



## Parapatric pied and red-handed tamarin responses to congeneric and conspecific calls

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### ABSTRACT

Aggressive behaviors are widespread among territorial species and asymmetrical aggressiveness may imply differential access to resources. At a larger scale, such asymmetry may also drive shifts in geographic distributions. The pied tamarin (*Saguinus bicolor*) is an endangered Amazonian primate species with a small natural range. In recent decades further reduction of its range has been observed coincident with the expansion of the range of the red-handed tamarin's (*Saguinus midas*), which appears to be encroaching into the area otherwise occupied by the pied tamarin. Here we test if, at range boundaries, red-handed tamarin produces more aggressive vocalizations than the pied tamarin. We performed a series of 96 playback trials presenting both congeneric and conspecific long calls to sixteen groups of red-handed tamarins and fourteen of pied tamarins. We recorded their territorial, agonistic, alarm vocalizations, and the duration of their calling displays after broadcasts. In doing so, we assessed whether agonistic displays were more likely to occur in response to congeneric than conspecific calls in areas of sympatry. We found that the red-handed tamarin was more likely to emit more territorial calls when listening to pied tamarins than to its own species in sympatric areas, but found no differences in vocal responses from either species in relation to agonistic calls or duration of display in sympatric and allopatric areas. Furthermore, the red-handed tamarin emitted more alarm calls when listening to pied tamarin, independently of the geographic circumstances. Overall, we found that acoustic displays may be mediating species interaction in areas of sympatry. Together, these observations are suggestive of behavioral interference, including the competitive displacement of pied tamarin by red-handed tamarins.

### 1. Introduction

Aggressive behaviors are widespread among territorial animals, and are usually associated with dominance and interference competition within and between species (Drews, 1993; Anderson and Grether, 2010; Grether et al., 2013). Competing parapatric species commonly respond differently to interspecific stimuli, depending on how far individuals or groups are from the areas where the two species meet. Such behavior is known from a variety of animals (including damselflies: Anderson and Grether, 2010; lizards: Ord and Stamps, 2009; birds: Jankowski et al., 2010; and mice: Pasch et al., 2013). When asymmetrical patterns of

aggressive responses occur in contact areas this may indicate that one of the species is competitively dominant (Jankowski et al., 2010; Pasch et al., 2013). In many species of fish, lizards, birds, and primates, resolution of such interactions appears to be especially important as a factor driving species diversity, the extent of geographic ranges, and abundance (Iwanaga and Ferrari, 2002; Levi et al., 2013; Robertson et al., 2013; de Almeida Rocha et al., 2015).

When engaging in intra- and interspecific interactions, species often mediate their exchanges via vocalizations (Cheney and Seyfarth, 1982; Norconk, 1990; Windfelder, 2001; Suwanvecho and Brockelman, 2012), since sound components can contain information about the caller, such

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as species, emotional state, and body size (Morton, 1977; Fischer et al., 2004; Briefer, 2012; Pasch et al., 2013; Ordóñez-Gómez et al., 2015). Consequently, vocal displays with aggressive intent are a lot safer, and less energetically costly, than active physical engagement (Seyfarth and Cheney, 2009), and are usually deployed at the beginning of a series of potentially aggressive behaviors, most likely as an attempt to avoid escalation (Clutton-Brock and Albon, 1979; Hof and Podos, 2013). Many studies have shown that vocal displays are especially important for territorial species, and may be a good proxy for understanding their aggressive contests (Orians and Willson, 1964; Clutton-Brock and Albon, 1979; Caselli et al., 2018). Furthermore, both the duration of such vocal displays and sizes of groups involved are often central to how such conflicts are resolved (Clutton-Brock and Albon, 1979; Robinson, 1981; Radford and Du Plessis, 2004; Van Belle and Scarry, 2015).

In Amazonia, pied (*Saguinus bicolor*) and red-handed (*Saguinus midas*) tamarins are two closely related arboreal primate species with parapatric distributions (Rylands et al., 2016; Gordo et al., 2017). Yet, while the red-handed tamarin occurs over much of the northeastern portion of the region, the pied tamarin has one of the smallest primate distribution ranges in the world (~7500 km<sup>2</sup>) (Gordo et al., 2017), much of which lies northeast to the confluence between the Amazon and Negro rivers, within the largest urban area of Amazonia (Gordo et al., 2013). Habitat loss in this naturally small range frequently restricts individual groups to isolated forest fragments, with consequent effects on population size (Gordo et al., 2013, 2017). Largely because of this, the pied tamarin is currently classified as Critically Endangered by the International Union for the Conservation of Nature (Gordo et al., 2019). Over the last 30 years, the range of the species appears to have decreased, while that of red-handed tamarin has not only increased but done so towards the area occupied by the pied tamarin (Röhe, 2006; Gordo et al., 2017). As shifting parapatric boundaries frequently indicates high niche overlap (Bull, 1991), the pied and red-handed tamarins are considered potential competitors (Hershkovitz, 1977; Ayres et al., 1982; Subirá, 1998; Röhe, 2006).

