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## Do pied tamarins increase scent-marking in response to urban noise?

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Sounds produced by human activities are often loud and may mask acoustic signals used by other species for communication. To circumvent this, some animals use various strategies, including shifting modality completely or complementing acoustic information by using additional modalities to communicate. Here we used pied tamarins (*Saguinus bicolor*) as models to explore whether shifts in communication modalities occur under increased anthropogenic noise or deploy them complementarily. We predicted that in circumstances where noise could impede acoustic communication the study animals would exhibit more scent-marking behaviour (i.e. olfactory communication) while reducing the emission of long calls (i.e. acoustic communication). We collected information on vocal and scent-marking behaviour in nine groups of wild pied tamarins in urban forests in Manaus, Amazonian Brazil. We found that scent marking occurrence increased with noise amplitude, though long call numbers did not change. Thus, our results do not suggest a complete shift between channels but complementation of information, where scent marking may compensate for the impacts of anthropogenic noise on the acoustic channel. This is an interesting result from a conservation perspective as pied tamarins may be capable of coping with city noise to communicate with conspecifics, a key tenet of species survival.

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KEY WORDS: animal communication, urban soundscape, multimodality, olfactory, Amazon, *Saguinus bicolor*.

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## INTRODUCTION

Many species depend on the acoustic channel to communicate with conspecifics about essential information regarding foraging, mate attraction, predator, and territorial defence (Bradbury & Vehrencamp 1998). The environments in which animals reside are naturally noisy. However, humans have contributed many additional stimuli to the soundscapes that animals have evolved to deal with (Kight & Swaddle 2011). Sounds produced by human activities (anthropogenic noise) are often loud and may mask natural sounds. To circumvent this, animals deploy a variety of strategies, such as changing the physical parameters of acoustic signals (Duquette et al. 2021), completely shift to a different communication modality, or complementing acoustic communication with another modality (Partan 2017). Humpback whales, for instance, usually display more surface-active behaviours (which may be considered both acoustic and/or visual) when background noise is high (Dunlop et al. 2010). In human speech, in what is called the “cocktail party” phenomenon, people also rely on visual cues (e.g. movement of the mouth and eye position) when the acoustic environment is too noisy, and the auditory channel is compromised (Arons 1992; Best et al. 2021).

Multimodality, or the capacity to communicate using signals in more than one sensory channel, is widespread among animal species (Partan & Marler 1999; Uetz et al. 2009; Muramatsu 2011). These signals can contain complementary or redundant information that serves various functions, such as attracting additional attention to the signaller, or acting as a backup signal in noisy contexts (Partan & Marler 1999; Hebets & Papaj 2005). While signals evolve the emission of information that influence the behaviour of a receiver, cues do not contain any intrinsic information and is not intentionally emitted (Bradbury & Vehrencamp 1998; Maynard-Smith & Harper 2003). In multimodal communication in noisy contexts, both signals and cues can act to enhance detectability of signals from the main communication channel (Rowe 1999; Akçay & Beecher 2019; Pouw et al. 2021). The ability to switch from reliance on one modality to another during communication in a noisy context is known as a “Multimodal Shift Hypothesis” (Partan 2017), and is more likely to be effective if the information contained in both channels is redundant (Partan 2017) – i.e. the same message can be sent using either modality.

While many studies evaluating the impact of anthropogenic noise have been published (Swaddle et al. 2015; Kunc & Schmidt 2021), studies on multimodal communication remain rare (Liebal et al. 2022). Among primates, such investigations have been restricted mainly to captive environments or unimodal senses (Duarte et al. 2011; Slabbekoorn et al. 2018; Lineros et al. 2020), with a focus on captive and semi-captive apes (Liebal et al. 2013; Taglialatela et al. 2015; Fröhlich & van Schaik 2018). The majority of such studies have evaluated the importance of social determinants to multimodal communication and the evolution of language (Slocombe et al. 2011; Liebal et al. 2013), while hypothesis testing regarding the importance of environmental factors is scarce (Partan 2017; Fröhlich & van Schaik 2018). To our knowledge, the possibility of multimodal shifts in response to noise pollution has never been tested in primates.

South American primates use a great variety of signals in communication, including visual, chemical, and acoustics modalities (Snowdon 1989; Oliveira & Ades 2004; Bradley & Mundy 2008; Santana et al. 2012; Snowdon & Ziegler 2020), and are highly susceptible to habitat loss due to urbanisation and its consequences, such as increases in anthropogenic noise (Estrada et al. 2018). Therefore, South American primates have a great potential to exhibit multimodal shifting.

