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Research article

Olfactory communication in tamarins: A comparative analysis of scents from wild and captive populations

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Abstract

Animals deposit odorant signals during social interactions, and to mark territories and resources. Odorants may be direct by-products of essential biochemical pathways, derived from diet and the environment, and/or produced by commensal bacteria. Accordingly, animals in captivity, which are provisioned with artificial diets and environments, may produce a different range of odorants than their wild counterparts. Few studies have compared chemosignalling in wild and captive conspecifics. This study begins to address this gap by investigating the effect of captivity on chemosignalling in the bearded emperor tamarin, *Saguinus imperator subgrisescens.* Scent samples collected from eight wild tamarins and investigated by headspace solid-phase microextraction coupled with gas chromatography-mass spectrometry contained a greater number of identified odorants than those collected from five captive tamarins and analysed under the same conditions. Wild and captive scent samples also showed a marked overall difference in chemical composition, although some of this variation may be due to demographic differences between the study populations, the limited sample size and different storage conditions. These results suggest that captivity might alter primate chemosignalling, with potential implications for primate captive husbandry practices and conservation breeding programmes.

Introduction

Mammals use semiochemicals—the chemicals used in olfactory communication—during territorial and resource marking, as well as during more direct social interactions (reviewed by Wyatt 2014). Semiochemicals can be by-products of essential biochemical pathways (Charpentier et al. 2012), derived from the diet and the environment (Havlíček et al. 2019) or produced and/or modified by commensal bacteria (Ezenwa and Williams 2014). For instance, diet has been shown to affect the chemical composition of genital secretions of various strepsirrhine primate species (Lemuridae; Drea et al. 2013), femoral gland secretions of lacertid lizards (Lacertidae; Kopena et al. 2011) and urinary proteins produced by mice *Mus musculus* (Kwak et al. 2008; Schaefer et al. 2010). Although attempts are made to provide captive animals with naturalistic diets, the extent to which this is possible varies and captive diets may contribute to the production of a different range of semiochemicals than are produced by wild animals. Moreover, in captive environments variation in husbandry procedures and cleaning protocols may influence the commensal microbial communities of the animals, resulting in distinct odour production (Clayton et al. 2016).

To date, few studies have directly compared the semiochemicals produced by wild and captive conspecifics, and results previously reported are inconsistent. In a recent study

on chemosignalling in giant pandas *Ailuropoda melanoleuca,* Zhou et al. (2019) reported a more diverse composition of anogenital scent gland samples from wild pandas than from their captive counterparts. On the contrary, Spence-Aizenberg et al. (2018) reported a more diverse chemical composition of glandular secretions from captive owl monkey *Aotus* spp. than wild congeners and Rudie (2015) found that female red-sided garter snakes *Thamnophis sirtalis parietalis* showed an increased diversity of skin lipids when kept in captivity. Spence-Aizenberg et al. (2018) attribute their findings to the lower quality of the wild owl monkey scent samples compared to the captive samples, while Rudie (2015) argues that captive snakes had access to a greater quantity of food than in the wild and as a consequence were able to invest more energy into the production of chemosignals than their wild counterparts. Yet a review by Rasmussen and Krishnamurthy (2000) investigating the chemical composition of urine and temporal scent gland secretions of Asian elephants *Elephas maximus* reported a high similarity in the chemicals retrieved, as well as their relative concentration throughout the reproductive cycle, between captive and wild animals.

This study examined the chemical profiles of wild and captive bearded emperor tamarins *Saguinus imperator subgrisescens* (Hershkovitz 1979), a small callitrichid primate distributed across Peru, Brazil and Bolivia (Rylands et al. 2016). Callitrichids are excellent models for the study of primate olfactory communication, since they have a well-developed olfactory system and rely heavily on odour signals in their ecology and socio-reproductive behaviour (Epple et al. 1993; Smith et al. 2011; Snowdon and Ziegler 2021). Tamarin odour secretions are produced by three specialised scent glands on the anogenital, suprapubic and sternal regions of the body (Epple et al. 1993; Fontani et al. 2014; Perkins 1966) and then conspicuously deposited on branches and lianas in the environment (i.e. via scent-marking; Epple 1974; Epple et al. 1993; reviewed in Wyatt 2014). Sniffing, licking and overmarking of the marked substrates by conspecifics are commonly observed behaviours (Snowdon and Ziegler 2021). Numerous potential functions have been attributed to callitrichid scent-marking behaviour; these include signalling identity, reproductive and dominance status, territorial defence, spatial orientation and food resource location (Heymann 2006a).