To better understand the interspecific interactions between red-handed and pied tamarins, we compared their vocal behavior in response to playback of congeneric and conspecific calls in sympatric and allopatric areas. During intergroup encounters pied tamarins use a complex range of calls such as long calls (territorial calls), chirps (alarm calls), and trills (agonistic calls) (Sobroza et al., 2017). Therefore, we used territorial, agonistic, and alarm calls, as well as vocal display duration, as proxies for dominant behavior. Little is known about the red-handed tamarin vocal repertoire, but we assumed, based on field observations, and their frequent use by other members of the genus *Saguinus* (Moody and Menzel Jr, 1976; Cleveland and Snowdon, 1982; Kirchoff and Hammerschmidt, 2006; Rueda and Ordóñez, 2009), that these calls would also be present, and used in a similar context, in this species. Based on recent shifts in geographic ranges, we hypothesized that the red-handed tamarin is competitively superior to pied tamarin, which should translate into differential calling responses and display durations while listening to congeners in sympatric areas (Table 1). We also expected that both species would have stronger responses while in larger groups as they would be in numerical advantage to engage in vocal battles, as it occurs in intraspecific group encounters (Van Belle and Scarry, 2015). By testing in this manner, we also aimed to generate behavioral information to help understand the mechanism behind recent pied and red-handed tamarin range shifts.

## 2. Materials and methods

### 2.1. Study site

We carried out the study in central Brazilian Amazon, in an area between the Negro, Amazonas, Cuieiras, and Urubu rivers in Amazonas State, and at a second site between the Branco and Anauá rivers at Viruá National Park, Roraima State (Fig. 1). Mean annual rainfall at the two

**Table 1**

Summary of expected responses to playback of congeneric and conspecific calls if the red-handed tamarin (*Saguinus midas*) is competitively superior to pied tamarin (*S. bicolor*) in sympatric areas.

Species	Response variables	Geographic condition	Expectation
<i>S. midas</i>	Territorial, agonistic, and alarm calls	Allopatry	Responses towards conspecific calls would be greater than to congeneric calls
		Sympatry	Responses towards congeneric calls would be greater than to conspecific calls
	Calling display duration	Allopatry	Display duration would not differ in response to conspecific and congeneric calls
		Sympatry	Display duration would be greater in response to congeneric than to conspecific calls
<i>S. bicolor</i>	Territorial, agonistic, and alarm calls	Allopatry	Responses towards conspecific calls would be greater than to congeneric calls
		Sympatry	Responses towards conspecific calls would be greater than to congeneric calls
	Calling display duration	Allopatry	Display duration would not differ in response to conspecific calls and congeneric calls
		Sympatry	Display duration would be shorter in response to congeneric calls than to conspecific calls

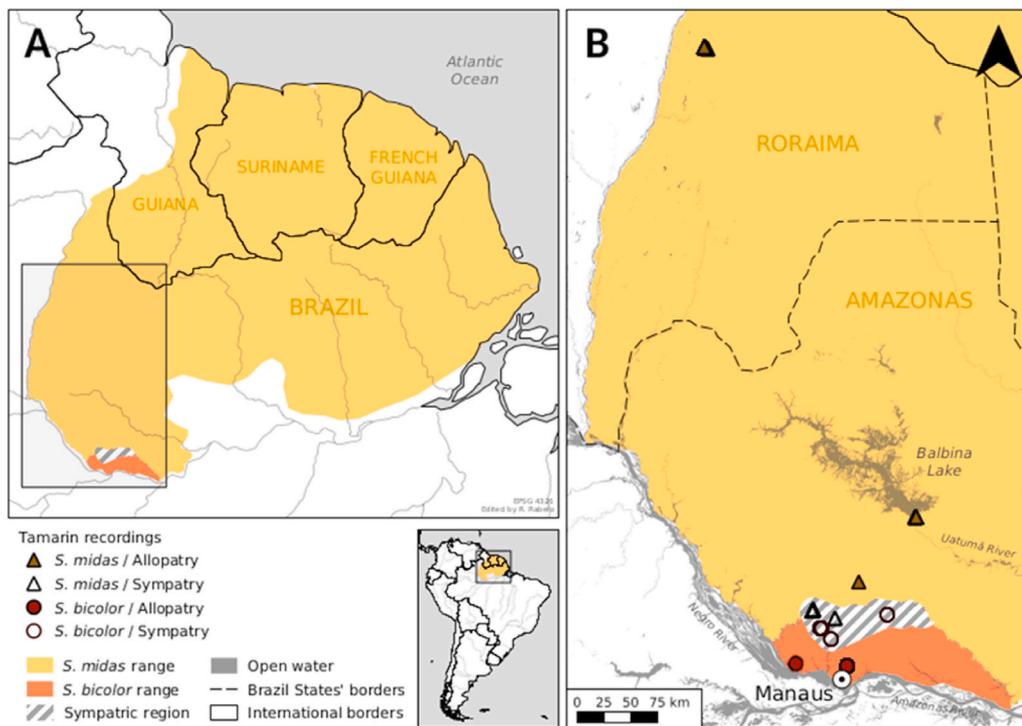
sites varies from 1200 to 2800 mm, and the annual mean temperature is 26 °C. Topography is predominantly flat, although slopes and stream-side forest areas (*baixios*) are present. Vegetation cover at the Amazonas State site consisted of tropical humid *terra firme* forest (Oliveira et al., 2008). In Viruá National Park, the vegetation is a mosaic of white-sand forest (*campinarana*), shrubby *campinarana* (white-sand shrubland), and open-canopy rainforest. All sampled areas contained forests with both primary and secondary growth, but the vegetation was continuous in all cases.