The pied tamarin (*Saguinus bicolor*) is a callitrichid from central Brazilian Amazonia with a narrow geographic range, much of which lies within the urban and peri-urban areas of the city of Manaus (Gordo et al. 2013). Urbanization has restricted individual groups to isolated forest fragments surrounded by a noisy anthropized matrix. Mainly due to fragmentation and its consequences (e.g. road-kill, electrocution, and attacks from domestic animals), the species is considered Critically Endangered by the IUCN (Gordo et al. 2019). Pied tamarins deploy several types of scent marking, behaviours that are usually associated with olfactory communication (Wormell & Feistner 1992; Epple et al. 2002). As in other tamarin species, these may have multiple functions, including reproductive and territorial information (Snowdon & Ziegler 2020; Heymann 2022). The species also produces various sounds, including long calls, used for territoriality and group cohesion (Sobroza et al. 2017), which in captivity average 74 dB (up to 89 dB) (F. Steinbrecher unpublished data). Long calls are especially important in fragmented landscapes, as they potentially regulate animal movements and intergroup communication. Here, we aim to investigate whether pied tamarins shift the use of communication modalities in response to anthropogenic noise. We predict that the occurrence of scent-marking behaviours will increase in noisier areas to compensate for the possible compromising of acoustic-based communication. If such a shift happens, we also expect that the number of long calls will decrease in noisier areas.

## MATERIAL AND METHODS

### *Study site*

This study was conducted in the Central Brazilian Amazon, in the city of Manaus, Amazonas State, Brazil. We followed a total of nine groups of pied tamarins in five forest fragments ranging from 24 to ~ 700 ha within the city of Manaus (Fig. 1). Vegetation is categorized as non-flooded lowland tropical forests (“terra firme”) with different vegetation structures ranging from forests in various stages of succession to mature forest (Marcon et al. 2012). Other primate species present in the area include saki monkeys (*Pithecia chrysocephala*), squirrel monkeys (*Saimiri sciureus*), and, at one site, an introduced group of night monkeys (*Aotus* sp.). All forest fragments are surrounded by a urbanized matrix. For each, the most common source of anthropogenic noise was road traffic, though there was also air traffic, park visitors, talking and screaming from children and university students, singing and gunshots from military activities.

### *Subjects*

The number of individuals within the study groups varied from 3 to 13, sex and age classes were known for all but one group (Table 1). Two groups were relatively well-habituated to human presence due to frequent public visitation to the parks in which they occurred (Table 1). We followed most of non-habituated groups by radio-tracking. We captured the groups using baited Tomahawk TH105 (10 × 10 × 40 cm) live traps to attach the radio-collars onto the animals

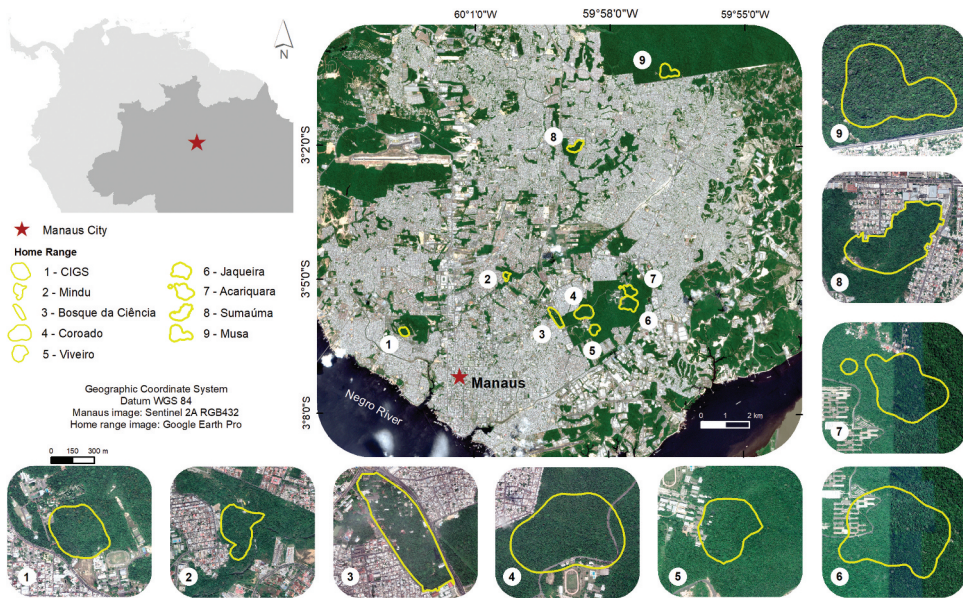


Fig. 1. — Home ranges of pied tamarin (*Saguinus bicolor*) groups (1–9) (small maps) studied in the urban area of Manaus, Brazil (larger map) from November 2018 to December 2019.