This study aimed to 1) describe the chemical composition of emperor tamarin scent gland and body odour and 2) compare odours produced by wild and captive animals. The volatile chemical profiles of wild and captive tamarin scent samples were investigated in terms of both the richness of compounds and their relative abundance in the samples. It was predicted that wild tamarins, which have access to a greater variety of food items and interact with a greater diversity of organisms, would produce i) different and ii) more diverse chemosignals than their captive counterparts. Potential implications of the findings for captive welfare and breeding of callitrichids are discussed, and future directions for research in primate chemosignalling are considered.

Methods

Sample collection

A wild population of bearded emperor tamarins *Saguinus i. subgrisescens* (Figure 1a) was studied in June 2018 at Estación Biológica Los Amigos (EBLA) in south-eastern Peru (12°34'S, 70°05'W) during an annual capture-and-release programme led by Field Projects International (www.fieldprojects.org; Watsa et al. 2015). MW and GAE collected 27 swab samples from the anogenital, suprapubic and sternal scent glands and a body region on the skin of the inner arm, of five females (four adults and one subadult) and three adult males of unknown relatedness, belonging to two groups of emperor tamarins (Figure 1b; Table S1).

The sampling procedure consisted of gently wiping a 1 cm^2 viscose swab held by forceps over the scent gland or body area ten times in an up-and-down movement. A single scent gland or body

Figure 1. a) Adult male bearded emperor tamarin *Saguinus imperator subgrisescens* (photo credit M. Guerra Vargas); b) Location of the three scent glands (anogenital: green circle; suprapubic: blue triangle; sternal: yellow square) and body regions (inner arm or flank: orange diamond) sampled in this study.

area was sampled with each swab, allowing for comparisons across swabbing locations. In addition, two air controls (i.e. swabs left out for 30 sec to control for background volatiles) and two blank controls (i.e. empty vial and unused swab) were collected. Prior to use, swabs were washed in HPLC-grade methanol and pentane (ACROS OrganicsTM, London, UK), then baked at 130°C for 30 min, as recommended by Birkemeyer et al. (2016) and transported to the field site in air-tight containers to avoid contamination. Upon collection, swabs were stored in brand new 4 mL glass screw-top vials fitted with a polytetrafluoroethylene/rubber septum (Supelco, Bellefonte, PA, USA). Vials were kept for a maximum of seven hours in a cool Thermos® flask filled with gel packs pre-chilled in a freezer at approximately 0°C, before being transferred to a freezer at the field station (mean±SD temperature: -1.4±4.3°C, recorded hourly by an automatised temperature data logger). At the end of the capture-and-release programme (after 25 days), samples were shipped to Anglia Ruskin University (ARU) in the UK, where they were stored at -80°C until analysis. Temperature varied between below zero and room temperature during transportation, since owing to unforeseen logistical difficulties sample shipment between Peru and the UK was executed in several steps, during some of which the samples were left to thaw.

A captive population of emperor tamarins housed together at Twycross Zoo in the UK were also studied (Table S1). The study group was composed of five related individuals, one adult female and two pairs of twins (a male and a female adult and a male and a female juvenile). The animals were fed twice daily a mix of vegetables, once daily invertebrates, and more rarely fruits. Eight scent swabs of the suprapubic scent gland and a body region on the flank were collected by veterinarians during routine health checks in September 2017, following the same sampling procedure as used in wild conditions (Figure 1b). Animals were removed from their enclosure one at a time and underwent anaesthesia. Sampling also included the collection of two air controls, to account for background odours emanating from the environment and from the personnel involved in sample collection, which differed between the captive and wild studies. Upon collection, sample vials were kept in an insulated cool box filled with frozen gel packs at a temperature close to 0°C, then stored in a freezer onsite (-20°C) within two hours (usually 30 min). Samples were then transported in the cool box to ARU, where they were stored at -80°C until analysis.