### 2.2. Experimental design

Our experimental design was based on comparing the pied and red-handed tamarin behavior in response to playback of congeneric and conspecific calls. We conducted experiments in areas of sympatry, and in allopatry for both species. We defined sympatric areas based on a variety of evidence (Table A.1), including previous studies that used interviews with local population and field-censuses (Ayres et al., 1982; Subirá, 1998; Röhe, 2006), and geographic distributional modelling (Röhe, 2006), as well as data from long-term studies such as the Pied Tamarin Project (Projeto Sauim-de-Coleira, UFAM), and Tropical Ecology, Assessment and Monitoring Network (TEAM). It is worth mentioning that the sympatric surveyed area comprised sites where both tamarin species had either been recorded in syntopy or had been modeled as having a high probability of co-occurrence (Röhe, 2006).

### 2.3. Characteristics of experimental stimuli

We used as stimuli (from here on called “treatments”) playback of pied and red-handed tamarins vocalizations originally recorded from the same groups that were tested in the survey. When recording initially, we were not able to count how many animals contributed to the playback library, nor the sex of the recorded individuals. In this study, mean pied tamarin group size was 5.2 (sd = 2.2), and 5.1 (sd = 2.03) for red-handed tamarins. Therefore, the potential number of individuals contributing to each of the recordings and final sound library varied



**Fig. 1.** Map of A) red-handed tamarin (yellow) and pied tamarin (orange) ranges and putative sympatric areas (dashed) (based on Röhe 2006). B) Open circles show pied tamarin sympatric sampling sites and filled circles represent pied tamarin allopatric sampling sites. Open triangles are red-handed tamarin sympatric sampling sites and filled triangles red-handed tamarin allopatric sampling sites. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

between 3 and 7 per group. One of the recorded groups contributing to the sound library had infants, but treatments consisted only of adult calls. We recorded sounds as wav. files, using an HTDZ HT-81 microphone (Frequency response: 1–16.0 kHz) attached to a Zoom H1 recorder (16-bit, 44 kHz). Distance between animals and recorder varied from 5 to 30 m. A total of 46 sound treatments were built (28 of red-handed tamarin, 18 of pied tamarin). The sound library used during the playback experiments was composed of 58% long calls from allopatric areas and 42% from sympatric areas. We presented treatments in a balanced way across species and geographic conditions throughout the experiment. One single recording was deployed from one to four times during 95 playback trials. Even though each recording was never presented to the same group more than once, we recognize that some pseudoreplication may be present in this experimental design (Kroodtsma et al., 2001).

The treatments used during the study consisted of long calls which, in *S. bicolor*, generally measure from 6 to 8 kHz, and have a territorial function (Sobroza et al., 2017). Each recording presented to the tamarins was 2 min long and contained four long calls spaced by intervals of ~30 s of silence in an mp3 extension. Such a calling rate does not necessarily equate to natural rates. Instead, the presented form was designed to maximize the chances of tamarins perceiving the stimulus. In nature, pied tamarins emit on average one long call per hour ( $sd = 1.84$ ), although this number tends to be much higher during group-encounters. To standardize playback treatment sound quality, we filtered sounds below 5 kHz and estimated signal-to-noise ratio (SNR) by dividing the signal peak amplitude by the Root Mean Square amplitude (RMS amplitude). We only used high SNR sounds to build playback treatments. We digitally normalized treatment sounds amplitudes using the Batch Amplify Tool. All sound manipulations were made in Raven Pro 1.5 (Cornell University Laboratory of Ornithology, 2014).

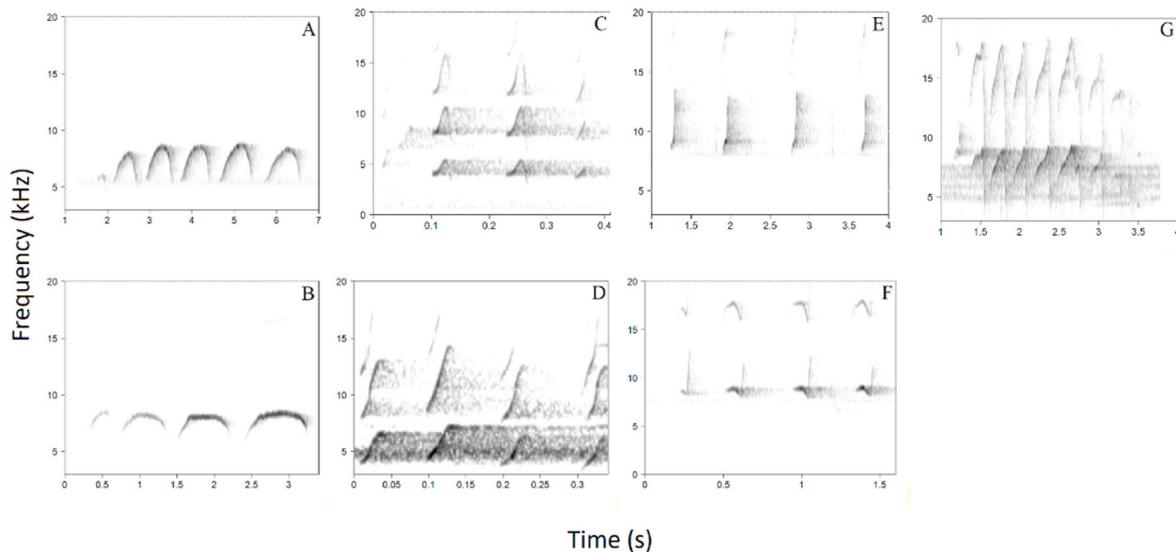
#### 2.4. Data collection

Fieldwork was carried out during 11 expeditions from January 2014 to February 2015. Sampling effort totaled 754 km walked, spread over 106 days, at 10 sampling sites, averaging nine sampling days at each