Table 1.

Characteristics of sampling locations and pied-tamarin (*Saguinus bicolor*) groups studied in urban areas of Manaus, Brazil.

Group	Group size	Group composition	Radio-collar	Scent-marking observations
Viveiro	8	1F + 2M + 3JF + I + 1UN	Yes	No
Jaqueira	13	3F + 5M + 2JF + 1JM + 1I + 1UN	Yes	No
Coroado	7	3 M + 1JM + 1I + 2UN	Yes	No
Acariquara	7	2F + 1JF + 1MF + 3UN	Damaged during the study	Yes
CIGS	5	1F + 2M + 1FJ + 1UN	Yes	Yes
Mindu*	6	2F + 1M + 1MJ + 2UN	No	Yes
Sumaúma	9	3F + 3M + 1FJ + 2MJ	Yes	Yes
Bosque da Ciência*	3	2F + 1M	No	Yes
Musa	10	NA	No	No

Group composition: M = adult male; F = adult female; JF = juvenile female; JM = juvenile male; I = infant; UN = adults of unknown sex. \*Habituated groups.

(Sobroza et al. 2017). Once captured, we sedated the animals with 0.2 mg/kg Ketamine® (Sobroza et al. 2017) and attached a SOM 2380 transmitter (164.00–164.99 MHz) (Wildlife Materials) to the alpha female of each group, as they tend to be philopatric (M. Gordo unpublished data). The frequencies emitted by the transmitter were detected with a two or three-element directional antenna and an ATS® receiver (164–168 MHz). We also followed one non-habituated group with no radio-collar and one of the groups had its radio damaged during the study (Table 1), therefore, data collected for these groups may not be optimal.

### Data collection

Data collection took place from November 2018 to December 2019. We followed each of the nine tamarin groups for 10 complete days from 06:00 am to 05:00 pm, for a total of 90 days of behavioural sampling. In the field, we collected data during 5-min behavioural sampling bouts (followed by 5-min intervals), recording all occurrences of scent marking and counting the number of long calls emitted by any individuals in the group during each sampling. During these 5-min sampling bouts, we also took a 1-min sample of noise amplitude by calculating the equivalent continuous sound levels (LEeq) with a C weighting (dB(C)). The LEq is a time-averaged sound level that, in this survey, was estimated based on sound pressures assessed every second during 1-min readings of a calibrated CEL-246 sound level meter (Casella Solutions).

### Data analysis

To test whether pied tamarins scent mark more often in noisier areas, we used a zero-inflated Generalized Linear Mixed Model (GLMM), assuming a binomial distribution and logit link function. In this analysis, each behavioural sampling was deployed as a sample unit – the occurrence of scent marking as the response variable and the noise amplitude interacting with the number of long calls as a predictor. Both variables (amplitude and number of long calls) were scaled to zero mean and unit standard deviation to facilitate parameter estimation. Additionally, we included both fragment and group identity as random factors to control for any landscape-induced variation, non-independence between observations of the same group, or different sample sizes (Zuur et al. 2009). To test whether the number of long calls diminished in response to anthropogenic noise we ran another GLMM model assuming a negative binomial distribution and log function. We chose this distribution because it is usually considered more appropriate when using count data that suffers from overdispersion (Zuur et al. 2009; Lindén & Mäntynjemi 2011). As before, we included both fragment and group identity as random factors. The two models can be summarized as follows:

- (1) Scent marking occurrence (binomial data) ~ amplitude \* number of long calls | fragment/group id
- (2) Number of long calls (count data) ~ amplitude | fragment/group id

We performed all analyses in R version 3.5 (R Core Team 2018), using the *glmmTMB* and *visreg* packages (Breheny & Burchett 2017; Brooks et al. 2017). The datasets generated and analysed during the current study are available in the Dryad repository (<https://doi.org/10.5061/dryad.np5hqbtzm>) (Sobroza et al. 2021).

