Cheraebebus or Plecturocebus or Pithecia or Chiropotes or Cacajao)” and constrained the search to papers published after 2006. Additionally, I screened the primatological literature (journals, books, theses) and extracted information on sex-specific rates of scent marking; spatial, temporal patterns and contexts of scent marking; chemical composition of scent marks and gland secretions; and other pertinent information.

RESULTS AND DISCUSSION

In the first part of this section, I summarize the findings of taxon-specific studies. In the second part, I synthesize this information in order to compare patterns and to examine their implications for the postulated functions of scent marking. The section ends with some ideas and hypotheses for future research.
Summaries of taxon-specific studies

Saguinus imperator (wild; Aragón Romero 2007). In a trio composed of two adult males and one adult female, anogenital marking was the most frequently observed type of scent marking (71.7%), followed by suprapubic (18.9%) and sternal marking (9.4%). The single female marked 4.3-times more often than the two males.

Saguinus oedipus and Saguinus imperator (captive; Poirier et al. 2021a). In a study on two groups of each species, adult females scent-marked significantly more often than adult males. In both species, anogenital marking was the most frequently employed type of scent marking followed by suprapubic marking and very low levels of sternal marking. The chemical composition of anogenital marks differed between species, sexes and reproductive/non-reproductive individuals. Several of the identified compounds must come from the diet, as animals do not possess the metabolic pathways for their production.

Saguinus imperator and Leontocebus weddelli (wild; Poirier et al. 2021b). In the first study that used a portable GC-MS device for analysing scent-gland secretions in wild tamarins (57 individuals from 13 groups), the authors found significant differences between species. The chemical composition was also significantly different between males and females, and between primary and secondary breeders. Samples from individuals of the same group were more similar to each other than those from different groups.

Leontocebus nigrifrons (wild; Lledo Ferrer 2010; Lledo Ferrer et al. 2010, 2011). In three groups (1–4 adult males, 1–2 adult females) scent-marking rates of females were significantly higher than those of males. All groups marked more at the periphery of their respective home ranges, and feeding trees in overlap areas that were also visited by neighboring groups received more scent marks than feeding trees in other parts. Scent-marking rates did not increase during intergroup encounters. The spatial pattern was interpreted as a strategy to optimize signal transmission between neighboring groups, perhaps as part of reproductive strategies. In one group (two adult males, one adult females) where a consort period occurred during the observations, all individuals scent marked less during the consort period. Scent-marking rates did not differ between the two males outside the consort period, but the consort marking male marked more often than the other. Both males overmarked the same proportion of female scent-marks (15.8 and 13%, respectively), but the proportion increased to 48% in the consort marking male and decreased to 5% in the other male. The consort marking male also showed significantly more allomarking of the female compared to the other male. These patterns were interpreted as “chemical mate guarding”.

Leontopithecus rosalia (wild; Franklin et al. 2007). This study examined an interesting question not explicitly addressed in studies of scent marking in other Neotropical primates, namely that the temporal pattern of scent marking should reduce the risk of attracting or cueing in predators. Specifically, the authors predicted that scent-marking rates should decrease in the 30-min period before retiring to a sleeping site. In contrast to the prediction, scent-marking rates increased which was due to increased rates of male scent marking. When specifically comparing scent-marking rates before retiring between the dry (breeding) and wet (non-breeding) season, increased rates were found for both sexes in the wet season. Increased scent-marking rates were interpreted as means of rapidly relocating
sleeping sites and maintaining group integrity, as an alternative strategy to reduce predation risk.

*Callithrix jacchus* (wild; Ribeiro 2007). In a study on juvenile behavioral development, scent marking rates of juvenile females (n = 5) were higher than those of juvenile males (n = 3). Scent marking took place almost exclusively in gum trees.

*Callithrix jacchus* (captive; Barbosa & Da Silva Mota 2009). In a study of five groups aimed at examining behavioral and hormonal responses to environmental conditions (non-quiet weekdays, quiet weekends), all age sex classes scent marked more on weekdays, and scent-marking rates of adult males and females did not seem to differ, but were higher than those of subadults and juveniles on weekdays (see fig. 2 in Barbosa & Da Silva Mota 2009).

*Callithrix jacchus* (captive; Massen et al. 2016). In an experimental study on behavioral contagion involving two groups with seven individuals each (breeding pair and adult offspring), scent-marking rates were higher in males than in females. The offspring tended to scent mark more than the breeding pair. Scent marking and gouging were clustered in time, and both seemed to be contagious between group members. The authors concluded that contagion enhances rapid spread of information within a group.