site. Data collection occurred between 06:30 and 16:30, the period when tamarins were most active (Day and Elwood, 1999; Egler 1986). Using existing trails and roads, two people (TVS plus one) walked through study areas. Upon encountering groups, we broadcast the treatments. We marked each encounter point with a Garmin GPS, and recorded the per-group number of adult individuals. As home ranges do not exceed 1 km<sup>2</sup> (Day and Elwood, 1999; Gordo et al., 2008; Hershkovitz 1977), groups separated from each other by one km or more were considered independent. During our sampling, we never detected any interspecific group encounters, and whenever we detected a conspecific group encounter, we avoided performing playback trials.

For playbacks, we used a Pignose 7–100 portable amplifier (Pignose, Las Vegas, NV; Frequency response: 0.1–12.0 kHz; power output: 5 W) and an mp4 player. Whenever possible, we tested both treatments (pied and red-handed tamarin calls) on the same day, with minimum intervals of 1 h, although it was usually greater (mean = 29.63 h). Congeneric and conspecific treatments were played to the same group multiple times ( $n = 1$  to 3). We alternated treatments to avoid order effects (Kroodtsma et al., 2001), and one specific treatment (congeneric or conspecific call) was only played to the same group after an interval of at least 48 h to avoid habituation (Bezerra et al., 2009). Distance between animals and playback sources varied from five to 30 m, with or without visual contact between the observer and the focal group. During trials, the speaker remained attached to the observer ~1.10 m above the ground, with volume held at a constant level.

We conducted a total of 96 playback trials with 16 groups of red-handed tamarin and 14 pied tamarin groups. Tamarin responses were recorded during the 10 min immediately following playback trials. We chose this duration because the groups were non-habituated and, for about half of recorded events, displays lasted 10 min or less. From the responses to playbacks, we quantified the number of territorial (*long call*), agonistic (*trills*) and alertness (*chirp*) calls because these are the most common vocalizations emitted during intergroup encounters (Sobroza et al., 2017). The red-handed tamarin vocal repertoire is not known, although they appear to produce sound types similar to the pied tamarin, except for an additional alert call (Fig. 2) (TVS, unpublished data). We counted each chirp, and the number of trill and long calls



**Fig. 2.** Vocalizations emitted in contexts of A-B) territoriality (*long calls*), C-D) agonism (*trills*) and E-G) alarm (*chirp*) of red-handed tamarins (upper line) and pied tamarins (lower line).

sequences through visual and auditory inspection of spectrograms. We defined a long call as a signal composed of a variable number of syllables with relatively constant intervals between syllables (mean = 0.129 s,  $sd = 0.045$  s). The duration of each calling display (the amount of time the animals spent near the playback speaker) was inferred from the recorder timer or by the last call showing on the spectrogram. The number of individuals in each group was never inferred based on the spectrograms, only through direct visual counts. The study was non-invasive and complied with Brazilian law (permit for Viruá National Park access 47755-1; and for red-handed tamarin and pied tamarin research 10286-3 issued by SISBIO/MMA).

## 2.5. Data analysis

We used Generalized Linear Mixed Models (GLMMs) to test if the two species showed asymmetrical response patterns to conspecific and congeneric calls in sympatric vs. allopatric conditions. We created a separate model for each species and used the number of territorial, agonistic, and alarm calls, as well as the duration of calling display, as response variables in these models, treating each playback event as a sample unit (red-handed tamarin:  $N = 54$ ; pied tamarin:  $N = 42$ ). For models using call number as the response variable, we used a negative binomial error structure, and for the duration of the calling display models, we used a gamma distribution to investigate the influence of continuous or categorical explanatory variables (Zuur et al., 2009). Predictors were: the geographic condition (two levels: sympatry or allopatry), treatment (two levels: congeneric or conspecific call), group size, and whether the group was in visual contact with the observer during the playback experiment. We included categorical information concerning the visual contact between the tamarins and observer (two levels: no visual contact or with visual contact) to control for possible observer effects (Martin and Bateson, 1993). Group identity and the locality where the experiment took place were used as hierarchical random factors to control for the non-independence of pairs of observations from the same group and potential non-independence of neighboring groups.

It should be mentioned that we made an exploratory analysis including the “playback identity” as a random factor, as our design could have some playback pseudoreplication (see methods). Since the inclusion of playback identity did not alter our results, we chose to not include them in the final models to avoid overfitting (Zuur et al., 2009).

In all models, we tested for the interaction between geographic condition and treatment. In our final models, we included all the variables defined *a priori* as they would be biologically relevant to interactions between species, or accounted for possible confounding factors. All analyses were performed using the *lme4* package (Bates et al., 2015) in R 3.4 (R Development Core Team, 2013). The data used for this study are available from the authors upon request.