Chemical analyses and interpretations

Scent samples were analysed by solid-phase microextraction coupled with gas chromatography-mass spectrometry (SPME–GC-MS) on a Clarus 500 GC-MS (PerkinElmer), following the methods established in Poirier et al. (2021a). For each GC-MS chromatogram, automatic peak detection, deconvolution and integration were performed using the Automated Mass Spectral Deconvolution and Identification System (AMDIS 2.73; Stein 1999). The deconvolution parameters used were medium resolution, sensitivity and peak shape requirements. Only peaks with a minimum area of 0.1% of the chromatogram's total signal (after removing compounds whose identity was clearly inorganic e.g. silane derivatives) were selected. This step limited the inclusion of background noise, as peaks under this threshold were generally too flat to be distinguished either from the baseline or from a neighbouring peak. In addition, all peaks found in at least one of the blank controls were removed from further analysis, and peaks present in air controls in higher abundances (i.e. higher mean peak area) than in the scent gland and body samples were discarded. Relative abundance of all selected peaks, i.e. peak area divided by the sum of all included peak areas multiplied by 100, was calculated for each sample to account for variation in absolute abundance that might be due to the amount of sample swabbed.

Compounds were tentatively identified using the National Institute of Standards and Technology mass spectral library (NIST14; Shen et al. 2014) on the basis of their mass spectra and retention indices, which were calculated based on an n-alkane reference mixture analysed under identical conditions. Careful visual inspection of peaks' mass spectra distinguished between peaks with similar retention times. The identities of nine compounds were further confirmed by comparison of their retention times with those of commercially obtained compounds analysed under identical conditions as part of a different study (Poirier et al. 2021b).

Statistical analyses

All statistical analyses were conducted in R v.4.1.0 (R Core Team 2021) operated in RStudio (RStudio Team 2021). Differences in the chemical composition of wild and captive tamarin scent samples were investigated both in terms of the number of compounds detected and their relative abundance in the samples, only including body samples (wild n=8; captive n=3) and suprapubic scent gland samples (wild n=7; captive n=5), which were collected in both conditions. Differences in the number of compounds detected in the samples were tested using non-parametric Wilcoxon rank sum tests (wilcox.test function in R package stats; α=0.05). Similarity between chemical profiles of samples was assessed based on pairwise Bray-Curtis dissimilarity indices, calculated from the log(arcsin(x+1))-transformed relative peak abundances using the vegdist function in R package vegan v.2.5-7 (Oksanen et al. 2020). A graphical visualisation of sample chemical dissimilarity using two-dimensional non-metric multidimensional scaling (NMDS) was produced using the metaMDS function in vegan. Analyses of similarity (ANOSIM, anosim function in vegan with 999 permutations on Bray-Curtis distances) were then performed to test whether the chemical composition of groups of samples was more similar than that of samples from different groups. There was no significant difference in the number of compounds detected in samples collected from the two wild groups of tamarins studied (Wilcoxon rank sum test: W=22, P=0.59), so these samples were combined into a single 'wild' category. Moreover, there was no significant difference in the number of compounds detected between suprapubic scent gland and body swabs collected in wild conditions (W=27, P=0.95) nor in captive conditions (W=8, P=1). Similarly, the difference in chemical composition between suprapubic scent gland and body samples was non-significant (ANOSIM with argument 'strata' to test within condition: R=-0.03, P=0.62). Therefore scent gland and body samples were combined for subsequent comparisons of the 11 individuals for which both sample types were collected, in order to increase sample sizes for the variable of interest (i.e. captivity versus wild condition). Combining samples provided sufficient sample size to allow statistical analysis but did lead to pseudoreplication in the dataset; this limitation is acknowledged in interpretation of the results.

The difference in log(arcsin(x+1))-transformed relative peak abundance was examined between wild and captive samples for each identified compound found in common between the two study conditions, using independent Wilcoxon rank sum tests.