## RESULTS

Anthropogenic noise levels varied from 40 to 80 dB across the five forest fragments averaging 58.6 dB (Fig. 2). Calling and scent marking activities were recorded from all nine pied tamarin study groups, but we only detected scent-marking behaviour in five of these. Accordingly, to evaluate calling behaviour, we used information from all nine observed groups, and for scent-marking analysis from five. We observed 50 scent-marking events (mainly sternal and anogenital) during 801 behavioural sampling bouts and 490 long call events during 1910 behavioural sampling bouts. During the 10 days of sampling for each group, the occurrence of scent markings per group varied from 0 to 33 events, while the frequency of long calls varied from 143 to 1140. As predicted, we found that the occurrence of scent marking was positively related to an increase in noise amplitude (Fig. 3, Table 2): noise levels of 65 dB implies in an increase in the probability of scent marking of approximately 60% (see Fig. 3).

## Group identity

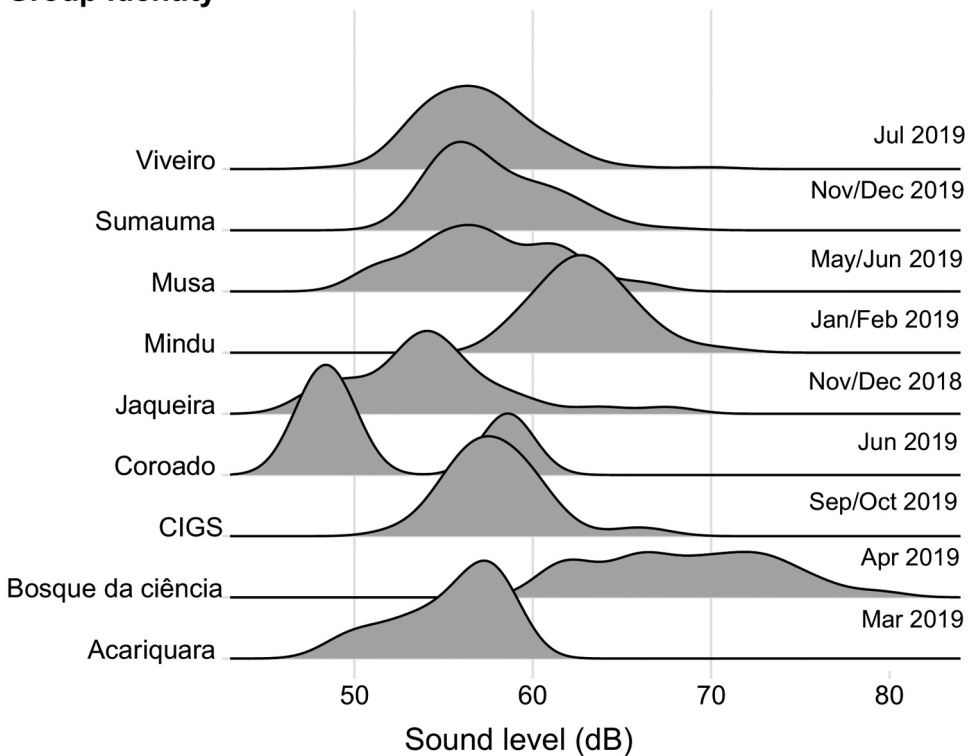


Fig. 2. — Distribution of noise levels (dB) in the sampled areas where nine pied-tamarin (*Saguinus bicolor*) groups were studied in the urban area of Manaus, Brazil. Sound levels estimated during 1-min in each 5-min behavioural sample ( $N = 1910$ ).