## 3. Results

Pied and red-handed tamarins responded to playbacks of long calls of both species by emitting trills, chirps, and long calls (Fig. 2), and by exhibiting vigilance behavior (moving towards playback source and visually scanning the environment). As expected, we found that the number of long calls emitted by red-handed tamarins was higher when listening to congeneric than to conspecific calls in sympatric areas, whilst in allopatric areas the red-handed tamarin emitted more long calls to its own species, as shown by the interaction factor (Table 2, Fig. 3). For the pied tamarin, the number of long calls responded to was not different when listening to either congeneric or its conspecific calls, independent of geographic conditions (Table 3). Similarly, none of the predictors, including treatment, geographic condition (i.e. sympatry or allopatry) or group size, had any significant effect on the number of aggressive calls, or calling display duration for either the red-handed or pied tamarin (Tables 2 and 3). We found that the number of alarm calls was positively affected by the visual contact with the observer for both species (Tables 2 and 3). However, when controlling for this effect, the red-handed tamarin emitted more alarm calls while listening to pied tamarins than the converse, independently of geographic condition (Table 2, Fig. 4). Nevertheless, the number of alarm calls emitted by the pied tamarin was influenced only by group size (Table 3) (Fig. 5).

## 4. Discussion

In recent decades, a shift in the pied tamarin range has been observed, and the red-handed tamarin appears to be encroaching into the range of the pied tamarin (Röhe, 2006). Thus, we expected that the red-handed tamarin would be more aggressive/territorial than the pied tamarin. Indeed, the red-handed tamarin displayed more long calls (but not agonistic calls) while listening to pied tamarins calls than to its own species in sympatric areas. However, in allopatric areas, red-handed

**Table 2**

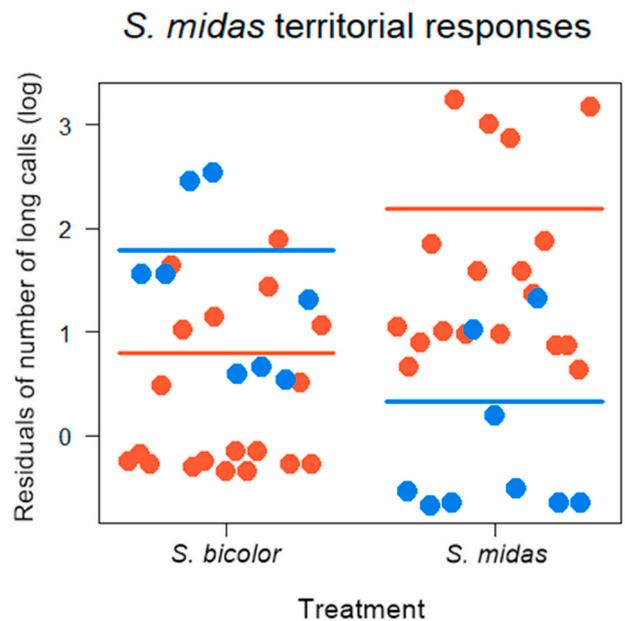
Generalized mixed-effects models for different descriptors of vocal behavior by the red-handed tamarin (*Saguinus midas*) in sympatric and allopatric areas in response to playback trials (N = 54).

Response variable	Predictor	Estimate	SE	Z	P
Territorial	Intercept	2.9685	1.2646	2.347	0.0189
	Treatment	-1.4641	1.0725	-1.365	0.1722
	Condition	-1.0029	0.9860	-1.017	0.3091
	Group size	0.1630	0.1492	1.092	0.2747
	Observer presence	1.7878	0.9535	1.875	0.0608
	Treatment*	2.8613	1.3472	2.124	0.0337
Alarm call	Intercept	3.4089	1.4445	2.360	0.0182
	Treatment	-2.5580	1.1964	-2.138	0.0325*
	Condition	-0.4766	1.0461	-0.456	0.6486
	Group size	0.1438	0.2383	0.603	0.5462
	Observer presence	-2.5131	0.9392	-2.676	0.0074
	Treatment*	1.1655	1.3583	0.858	0.3908
Agonistic call	Intercept	0.5395	2.5594	0.2111	0.833
	Treatment	-2.9341	1.9250	-1.524	0.127
	Condition	-0.0623	1.6883	-0.037	0.971
	Group size	0.2415	0.4502	0.537	0.592
	Observer presence	-0.959	1.6532	-0.580	0.562
	Treatment*	1.3837	2.2654	0.611	0.541
Calling display duration	Intercept	2.938e-03	5.864e-04	5.010	5.44e-07
	Treatment	-3.348e-05	0.0007	-0.046	0.963
	Condition	2.668e-04	0.0006	-0.428	0.669
	Group size	-1.483e-04	0.00007	-1.911	0.056
	Observer presence	-1.817e-04	0.0005	-0.339	0.735
	Treatment*	1.329e-04	8.467e-04	0.157	0.875

Treatment = Sound emitted to the species (≠ *S. bicolor* or *S. midas*); Condition = geographic position of the groups (≠ contact and non-contact areas, i.e. sympatric and allopatric); Group size = number of adult individuals per group; Observer presence = effect of visual contact between the tamarins and observer (no visual contact = ≠ 0, or with visual contact = 1). ≠ Baseline categories \* Results statistically significant (P < 0.05).

tamarins responded more to calls of their own species than to those of the congener. Surprisingly, we also found that red-handed tamarin groups emitted more alarm calls while listening to the pied tamarin, than vice-versa. However, these alarm responses were not spatially structured, and responses were similar both in sympatric and allopatric areas.