*Callithrix jacchus* (captive; Thompson et al. 2018). In an experimental study, two males were confronted with branches modified to mimic exudate sources with large or small amounts of exudate, and with branches that contained the same amount of exudate but one being labelled with marmoset urine. Over 24 hr, the males placed more scent marks on the branch with more exudate. The males did not feed differentially on labeled and unlabeled branches, but one male gouged more on the labeled branch. The authors concluded that marmosets use scent marking to communicate the quality of food resources.

*Callithrix penicillata* (wild; Decanini & Macedo 2008). In a group of 11 individuals (including five adult males and one subadult male) that was observed to study male behavioral profiles, scent-marking rates (only anogenital marking observed) did not differ between males, which also did not show a clear dominance hierarchy.

*Callithrix penicillata* (wild; Oliveira & Macedo 2010). In a group of 13 individuals (breeding pair and adult and subadult offspring; the same group as the one studied by Decanini & Macedo 2008), all 201 except two scent marking events involved anogenital marking. No sex difference in scent-marking rates was observed. The number of scent marks in core and peripheral parts of the home range was proportional to size of the respective area. However, the proportion of female marks in the periphery was significantly higher than expected. Of the 36 scent marks observed during intergroup encounters, none were by the reproductive pair, 64% of them were associated with non-aggressive interactions. The majority of scent marks was associated with gum feeding. The authors conclude that scent marking has no territorial function, but rather is involved in the search for mates and in resource labelling.

*Callithrix penicillata* (captive; Ågmo et al. 2012). In this study which aimed primarily at analyzing the development of pair bonding in newly formed pairs (n = 5 pairs, with males vasectomized), males and females did not differ in scent-marking rates.

*Callithrix penicillata* (captive; Sgai et al. 2015). In a study on reproductive endocrinology and socio-sexual behavior of four adult pairs, scent-marking rates were significantly higher during the periovulatory phase compared to the follicular and
luteal phases of the female ovarian cycle. The authors do not report whether this is true for both males and females.

*Aotus nancymaee* (captive; Wolovich & Evans 2007; Wolovich et al. 2010). In a study with 12 captive pairs, scent-marking rates did not differ between sexes. However, females of newly formed pairs marked significantly more often than females in established pairs, while no difference was observed in males. Rates of partner sniffing were significantly higher in males, and in females of newly formed pairs compared to females in established pairs, but not in males. Scent-marking rates did not differ between periods with and without mountings, but during the latter period more anogenital sniffing was recorded. In a subsequent study, 10 established pairs were confronted either with an unfamiliar male and an unfamiliar female in separate trials (five pairs), or only with an unfamiliar male (four pairs) or an unfamiliar female (one pair). Scent-marking rates did neither increase in males nor in females, and the sex of the unfamiliar animal also had no effect on scent marking.

*Aotus nancymaee* (captive; Macdonald et al. 2008). Chemical analyses of the subcaudal gland revealed 300 different compounds. Sex, age and family could be reliably classified; for sex classification a combination of only five compounds sufficed. The chemical composition of secretions from younger animals (adult offspring still residing in their family group) was less complex than that of their parents. Female secretions included higher concentrations of plant aromatic compounds, which raised the question whether this is based on different diets or differences in metabolism.

*Aotus azarae* and *Aotus nancymaee* (wild and captive; Spence-Aizenberg et al. 2018a, 2018b). Chemical analyses of samples from 33 wild *A. azarae* and 104 captive *A. nancymaee* revealed that secretions of the subcaudal and sternal gland are different from each other and differ between sexes and possibly between individuals. Individual differences were larger in males compared to females. In wild *A. azarae* secretions vary with age, but not in captive *A. nancymaee*. Closely related individuals (determined through pedigree) were chemically not more similar compared to unrelated individuals. The subcaudal gland tends to be larger in males (P = 0.07), but females scored significantly higher (P = 0.007) on the amount of staining of the perianal region. Scent-marking rates of males and females were similar for all types of scent marking, but males sniffed significantly more at female scent marks than vice versa.

*Alouatta guariba clamitans* (wild; Braga Hirano et al. 2008). In three groups, each with one adult male and one to three adult females, different types of rubbing behavior were recorded that were assumed to serve a function in scent marking (hyoid, sternum, anogenital, dorsum, abdomen, mandible). Adult males rubbed significantly more than other age-sex classes. Hyoid and sternal rubbing were significantly associated with intergroup encounters, leading the authors to tentatively suggest a territorial and agonistic function. However, the overall number of hyoid and sternal rubbings was very low (17 out of totally 123 rubbing events, of which seven preceded and six followed an intergroup encounter).