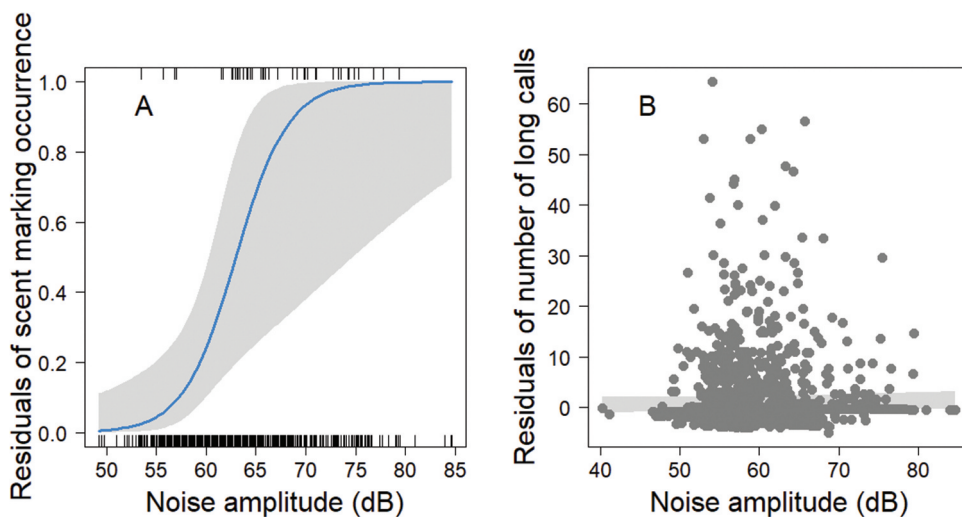


Fig. 3. — (A) Relationship between scent mark occurrence and noise amplitude (dB) (sample unit = behavioral bout;  $N = 801$ ); and (B) relationship between the number of long calls and noise amplitude (dB) in wild pied tamarins (*Saguinus bicolor*) in Manaus, Brazil (sample unit = behavioral bout;  $N = 1910$ ). Lines represent the best-fitting model (Table 2).

Table 2.

Summary of results from generalized linear mixed-effects models for observations of scent marking ( $N = 801$ ) and emission of long calls ( $N = 1910$ ) in response to noise amplitudes in nine groups of wild pied tamarins (*Saguinus bicolor*), Manaus, Brazil.

Response variable	Predictor	Coefficient	SE	Z	P
Scent marking occurrence	Intercept	- 0.19	0.633	- 0.30	0.76
	Noise amplitude (dB)	1. 91	0.68	2.78	0.005
	Number of long calls	- 0.41	0.41	- 0.99	0.31
	Noise amplitude (dB)* Number of long calls	- 1.00	0.78	- 1.28	0.19
Number of long calls	Intercept	0.93	-	-	-
	Noise amplitude (dB)	0.11	0.11	1.00	0.31

Model for scent marking occurrences with parameters estimated with a zero-inflated single model.

\*Results statistically significant ( $P < 0.05$ ).

## DISCUSSION

Here we explored whether pied tamarins can shift the use of communication modalities or use complementary ones in noisier contexts. We found that pied tamarins increase scent marking in noisier contexts. However, this change cannot be considered a multimodal shift, as the interaction between the number of long calls and noise amplitude was not a significant predictor of scent marking occurrence, and the



number of long calls was not reduced significantly when anthropogenic noise increased (Table 2). Our observations do not indicate a complete shift between channels, but possibly the complementation of information by using multimodal communication. Although preliminary, since more detailed data are recommended, it is likely that the recorded scent-marking may represent a strategy to compensate for the possible compromising effects of the acoustic communication channel by noisy environments.

Acoustic signals are ideal for immediate communication over distance in forest environments due to their capacity to circumvent physical obstacles. One downside is that they are ephemeral, while chemical cues persist longer in the environment (Bradbury & Vehrencamp 1998). Also, acoustic and chemical signals have different propagation capacities, and act in long- and short-range communication, respectively, therefore, signals from these different channels are unlikely to be redundant. However, in the presence of high-intensity noise, short-range modalities may become more relevant (Bradbury & Vehrencamp 1998) as they can function as complementary signals where inter-signal interaction causes disambiguation and refinement of information (Fröhlich & van Schaik 2018). One possibility is that pied tamarins may enhance detection and discrimination of territorial long calls in the presence of scent marks due to enhanced attention by receivers. Humans, for example, use gestural information to enhance receivers' perception of speech in the presence of noise (Grant & Seitz 2000).

Three main non-exclusive selection pressures are considered likely to act to promote multimodal communication (Hebets & Papaj 2005): (1) selection based on the content – where signals may be redundant and contain similar information, or not, but both work together during communication of a particular context; (2) selection based on efficiency – where one signal may act as a backup for another, so enabling multimodal shifts to occur effectively in noisy environments; (3) selection based on inter-signal interaction – where the response to a signal depends on another. In the current study we found no support for the “Multimodal Shift Hypothesis”, but selection based on inter-signal interaction may be acting to improve communication in noisy contexts. It would be interesting to test such hypotheses on captive tamarins by testing whether their responses to long calls in noisy environments vary when olfactory cues are present.

Scent marking has been traditionally correlated with territoriality across mammalian taxa, and in callitrichids it may function both as a signal and a cue [i.e. with or without the intentionality of communication (Pouw et al. 2021)] across a variety of contexts (Snowdon & Ziegler 2020). The territorial function of scent marking has been debated (Rylands 1981; Heymann 2000; Lledo-Ferrer et al. 2011, 2012; Roberts 2012), but such refutation of the territorial role of scent marks comes primarily from unimodal studies (Heymann 2000; Lledo-Ferrer et al. 2011). If we consider the context of multiple channels being used, and that the meaning of chemical signals may be learned (Snowdon et al. 2011), there is still a possibility that scent marking has a territorial function, one that should be tested with a multimodal approach.