Long calls are territorial vocalizations typically employed during intergroup encounters (Oliveira and Ades, 2004; Sobroza, 2017). During intraspecific tamarin group encounters, long calls often precede aggressive encounters where acoustic signaling escalates to visual displays and chasing (Garber et al., 1993). If similar trends occur during the pied and red-handed tamarin encounters, it is likely that the red-handed tamarin will be more prone to engage in aggressive contests. Such asymmetric responses may result in differential access to resources and is suggestive of behavioral interference, including (but not restricted to) competitive displacement (Bull 1991; Weber and Strauss 2016; Grether et al., 2017) of pied tamarins by the red-handed tamarins, which would explain, at least partially, the range shifts documented by Röhe (2006). Besides the greater number of long calls, we also found that the red-handed tamarin emitted more alarm calls when exposed to congeneric calls regardless of the geographic condition (i.e. sympatry or allopatry). In areas of sympatry, such pattern may be explained by a possible learned association of sound with the pied tamarin presence,



**Fig. 3.** Differences of long calls (territorial) responses displayed by the red-handed tamarins (*Saguinus midas*) relative treatments (calls of *S. bicolor* and *S. midas*), and geographic condition (red = allopatry; blue = sympatry), based on the Generalized Linear Mixed Model (GLMM) given in Table 2. Each point represents the responses to a playback trial (n = 54); lines represent predicted means for each group of observations. Plots use partial residuals of the response variable, thus show the effect of a given interaction while controlling for the effects of remaining predictors. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

while in allopatric areas it may be a result of the novelty of such a sound at the site. Alarm calls are usually used to communicate with conspecific about possible threats, but it may also function as *perception advertisement signals* that communicate to predators and competitors that they have been detected, and it would be unprofitable to invest in an aggression-based contest (Zuberbühler et al., 1999; Bearder, 2007). Nevertheless, at least in intraspecific interactions, senders take advantage of alarm calls to establish territory borders (Smith 1986), and calling frequency often correlates with differences in potential benefits (Smith 1986), which in the case of pied and the red-handed tamarins may lead to asymmetrical capacities for territory holding.

Generally, it seems that the red-handed tamarin is more responsive to congeneric calls than the pied tamarin. One possible explanation is that the pied tamarin does not recognize the red-handed tamarin as a threat, or perhaps not recognize the congener at all. Interspecific interactions such as aggressive displays and mating often are results of recognition errors (e.g. Schultz and Switzer, 2001; Pasch et al., 2017). For example, in parapatric *Scotinomys* mice asymmetric species recognition capacities occur even when their vocal signals are highly divergent (Campbell et al., 2010; Pasch et al., 2017). Similarly, recognition asymmetries occur in pairs of howler monkey species (Bergman et al., 2016; Kitchen et al., 2018). Also, the weaker responses to congeneric vocalizations by the pied tamarin could influence the occurrence of hybridization between species. Indeed, red-handed tamarin x pied tamarin hybrids are known, both from captivity and in the wild (Hershkovitz, 1977; Gordo et al., 2017). Hybrids can be a sign of genetic introgression between species (Matsudaira et al., 2013), and may occur even when species are vastly different phenotypically (e.g. howler monkeys: Mourthé et al., 2018). The generation of hybrids, however, does not exclude the possibility of competition (Goodman et al., 1999; Agostini et al., 2008, 2010; Suwanvecho and Brockelman, 2012; Holzmann et al., 2015).

In the current study, we also found that the pied tamarin emitted

**Table 3**

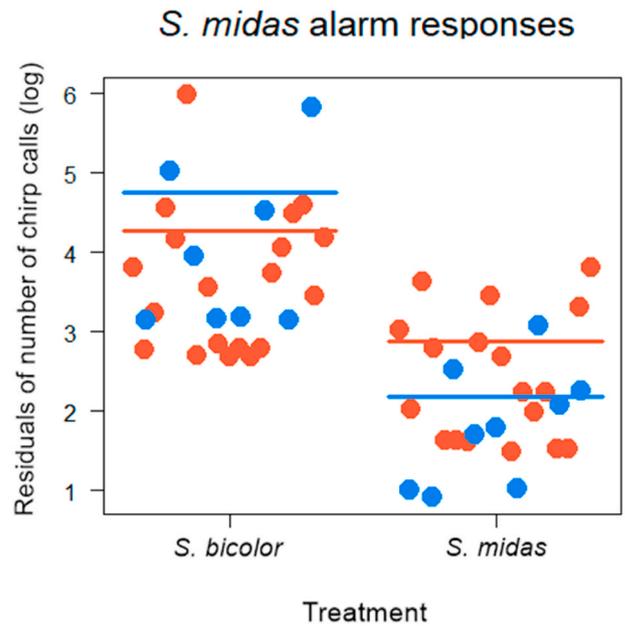
Generalized mixed-effects models for different descriptors of vocal behavior by the pied tamarin (*Saguinus bicolor*) in sympatric and allopatric areas in response to playback trials (N = 42).