Ethics approval

The wild tamarin capture-and-release programme led by Field Projects International is conducted with annual authorisation from the Peruvian Ministry of the Environment (SERFOR), as well as the Animal Care and Use Committees of the University of Calgary (ACC protocol # AC19-0167) and Washington University in St. Louis (IACUC protocol # 21-0084). This study was approved by the Faculty of Science and Engineering Departmental Research Ethics Panel (DREP) at Anglia Ruskin University (ARU) and received support

from the British and Irish Association of Zoos and Aquariums. It adheres to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates, and follows the Animal Behavior Society Guidelines and the American Society of Mammalogists' Guidelines on wild mammals in research.

Data availability

The supplementary material supporting this article can be found at https://github.com/AlicePoirier/Poirier-et-al_JZAR_Oct2021.git

Results

Chemical composition of tamarin scent gland and body odour

A total of 69 animal-sourced compounds were detected in the scent gland and body swabs of emperor tamarins. These compounds were absent from blank controls and present either only in the tamarin samples or in higher abundance (i.e. higher mean peak area) in the tamarin samples than in the air controls. It was possible to tentatively identify 63 of these compounds, including alcohols, carboxylic acids, ketones, aldehydes and esters. The identities of nine compounds were confirmed by comparison of their retention times with those of commercially obtained compounds (Table 1). Most compounds (74%) were retrieved from at least two sample types (Table S2), but some were only retrieved from a single location: body swabs (2,5-dipropyltetrahydrofuran [#41] and 3-methoxy-5-pentylphenol [#66]); suprapubic scent gland (p-cresol [#27], methyl 3-oxo-4-methylhexanoate or methyl 3-oxoheptanoate [#36] and tetrahydro-6-propyl-2H-pyran-2-one [#50]); anogenital gland (heptan-2-one [#09], branched C9 alcohol [#12], ethyl 2-hydroxy-3-methylbutanoate [#14], phenylacetaldehyde [#23], 2-phenylethanol [#38], ethyl tetradecanoate [#67] and ethyl pentadecanoate [#68]); and sternal gland (e.g. ethyl non-3-enoate [#48], branched C10 carboxylic acid [#54], ethyl dec-3-enoate [#56] and octyl 2-methylpent-4-enoate [#61]).

Comparison of odours produced by wild and captive tamarins

Fifty-two of the detected compounds were only found in wild samples (75%) and eight only in captive samples (12%; Table 1). Nine compounds (13%) were common to the two datasets: 4-hydroxy-4-methylpentan-2-one [#07], 2-butoxyethanol [#11], benzaldehyde [#13], phenol [#17], 2-ethylhexan-1-ol [#21], nonanal [#34], 4-methoxybenzaldehyde [#47], 'unknown compound 2' [#49] and butyl octanoate [#53] (Table 1).

When considering only body and suprapubic gland samples, which were collected in both wild (n=15) and captive (n=8) conditions, the number of compounds per sample detected from wild emperor tamarin samples (mean±SD=15.8±5.7, ranging 9–27 per sample) was significantly greater than that found in captive emperor tamarin samples (7.3±2.7 compounds, ranging 4–11 per sample; Wilcoxon rank sum test: W=6, P<0.01; Figure 2a). Wild samples consistently showed a greater number of compounds than captive samples, except for two wild suprapubic gland samples with a lower compound richness (n=9 compounds) than some of the captive samples. In addition, sample chemical composition differed significantly between captive and wild emperor tamarins (ANOSIM: R=0.94, P<0.01); the two study conditions appear well separated on the NMDS plot (Figure 2b).

Among the eight compounds found in common between the two study conditions (4-methoxybenzaldehyde was absent from