Group sizes and the rate of intergroup encounters may influence the frequency of communication behaviour (Van Belle & Scarry 2015). Of the habituated groups with which we evaluated scent-marking behaviour, one had three individuals and no neighboring groups in the fragment (though, three other primate species were common in the area), while the other group was composed of six individuals, and often

encountered neighboring tamarin groups. Despite demographic and social differences, such a pattern of scent marking was evident only when we analyzed the data of all groups together, suggesting that the detected pattern is not group-specific and scent marking occurrence increases in response to local conditions (in this case, anthropogenic noise), as also reported in other mammal species (Mills 1987). Future studies, using long term data collection and an increased number of observed groups, should investigate the impact of both socio-demography and environmental variables on scent marking occurrence and frequency in urban primates.

The increase in scent-marking may be a widespread flexible response towards environmental change, as occurs in birds that increase the redundancy of acoustic and visual signals in noisier areas (Akçay & Beecher 2019). However, it is not clear whether this behavioural change is reversible (Suriyampola et al. 2020), which would be desirable if fragments are connected to pristine, quieter, areas (Barr 2016) and pied tamarin groups from very different soundscapes began to communicate. Tamarins reproduce quickly, giving birth to twins at least once (sometimes twice) a year (Gordo et al. 2017). The groups that we studied, and their relatives, have probably been in contact with a noisy urban matrix for at least 20 years (about 30 tamarin generations) (Gordo et al. 2013). Thus, it would not be impossible that our observations are related to shifts in gene expression associated with sensory channels – an event that has been observed in guppies (Ehlman et al. 2015). Experiments using playback techniques could help in understanding if the use of scent-marking by pied tamarin is an adaptive (i.e. gene based) or flexible (e.g. learning-based) response to anthropogenic noise.

Our study has some limitations, including the comparatively short period for which each study group was observed. As a result, we cannot rule out the possibility that seasonality might have influenced our results, since both the chemical composition and the information content of marked scents might vary between months (Scordato et al. 2007). In addition, some species use scent marking as a displacement activity to minimize the impact of environmental stressors (e.g. anthropogenic noise) (Watson et al. 1999; Troisi 2002). Accordingly, one possibility is that the scent marks that we observed were deposited not for communication but in response to stress caused by noise or other drivers, such as the presence of observers (though, under such circumstances we would expect a larger number of scent markings in non-habituated groups, which was not the case, see data), other visitors (Reyes et al. 2022), a lack of food resources, or social aspects (Price et al. 2019). Even if the intention of depositing these odours was not communicative, it could still function as a communicative cue. Future studies with free-range pied tamarins should consider their inner physiological state to further explore whether scent-marking under such circumstances functions as a displacement or communication behaviour or a mixture of both.

Overall, our results can be used as hints of a potential ecological effect of anthropogenic noise on scent-marking behaviour, which might relate to multimodal communication and indicate complementarity of communication channels. Further studies are still needed, both to ascertain whether the increase in scent marking is a successful strategy in response to anthropogenic noise and to evaluate if this change is adaptive. Additionally, studies that account for the possibility of scent marking functioning both for communication and behavioural displacement should also be developed. Our results are also interesting in terms of implications for conservation; as long as urban fragments where pied tamarins groups occur are functionally connected (Barr 2016; Campos et al. 2017), individuals are likely to cope with city noise by using

multiple sensory channels that enable effective communication, thus facilitating the presence of this Critically Endangered species within the largest city in the Brazilian Amazon.

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#### DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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#### ETHICAL STANDARD

The Project was approved by the Ethical Committee of the Instituto Nacional de Pesquisas da Amazônia (SEI.01280.009002018–58). SISBIO/MMA (Ministry of Environment) granted us the necessary licenses to capture, anesthetize, manipulate, and mark the subjects (N. 60347–1). Appropriate licenses were obtained to access municipal and state parks and military areas.

#### AUTHOR CONTRIBUTION

T.V. Sobroza, A.A. Barnett, M. Gordo and J.C. Dunn originally formulated the research topic. T.V. Sobroza raised funds, collected data, performed statistical analyses and wrote the original draft. A.A. Barnett, M. Gordo, and J.C. Dunn supervised. A.A. Barnett and J.C. Dunn checked the English. All authors contributed to the writing and reviewing

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