Response variable	Predictor	Estimate	SE	Z	P
Territorial call	Intercept	2.9685	1.2646	2.347	0.0189
	Treatment	-0.3128	1.1318	-0.276	0.78227
	Condition	-0.3529	1.0987	0.321	0.74806
	Group size	-0.1772	0.1903	-0.931	0.35183
	Observer presence	1.1787	0.7997	1.474	0.14052
	Treatment* Condition	-1.6040	1.3897	-1.154	0.24842
Alarm call	Intercept	-1.1993	1.5483	-0.77	0.4386
	Treatment	-1.503	1.0664	0.158	0.1586
	Condition	-1.9831	1.2700	1.561	0.1184
	Group size	0.9583	0.2814	3.405	0.0006*
	Observer presence	-4.3345	1.1758	-3.687	0.0002*
	Treatment* Condition	1.3466	1.7178	-0.784	0.4330
Agonistic call	Intercept	-0.454	1.427	-0.318	0.750
	Treatment	1.318	1.138	1.159	0.247
	Condition	0.707	1.236	-0.572	0.567
	Group size	1.747	0.1748	0.999	0.318
	Observer presence	-32.94	1.880e+06	0.000	1.000
	Treatment* Condition	-1.217	1.586e	-0.768	0.443
Calling display duration	Intercept	1.582e-03	0.0008	1.840	0.0658
	Treatment	8.389e-05	0.6898	0.122	0.9032
	Condition	-9.879e-06	0.0007	-0.013	0.9896
	Group size	1.166e-04	0.0001	0.926	0.3546
	Observer presence	5.825e-04	0.0006	0.854	0.3934
	Treatment* Condition	-4.141e-04	0.001	-0.414	0.6792

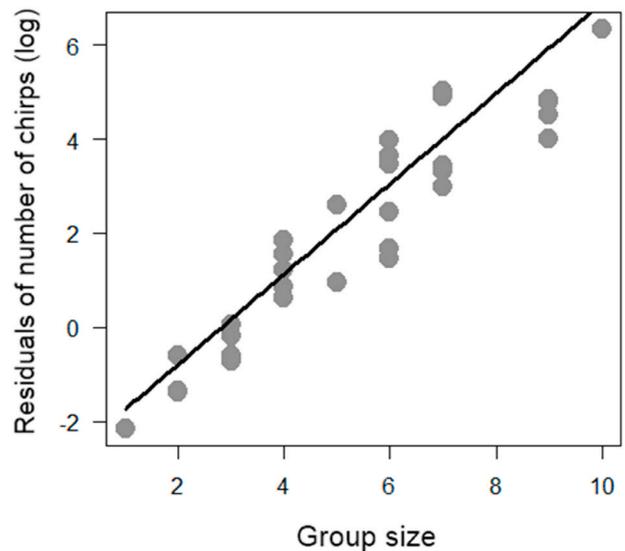
Treatment = Sound emitted to the species (≠ *S. bicolor* or *S. midas*); Condition = geographic position of the groups (≠ contact and non-contact areas, i.e. sympatric and allopatric); Group size = number of adult individuals per group; Observer presence = effect of visual contact between the tamarins and observer (no visual contact = ≠ 0, or with visual contact = 1). ≠ Baseline categories \* Results statistically significant (P < 0.05).

more alarm calls when in larger groups. Naturally, larger groups have more animals to produce alarm calls; however, such a tendency was not detected for red-handed tamarins, reinforcing the idea that this may be a strategy adopted by the pied tamarin for group encounters. Though, once again, pied tamarins responded in such a way under both sympatric and allopatric conditions, and response to congeneric and conspecific calls. It is common for some group-living animals to assess their own numerical strength prior to competitive events (Heinsohn, 1997; Wilson et al., 2002). Most probably, whenever group size is small, pied tamarins will retreat from neighbors and vocalize at a lower rate to avoid summoning attention, since they would be at a numerical disadvantage if the situation were to escalate to one involving physical aggression. On the other hand, if a greater number of individuals are present, then a dilution effect occurs, and the probability of each individual being attacked is proportionately smaller, then vocalizing becomes a viable strategy (Hamilton, 1971).

In the light of exploitation/interference competition, as well as general niche theory (Hutchinson 1957; Pianka, 1981), Ayres et al. (1982), in a pioneering study of pied and red-handed tamarin interactions, proposed three hypotheses: 1) the species compete and the red-handed tamarin is the superior competitor; 2) the species compete



**Fig. 4.** Differences in chirp (alarm) calls responses displayed by the red-handed tamarins (*Saguinus midas*) relative treatments (calls of *S. bicolor* and *S. midas*), and geographic condition (red = allopatry; blue = sympatry), based on the Generalized Linear Mixed Model (GLMM) given in Table 2. Each point represents the responses to a playback trial (n = 54); lines represent predicted means for each group of observations. Plots use partial residuals of the response variable thus show the effect of a given interaction while controlling for the effects of remaining predictors. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 5.** Chirp (alarm) calls responses displayed by the pied tamarins (*Saguinus bicolor*) relative to group size based on the Generalized Linear Mixed Model (GLMM) given in Table 3. Each point represents the responses to a playback trial (n = 42); lines represent predicted means for each group of observations. Plots use partial residuals of the response variable and thus show the effect of a given variable while controlling for the effects of remaining predictors.

and the pied tamarin is the superior competitor; 3) they do not compete and their niches are well separated. Following the study of Röhe (2006), we know that the fundamental niches of the two species (i.e. scenopoetic requirements) are similar, while the current study indicates that vocal displays are asymmetric between species, which gives support to Ayres'

first hypothesis. Other hypothesis remain to be tested, including habitat segregation; parapatric *Saimiri* spp, for instance, use habitat differently and vegetation composition is the main factor behind their habitat selection (Paim, 2008; Paim et al., 2018). To date, no equivalent fine-scale study has been made to evaluate possible habitat differences between pied and red-handed tamarin areas. Though, this should be considered, as differences in habitat use may imply in asymmetric capacities of colonization of disturbed areas and consequently to observed range shifts.