*Lagothrix lagotricha poeppigii* (wild; Camargo Peña 2020). This study involved four groups with two to five adult and subadult males and four to 10 adult and subadult females. Adult males marked more than any other age-sex class and performed significantly more sternal than anogenital marking, while females showed more anogenital than sternal marking. Scent-marking rates were not elevated during intergroup encounters, and scent marking occurred more frequently in core areas.
Also, scent marking occurred more often during the mating period, and particularly on days with copulations.

*Callicebus coimbrai* (wild; Souza-Alves et al. 2021). In two family groups (4–5 and 6–7 individuals) the authors observed 14 events in which titi monkeys “pressed the right hand against the gular and sternal body regions and then wiped the palm repeatedly on the nearby branch” (p. 1); most events (11) were observed in adult males. The authors suggest a function in intra- and intergroup communication.

*Plecturocebus (=* Callicebus) *cupreus* (captive; Ragen et al. 2012). In experiments aimed at determining the effect of social state (paired, natal, lone) on responses to external rewards, the authors found significant differences in rates of sternal marking (natal > paired > lone) and of anogenital marking (paired > natal and lone). Scent marking is interpreted as expressing arousal.

*Plecturocebus toppini (= Callicebus brunnneus)* (wild; Wright 2013). This paper provides qualitative information, namely that scent marking was not observed at the territorial boundary. Nevertheless, the author concludes that “scent-marking may function as a less-expensive form of mate, resource and territory defense” (p. 236).

*Pithecia aequatorialis* (wild; Di Fiore et al. 2007). In a case report on a male immigrating into a group after the death of the resident male, it was observed that the incoming male scent marked more than the resident male had marked, and that scent-marking rates increased in the female following the integration of the new male.

**Synthesis**

**Relative frequencies of different types of scent marking.** Most New World monkeys, particularly the callitrichids, employ two or more different scent glands for marking (Epple 1986; Epple et al. 1986). The studies by Aragón Romero (2007) and Poirier et al. (2021a) confirm the pattern reported earlier by Heymann (2001) for additional members of the genus *Saguinus*, namely that anogenital marking is more frequent than suprapubic marking and sternal marking the least frequent. Heymann (2001) also noted that in *Leontocebus nigrifrons* (previously *Saguinus fusccollis nigrifrons*) anogenital marking – while still ranking first – is less frequently and suprapubic marking – while still ranking second – more frequently employed than in *Saguinus mystax*. It will be interesting to see whether differences hold up in other pairs of sympatric tamarins (e.g., *S. imperator* and *L. weddelli*; *Saguinus labiatus* and *L. weddelli*), but also for *Saguinus* and *Leontocebus*, respectively, in general, be they sympatric or not. If they do, relating them to detailed information on social organization (which is superficially similar between *Saguinus* and *Leontocebus*; Heymann 2000a) and social structure will bring us closer to an understanding of how differences, be they even only fine-grained, in the social system relate to different communication strategies. This would necessarily have to be integrated with the chemical profiles of the different scent-gland secretions and bioassays to determine whether they elicit differential responses.

Few other studies report relative frequencies of different types of scent marking. In *C. penicillata*, most or all marking was anogenital, but since the same group was studied by Decanini and Macedo (2008) and Oliveira and Macedo (2010), a group-specific idiosyncracy cannot be ruled out; suprapubic and sternal marking is known from members fo the genus *Callithrix* (Stevenson & Poole 1976; Stevenson & Rylands 1988). In *A. nanymuae*, subcaudal marking is 14 times more frequent than sternal marking (Spence-Aizenberg et al. 2018b). Males of *L. l. popepigii* used relatively more
sternal, females relatively more anogenital marking (Camargo Peña 2020), a difference additional to the male-biased overall scent-marking rates (see below).