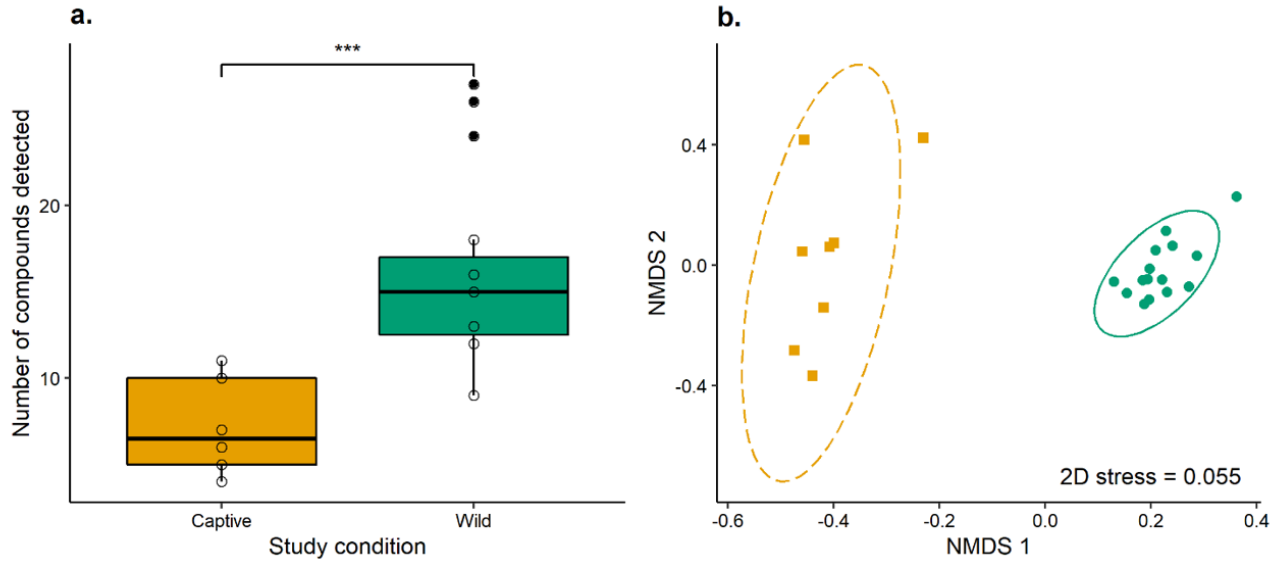

Figure 2. Difference in a) the number of compounds detected and b) sample chemical composition between captive (orange squares) and wild (green circles) emperor tamarin body and suprapubic scent gland samples. Non-metric multidimensional scaling (NMDS) was based on Bray-Curtis dissimilarities calculated using standardised relative abundance of the 69 peaks retrieved from the samples (stress=0.055). Points in close proximity indicate a higher chemical similarity of samples. Ellipses represent the 95% confidence interval for categories of samples.

Table 1. Volatile compounds detected in scent gland and body swabs of captive and wild emperor tamarins. SD=standard deviation. *Identity confirmed by comparison of retention times with those of commercially obtained compounds. RT = Retention Time (in min).

#	Mean RT±SD	Candidate compound identity	No. of captive samples containing compound (n=8)	No. of wild samples containing compound (n=27)
01	3.02±0.01	Butan-1-ol*	0	25
02	3.15±0.01	1-Methoxypropan-2-ol	5	0
03	4.44±0.04	3-Methylbutan-1-ol	0	4
04	5.08±0.56	Propane-1,2-diol	3	0
05	6.20±0.12	2-Methylpropanoic acid	0	15
06	6.22±0.01	Ethyl butanoate	0	2
07	7.59±0.12	4-Hydroxy-4-methylpentan-2-one	6	24
08	8.00±0.11	3-Methylbutanoic acid*	0	15
09	9.00±0.01	Heptan-2-one	0	1
10	9.19±0.01	Butyl prop-2-enoate	0	17
11	9.69±0.35	2-Butoxyethanol	3	24
12	10.80±0.00	Branched C9 alcohol	0	1
13	11.14±0.01	Benzaldehyde*	3	9
14	11.36±0.00	Ethyl 2-hydroxy-3-methylbutanoate	0	1
15	11.76±0.00	1-Octen-3-ol*	0	4
16	11.94±0.01	Branched C10 alkane	0	26
17	12.03±0.01	Phenol	4	2
18	12.11±0.05	Branched C6 carboxylic acid	0	16
19	12.38±0.00	Octanal	0	2
20	13.03±0.01	Branched C11 alkane 1	0	14
21	13.21±0.02	2-Ethylhexan-1-ol	4	25
22	13.43±0.01	3,3,5-Trimethylcyclohexanone	0	27
23	13.57±0.00	Phenylacetaldehyde*	0	1
24	14.23±0.00	Acetophenone*	0	17
25	14.39±0.01	2,6-Dimethyl-7-octen-2-ol	4	0
26	14.48±0.01	Branched C11 alkane 2	0	5
27	14.61±0.03	p-Cresol*	2	0
28	14.72±0.01	Branched C11 alkane 3	0	7
29	14.79±0.00	Branched C11 alkane 4	0	4
30	14.87±0.00	Branched C11 alkane 5	0	8
31	14.92±0.01	Branched C11 alkane 6	0	5
32	15.01±0.01	Branched C11 alkane 7	0	16
33	15.10±0.00	Branched C11 alkane 8	0	5
34	15.21±0.01	Nonanal	5	9
35	15.21± 0.00	Unknown compound 1	0	1
36	15.42±0.00	Methyl 3-oxo-4-methylhexanoate or Methyl 3-oxoheptanoate	1	0
37	15.50±0.01	Branched C11 alkane 9	0	4
38	15.57±0.00	2-Phenylethanol	0	2
39	15.77±0.00	Unknown (mixture containing a branched C12 alkane)	0	3
40	16.03±0.01	4,6-Nonadien-8-yn-3-ol	0	2
41	16.22±0.00	2,5-Dipropyltetrahydrofuran	0	1
42	16.35±0.04	Branched C7 carboxylic acid	0	6
43	16.43±0.00	3-Methylheptyl acetate	0	4
44	17.16±0.03	Branched C8 carboxylic acid	0	9
45	17.31±0.13	Branched unsaturated C10 aldehyde	0	3
46	17.59±0.01	Ethyl octanoate	0	5
47	19.13±0.07	4-Methoxybenzaldehyde*	5	2
48	19.65±0.00	Ethyl non-3-enoate	0	1