It is important to bear in mind that the presence of the observer during the playback trials appears to have had a significant influence on the alarm-related responses of both tamarin species, which could reduce our power to generalize about the studied interactions. Although the number of long calls, agonistic calls and display duration were not influenced by such factors and, in general, our results are likely to provide an accurate picture of the nature of vocally-mediated inter-group interactions between pied and red-handed tamarins.

One effect not compensated for by our experimental design is the inability to control if the playback trials occurred in core or peripheral areas of a group home range, since focal groups were unstudied, and the extent and disposition of their home ranges therefore unknown. This may be relevant since, at least in other callitrichids (such as *Callithrix jacchus*: Caselli et al., 2018), groups usually respond more to playback trials when in core areas than in peripheral ones. To try and ameliorate this potential influence, we made multiple playbacks in different places for each group, although our results must be treated with caution because of this possible complication. A second methodological consideration is that we only used the sounds of the two species. A future refinement would be to include playbacks of neutral sounds. Also, we broadcast the playback treatments at a height of some 1.1 m. Tamarins have been seen descending to the forest ground (Vidal and Cintra, 2006), but we have no information on how they use forest strata during group encounters and sound may propagate differently according to the height of the source within the forest (Waser and Brown, 1984).

## 5. Conclusion

Overall, our field playback-based results are consistent with the idea that red-handed tamarin is vocally more territorial than the pied tamarin. Such behavioral asymmetry may also be related to the capacity of the red-handed tamarin to retain territory and resources, giving the species competitive advantages that allow populations to advance into the pied tamarin range. As the capacity of species of judging threats by

means of vocal behavior also depends upon production and perception specific capacities (Bearder 2007), other tamarins' vocal behaviors such as the increased emission of alarm calls by pied tamarins when in larger groups, and red-handed tamarin alarm responsiveness to congeners in allopatric areas are more likely to be intrinsic to the nature of each species than be a reflection of any interaction between them. More studies are clearly needed to further investigate this system that provides unique opportunities for studying aspects of interspecific communication and its role in the mechanisms underlying shifts in the geographic ranges of parapatric neotropical primates. In this case the situation is made all more pertinent by the critical conservation status of one of the participating species, the pied tamarin.

## Author contributions

TVS, MG and WS originally formulated the research topic. WR, MG and JPB supervised. TVS and WRS raised funds, TVS conducted fieldwork, collected the data, performed statistical analyses and wrote the original draft. AAB helped with sampling design and checked the English. All authors collaborated substantially with writing and reviewing.

## Declaration of competing interest

None.

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## Appendices.

**Table A.1**

Geographic condition, location, number of groups and playback trials made for pied tamarin (*Saguinus bicolor*) and red-handed tamarin (*S. midas*) in each sampling location. We define as sympatric areas those sites with high probability of co-occurrence of species based on geographic modelling (Röhe 2006), and/or observation of mixed groups and hybrids.

Species	Geographic condition	Site	Coordinates	Number of groups sampled	Number of playback trials	Evidence of sympatry
<i>Saguinus bicolor</i>	allopatry	Ducke Reserve	59°55'26.23"W - 2°57'27.76"S	4	10	-
<i>Saguinus bicolor</i>	allopatry	Tupé Reserve	3°00'17.94"S - 60°12'57.57"W	2	12	-
<i>Saguinus bicolor</i>	sympatry	Pau Rosa Road	60°8'58.52"W - 2°43'35.44"S	4	10	Modelling and visual observation of mixed groups and suspected hybrids <sup>a</sup>
<i>Saguinus bicolor</i>	sympatry	Carapanã-açu Farm	59°37'56.9"W - 2°37.824"S	4	10	Modelling
<i>Saguinus midas</i>	sympatry	UFAM Experimental Farm	60° 03' 29.1"W - 02°39'41.4"S	2	5	Modelling and visual observation of a suspected hybrid <sup>a</sup>
<i>Saguinus midas</i>	sympatry	Silviculture Experimental Station	60°2'19.62"W - 2°35'54.96"S	2	4	Modelling

(continued on next page)

Table A.1 (continued)

Species	Geographic condition	Site	Coordinates	Number of groups sampled	Number of playback trials	Evidence of sympatry
<i>Saguinus midas</i>	sympatry	Cuieiras Reserve	60°13'15.45"W - 2°37'12.35"S	3	8	Modelling and visual observation of a mixed group <sup>b</sup>
<i>Saguinus midas</i>	allopatry	Balbina	59°27'20.41"W - 1°55'41.21"S	3	15	-
<i>Saguinus midas</i>	allopatry	Biological Dynamics of Forest Fragments Project	59°47'50.70"W - 2°26'23.83"S	3	9	-
<i>Saguinus midas</i>	allopatry	Virua National Park	60°58'40.97"W - 1°28'41.66"N	3	13	-
		<b>Total</b>		<b>16</b>	<b>96</b>	

<sup>a</sup> Gordo et al. (2017).

<sup>b</sup> Wilson Spironello unpublished data.

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