**Sex differences in rates scent marking.** Heymann (2003a, 2003b) had postulated that New World monkey scent marking is a sexually selected behavior and that sex biases in scent-marking rates are related to the relative contribution of males and females to infant care. He found that female-biased or unbiased scent-marking rates are found in New World monkey species with extensive paternal care and suggested that this reflects higher levels of female-female competition and male choice of females in such species. *Callicebus* did not fit this pattern, but data on scent marking in this genus were (and still are) very sparse. Spence-Aizenberg et al. (2018b) used the framework of sexual selection theory to examine the size and intensity of staining of the subcaudal gland (most frequently employed) and scent-marking rates in *A. nancymaea*. Following Heymann's (2003b) reasoning, one would have expected highly female-biased scent-marking rates, given the almost exclusive involvement of males in infant carrying in night monkeys (Huck & Fernandez-Duque 2012). Similar scent-marking rates of male and female *A. nancymaea* found by Spence-Aizenberg et al. (2018b) and Wolovich and Evans (2007) are inconsistent with Heymann’s hypothesis, and factors other than infant care need to be considered. I suggest that one such factor could be “floaters”, i.e., “individuals who range over a wide area rather than a fixed territory after having dispersed from their natal groups” (Fernandez-Duque et al. 2013, p. 1), which may represent a stronger challenge to existing pairs and create higher levels of intrasexual competition than previously conceived (Fernandez-Duque et al. 2013). In any case, Spence-Aizenberg et al. (2018b) emphasize the importance of using sexual selection as a theoretical framework for examining olfactory communication in general and scent marking in particular. The report by Di Fiore et al. (2007), albeit anecdotal, underlines this. Higher scent-marking rates of an immigrant male *P. aequatorialis* (compared to the previous resident male) and increased scent-marking rates in the female after the immigration, although both not reaching statistical significance, are consistent with the role of scent marking in mate selection and thus potentially subjected to sexual selection. Similarly, the differences between paired, natal and lone males reported in a study *C. cupreus* (Ragen et al. 2012) can be considered in relation to male competition, although it would be crucial to verify whether the pattern holds true in wild titi monkeys.

Findings on sex-differences in callitrichids – except for the male-biased scent-marking rates reported by Massen et al. (2016) – are in line with the direction and degree of the bias in other callitrichids (Heymann 2003a; see Table 1). Male-biased scent-marking rates in *A. guariba* and *L. lagotricha* (Table 1) are consistent with the supposedly higher levels of male competition in these polygynous or promiscuous primates.

**Spatial patterns of scent marking and relationship with intergroup encounters.** Few studies published since my last review (Heymann 2006) addressed the question of spatial patterns of scent marking, particularly the issue of whether scent marking has a territorial function. Camargo Peña (2020) refutes a territorial function in *L. l. poeppigii*. Similarly, Lledo Ferrer et al. (2011) conclude that scent marking in *L. nigrifrons* does not fulfill a territorial function (coinciding with Heymann 2000b), but rather functions in the exchange of information about reproductive opportunities. This has created a debate (Lledo Ferrer et al. 2012; Roberts 2012), centered around the
question of how to interpret the spatial distribution and context of scent marking when they seem to fit with predictions both from the territorial hypothesis and the mate attraction/mating competition hypothesis. Clearly, the issue can only be settled with data from more different populations and species, and long-term studies that examine the fitness consequences of scent-marking strategies.

**Chemical composition.** Several studies examined the chemical profile of scent-gland secretions. These studies revealed complex mixtures, but also that few individual compounds may be sufficient to distinguish the chemical profiles of male and female secretions. Also, variably between species or populations, chemical profiles can or cannot differentiate between sexes, age-classes or groups. Most interestingly a possible relationship of chemical profiles to diet and/or metabolism has been postulated in studies on night monkeys (Macdonald et al. 2008; Spence-Aizenberg et al. 2018a). If confirmed, this is particularly relevant in light of the suggestion made earlier (Heymann 2003a) that scent marks could include information on individual quality related to foraging success. At this point I want to hint to an error in Heymann (2003a), resulting from a misinterpretation of findings by Belcher et al. (1986). Tamarin scent marks do not include high amounts of unsaturated fatty acids, but other unsaturated compounds, e.g. dienes and squalene. Nevertheless, the presence of proteins in scent marks still is sufficient to maintain the general reasoning about a link between the presence of certain compounds in scent-marks and individual quality. There are still too few studies to identify specific patterns, but if such analyses are expanded to more species and different populations of the same species and to analyzing not only scent-gland secretions, but also scent marks in situ.