Table 1. (continued) Volatile compounds detected in scent gland and body swabs of captive and wild emperor tamarins. SD=standard deviation. *Identity confirmed by comparison of retention times with those of commercially obtained compounds.

#	Mean RT±SD	Candidate compound identity	No. of captive samples containing compound (n=8)	No. of wild samples containing compound (n=27)
49	19.72±0.01	Unknown compound 2	1	9
50	19.83±0.00	Tetrahydro-6-propyl-2H-pyran-2-one	0	1
51	19.96±0.01	Ethyl nonanoate or Branched C10 ethyl ester	0	4
52	21.35±0.01	Unknown compound 3	7	0
53	21.41±0.01	Butyl octanoate	1	27
54	21.61±0.00	Branched C10 carboxylic acid	0	1
55	21.66±0.02	n-decanoic acid	0	6
56	21.78±0.00	Ethyl dec-3-enoate	0	1
57	22.18±0.00	Ethyl decanoate	0	6
58	22.23±0.00	Tetradecane*	2	0
59	23.18±0.00	Diethylene glycol dibutyl ether	2	0
60	23.35±0.03	Unknown compound 4	0	4
61	23.57±0.00	Octyl 2-methylpent-4-enoate	0	1
62	23.84±0.00	Unknown compound 5	0	1
63	23.91±0.01	Cyclododecane	0	3
64	25.74±0.01	Dodecanoic acid	0	2
65	26.28±0.00	Ethyl dodecanoate	0	6
66	28.36±0.00	3-Methoxy-5-pentylphenol	0	1
67	29.97±0.00	Ethyl tetradecanoate	0	1
68	31.22±0.00	Ethyl pentadecanoate	0	1
69	33.98±0.01	Ethyl hexa- or hepta-decanoate	0	5

wild suprapubic and body swabs and was therefore not included in the comparison between captive and wild conditions), there was no significant difference in the log(arcsin(x+1))-transformed relative peak abundance between wild and captive samples (Table S3), except for 4-hydroxy-4-methylpentan-2-one [#07] and 2-ethylhexan-1-ol [#21], which were significantly more abundant in captive samples ($W=78$, $P<0.01$) and in wild samples ($W=6$, $P=0.02$) respectively.