### Table 1.

Comparison of male and female rates of scent marking.

| Species                  | Setting (C, captive; W, wild) | Relative scent marking rates (M, males; F, females) | Reference                  |
|--------------------------|-------------------------------|----------------------------------------------------|----------------------------|
| *Saguinus imperator*     | W                             | M < F                                              | Aragón Romero 2007         |
| *Leontocebus nigrifrons* | W                             | M < F                                              | Lledo Ferrer 2010          |
| *Callithrix jacchus*     | C                             | M > F                                              | Massen et al. 2016         |
| *Callithrix jacchus*     | W                             | M < F                                              | Ribeiro 2007               |
| *Callithrix penicillata* | C                             | M = F                                              | Ågmo et al. 2012           |
| *Callithrix penicillata* | W                             | M = F                                              | Oliveira & Macedo 2010     |
| *Aotus nancymae*         | C                             | M = F                                              | Spence-Aizenberg et al. 2018b |
| *Aotus nancymae*         | C                             | M = F                                              | Wolovich & Evans 2007      |
| *Alouatta guariba*       | W                             | M > F                                              | Braga Hirano et al. 2008   |
| *Lagothrix lagotricha*   | W                             | M > F                                              | Camargo Peña 2020          |
in the wild (see below), this will greatly expand our understanding of New World monkey olfactory communication.

**Methodological progress.** Two studies used portable GC-MS devices to analyze the chemical profiles of scent-gland secretions and scent glands in situ, respectively (Thompson et al. 2020; Poirier et al. 2021b). These studies will serve as a model for future studies of scent marking (and other aspects of olfactory communication) in wild New World monkeys.

**Perspectives for future research**

**Temporal changes of information content of scent marks.** Tamarin scent marks have been shown to degrade under controlled captive conditions: they remain attractive (and informative) for 1–3 days after experimental deposition, and sex discrimination is possible with 1–2 days old marks (Eppe et al. 1980). Given that natural surfaces (Eppe et al. used clean aluminium plates washed with ethanol) harbor microbiota (bacteria, fungi) that can metabolize compounds included in and thus degrade scent marks, it is quite likely that the information content of scent marks in the wild deteriorates much faster. This would make a territorial function of scent marking even less likely. Portable GS-MC devices could be used to monitor the temporal change in the composition of scent marks.

**The effect of floaters.** Reproductive competition may not only exist within groups or between neighboring groups, but also with “floaters”. Floaters can be single individuals, as e.g. in night monkeys (Huck & Fernandez-Duque 2017), but also duos and trios as in tamarins (Soini & de Soini 1990; Garber et al. 1993). In tamarins, floaters seem to behave rather inconspicuously, i.e., they are not very vocal, at least they do not utter calls (e.g., loud calls) that are audible over a wider distance and thus could call the attention of residents (personal observations). Would they also be olfactorily "silent", i.e., not scent mark? If scent marking functions in territoriality, they should not mark at all. However, if scent marking functions in the attraction of mates, they should scent mark, preferably at sites where their marks have a high probability of being detected, i.e., in and around food resources. This could result in familiarization of residents to the presence of potential (for non-breeding group members) or alternative (for breeding group members) mates without direct encounters (but note that this would depend on how fast scent marks degrade; see above). Admittedly, observing the behavior of rather inconspicuous floaters is a rather challenging task.

**Exploiting habitat fragmentation.** An increasing number of primates are facing fragmentation of their habitats (Marsh & Chapman 2013; Galán-Acedo et al. 2019). This provides quasi-experimental situations not only for the study of their ecological responses (Chaves et al. 2012; Bejar et al. 2020), but also of the effects of fragmentation on demography, physiology and behavior (Irwin et al. 2010; Rimbach et al. 2014; Klass et al. 2020). With regard to scent marking, fragmentation would allow to examine the disputed territorial function of scent marking by comparing scent-marking rates in fragments of variable size with a variable number of neighboring groups. If scent marking primarily fulfilled a territorial function, groups in fragments without or with very few neighbors should have much lower scent-marking rates than
groups in large fragments or in continuous forest with many neighbors. If the function is primarily in intragroup/intersexual communication, scent-marking rates should not vary, at least not for reproductive adults. Obviously, larger groups sizes and different group compositions in fragments compared to continuous forest, as a consequence of constraints on natal dispersal, need to be controlled for in such studies.

Microbially mediated olfactory communication. Carthey et al. (2018) devised an eco-evolutionary model of the role of microbes in mediating olfactory communication. Amongst others, they predict that microbial products can be used in signaling identity, but not in the assessment of individual quality and fitness; and that the ability to control the microbiome could represent an honest signal of individual quality and fitness, with a larger fraction of host-product compounds than microbial compound indicating higher fitness. The last years have seen an explosion of studies on microbiomes of primates and other animals (e.g., Clayton et al. 2018; Björk et al. 2019; Moeller & Sanders 2020). Integrating studies of scent marking behavior and the chemical composition of gland secretions and scent marks in situ with information on microbiomes in the framework provided by Carthey et al. (2018) is likely to provide highly exciting insights into New World primate olfactory communication.

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