Discussion

Tentative identification was possible for 63 out of 69 volatile compounds detected from the body and scent gland swabs of wild and captive emperor tamarins and included alcohols, carboxylic acids, ketones, aldehydes and esters. Most of these compounds have been found in glandular secretions, body swabs or urine of other primates and other mammalian taxa, mainly carnivores and rodents (reviewed in Apps et al. 2015; Poirier et al. 2021a,c). These may have a signalling role, although further investigation including behavioural assays testing the response of individuals to specific odours would be necessary to verify this assumption (e.g. in platyrrhines, Laska et al. 2004; Smith et al. 1997; in strepsirrhines, Greene and Drea 2014; Shirasu et al. 2020). The number of compounds per sample detected from the wild emperor tamarin body and suprapubic scent gland samples was significantly greater than that found in the captive samples collected and analysed using the same methods. This is consistent with the prediction that increased diversity of diet and species interactions (i.e. with con- and hetero-specifics, predators, prey, parasites and other micro-organisms) increases the range of odours produced. Only nine compounds were common to both the wild and captive datasets (4-hydroxy-4-methylpentan-2-one [#07], 2-butoxyethanol [#11], benzaldehyde [#13], phenol [#17], 2-ethylhexan-1-ol [#21], nonanal [#34], 4-methoxybenzaldehyde [#47], 'unknown compound 2' [#49] and butyl octanoate [#53]). These compounds did not differ in their relative abundance between wild and captive samples, except for 4-hydroxy-4-methylpentan-2-one [#07], which was significantly more abundant in captive samples and 2-ethylhexan-1-ol [#21], which was more abundant in wild samples, although reasons for this remain unknown. In a captive environment, diet, husbandry procedures (e.g. feeding and enrichment routines), cleaning protocols, climate and illumination can influence an animal's microbial environment and hence cause changes in the chemicals released as signals

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(Archie and Theis 2011; Clayton et al. 2016; Greene et al. 2019). Notably, recent studies have reported differences between wild and captive individuals regarding the oral and gut microbiome of long-tailed macaques *Macaca fascicularis* (Sawaswong et al. 2021) and the gut and scent gland microbiome of several lemur species (Greene et al. 2019). Since the production of body and scent gland odours is strongly influenced by commensal bacteria, wild tamarins have the potential to produce more complex chemical signals through bacterial mechanisms than their captive counterparts (Charpentier et al. 2012; Ezenwa and Williams 2014).

In this study, a number of compounds were retrieved from both wild and captive samples, suggesting that captive conditions, including diet and environment, may not completely transform an animal's odour. This strengthens the justification for the comparative value of studying captive animals to understand chemosignalling in the wild (Greene et al. 2019; Rasmussen and Krishnamurthy 2000). Callitrichids are common animal models, having been well studied in captivity and in the wild (e.g. reviewed in Epple et al. 1993; Heymann 2006b, 2022; Snowdon and Ziegler 2021). The study of captive callitrichid chemosignalling is anticipated to continue to provide valuable insight into the function of the sense of smell and chemical communication in the course of primate life history, notably throughout development, sexual maturation and senescence.

This study is one of very few having directly looked at differences in chemical communication between captive and wild specimens of the same species, adding to the existing data on owl monkeys (albeit a congeneric comparison; Spence-Aizenberg et al. 2018), giant pandas (Zhou et al. 2019), Asian elephants (Rasmussen and Krishnamurthy 2000) and red-sided garter snakes (Rudie 2015). In this study, a greater variety of samples were collected from the wild population (i.e. more animals sampled and belonging to two different groups containing several reproductive adults, different scent glands sampled) than from the captive population, which likely contributed to the greater diversity of compounds observed in the wild. Moreover, demographic differences (e.g. age and sex ratio, presence of multiple reproductive individuals, relatedness of individuals) between the wild and captive populations are an expected source of variation in the compounds found in this species, which could not be considered in this study due to the limited sample size. Previous semiochemical research on this wild tamarin population has shown differences in the chemical composition of scent gland samples across social groups, sex and breeding status (Poirier et al. 2021c). Future studies with longitudinal sampling and larger sample sizes would facilitate the study of individual variation and lend insight into inter-individual variation. The variation in chemical composition between samples from wild and captive emperor tamarins may also partly originate from natural differences between the two study populations. Indeed, even though captive and wild emperor tamarins sampled belong to the same subspecies *S. i. subgrisescens*, important genetic and ecological differences can be expected between the two populations, potentially leading to chemical differences in their produced scents. Chemical dissimilarity across populations was notably reported in studies on wild European rabbits *Oryctolagus cuniculus* (Hayes et al. 2002) and Eurasian otters *Lutra lutra* (Kean et al. 2017). Increased sampling of populations in wild and captive environments when opportunities arise will further enhance understanding of the impact of captivity on the chemical composition of primate scent gland secretions. Nevertheless, opportunities for collecting samples from endangered social animals such as primates are scarce, and appropriate datasets are hard to come by, underscoring the value of these data.

It is possible that some changes in the chemical composition of the wild samples resulted from the conditions of storage and transport. Logistical difficulties of sample shipment from Peru to the UK led to a multi-step shipping strategy, during which samples thawed for a short period of time. It is known that chemical composition of scent samples is susceptible to change over time in the absence of freezing, owing to loss of the most volatile compounds (Drea et al. 2013; Poirier et al. 2021b). Furthermore, bacterial activity inside the sample containers may have affected chemical composition (Charpentier et al. 2012); this can include formation of esters (Poirier et al. 2021b). Hence, esters uniquely retrieved from the wild samples in this study (ethyl decanoate and ethyl dodecanoate) could have arisen from the esterification, during shipping, of their carboxylic acid precursors, decanoic acid and dodecanoic acid, which were also found in these samples. Additionally, despite best efforts, spurious contamination of samples may have occurred. It is noted that 4-hydroxy-4-methylpentan-2-one and 2-ethylhexan-1-ol are common compounds used in cosmetics; therefore, their presence in the samples may have resulted from the tamarin handlers in the field and at the zoo facility. These considerations illustrate the extreme care that must be taken in the investigation of mammalian chemical signals. Advances in the development of collection and storage methods for thermally labile odorants and in the chemical interpretation of animal chemical signals in a variety of taxa foresee a flourishing future in the study of animal semiochemistry (e.g. Kücklich et al. 2017; Poirier et al. 2021c; Thompson et al. 2020; Weiß et al. 2018).

The findings raise important considerations for captive animal management and welfare given the importance of chemical communication in the social, reproductive and ecological lives of tamarin monkeys (Snowdon and Ziegler 2021). Chemosignals are recognised to be important regulators of mate choice, intrasexual competition and sexual receptivity in mammals (Wyatt 2014), and reproductive success can have important consequences for the conservation of rare mammal species. Modern breeding programmes are starting to make use of natural olfactory reproductive cues to artificially enhance breeding success in populations at risk (Lindburg and Fitch-Snyder 1994; Swaisgood and Schulte 2010). For instance, Swaisgood et al. (2004) exposed captive peri-oestrous female giant pandas and their future mates to each other's scents prior to the physical mating introduction, resulting in decreased aggression and increased sexual activity between the male and the female once placed in the same enclosure. Such approaches could very well be implemented to aid the conservation of wild populations of endangered callitrichids, such as golden lion tamarins *Leontopithecus rosalia* in the highly fragmented Brazilian lowland Atlantic rainforest (Kierulff et al. 2012). They may also be employed to enhance breeding in zoo facilities (Campbell-Palmer and Rosell 2011; Dehnhard 2011). Although animal olfactory communication may be largely inconspicuous to humans, it is of great importance to the animals. Captive husbandry protocols should take this into consideration and continue to improve incentives to provide zoo animals with naturalistic dietary and environmental conditions, in order to ensure welfare and to enhance breeding in captive facilities (Nielsen et al. 2015; Vaglio et al. 2021).

This study revealed differences in the chemical composition of scent gland and body odours produced by captive and wild emperor tamarins. Scent samples collected from wild tamarins contained a greater number of identified compounds than those collected from captive tamarins. Wild and captive scent samples also showed a marked difference in their chemical composition, though some of this variation may be explained by demographic differences between the wild and captive study populations, and by differences in storage and transport conditions. Overall, the findings indicate that captivity affects primate scents, which has important implications for chemosignalling. This research motivates further investigation into the mechanisms and

functions of olfactory communication in this taxon, which will help understanding of how captivity impacts the health and natural behaviour of these animals. It is hoped that these efforts will assist captive facilities to work towards improving conservation breeding programmes, captive husbandry and welfare of primates, especially for endangered species.

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