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RESEARCH ARTICLE

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High frequency/ultrasonic communication in a critically endangered nocturnal primate, Claire's mouse lemur (*Microcebus mamiratra*)

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The critically endangered Claire's mouse lemur, only found in the evergreen rain forest of the National Park Lokobe (LNP) and a few lowland evergreen rain forest fragments of northern Madagascar, was described recently. The present study provides the first quantified information on vocal acoustics of calls, sound associated behavioral context, acoustic niche, and vocal activity of this species. We recorded vocal and social behavior of six male–female and six male–male dyads in a standardized social-encounter paradigm in June and July 2016 at the LNP, Nosy Bé island. Over six successive nights per dyad, we audio recorded and observed behaviors for 3 hr at the beginning of the activity period. Based on the visual inspection of spectrograms and standardized multiparametric sound analysis, we identified seven different call types. Call types can be discriminated based on a combination of harmonicity, fundamental frequency variation, call duration, and degree of tonality. Acoustic features of tonal call types showed that for communication, mouse lemurs use the cryptic, high frequency/ultrasonic frequency niche. Two call types, the Tsak and the Grunt call, were emitted most frequently. Significant differences in vocal activity of the Tsak call were found between male–female and male–male dyads, linked primarily to agonistic conflicts. Dominant mouse lemurs vocalized more than subdominant ones, suggesting that signaling may present an honest indicator of fitness. A comparison of our findings of the Claire's mouse lemur with published findings of five bioacoustically studied mouse lemur species points to the notion that a complex interplay between ecology, predation pressure, and phylogenetic relatedness may shape the evolution of acoustic divergence between species in this smallest-bodied primate radiation. Thus, comparative bioacoustic studies, using standardized procedures, are promising to unravel the role of vocalization for primate species diversity and evolution and for identifying candidates for vocalization-based non-invasive monitoring for conservation purposes.

KEYWORDS
conservation, evolution, honest signaling, Madagascar, ultrasound, vocalization

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1 | INTRODUCTION

Vocal communication represents an integral part of animal societies and governs mate attraction, competition and conflict, group cohesion, parental care and antipredator strategies. In research on primate acoustic communication, the issue of signal reliability ("honesty") has gained increasing attention (Fitch, 2010; Hodges-Simeon, Gurven, Puts, & Gaulin, 2014; Wacewicz & Żywiczyński, 2012), based on the fact that body condition/social status may constrain the ability to vocalize in competitive interactions in various species. Thus, for example in peripubertal males of Bolivian Tsimane, a significant relationship between strength and vocal signaling was found, suggesting that vocal signaling acts as an honest indicator of threat potential and fitness (Hodges-Simeon et al., 2014; Wacewicz & Żywiczyński, 2012).

Most nonhuman primates, as well as humans, perceive sounds in the range between 20 Hz and 20 kHz, and primarily use the low frequency range (below 10 kHz) for vocal communication (e.g., Altenmüller, Schmidt, & Zimmermann, 2013; Andrew, 1963; Ghazanfar, Neuhoff, & Logothetis, 2002; Quam, Ramsier, Fay, & Popper, 2017; Sebeok, 1977). High frequency/ultrasonic communication, defined as communication via vocalizations above 10 kHz, is known from small insectivores (e.g., shrews), rodents, bats, as well as whales and dolphins, but is a rare phenomenon among primates (Zimmermann, 2018). Four of fourteen primate families (Galagidae, Lorisidae, Cheirogaleiidae, Tarsiidae) are known to emit ultrasonic vocalizations and only some members of the Malagasy dwarf and mouse lemurs use the high frequency/ultrasonic niche for adult social communication (Zimmermann, 2018). High frequency/ultrasonic signals have limited transmission potential, due to rapid atmospheric attenuation (Brown, 1984; Wiley & Richards, 1978), but provide benefits regarding to predation. Dwarf and mouse lemurs belong to the radiation with the highest predation pressure among primates (Scheumann, Rabesandratana, & Zimmermann, 2007). Raptors (birds of prey) represent about 50% of their predator species and are phylogenetically constrained to a hearing range up to 10 kHz (Fay, 1988) and consequently not able to locate their prey above this range. For carnivores, their other major predators, signals above 10 kHz are barely perceivable (Fay, 1988). Consequently, the evolution of high frequency/ultrasonic vocal communication in this primate group is suggested to represent a compromise between being cryptic for predators and noticeable for conspecifics.

Mouse lemurs are the world's smallest primates and often used as a model for the ancestral primate condition, due to their basal phylogenetic position within the primate order (Kappeler, 2012; Martin, 1990). The high cryptic species diversity of currently 24 phylogenetically described species with divergent geographic distribution in Madagascar, and the fact that the genome of the Grey mouse lemur is now available (NCBI genome assembly accession GCF 000165445.2), make mouse lemurs to unique models in biological research (Ezran et al., 2017; Lehman, Radespiel, & Zimmermann, 2016). Socioecology (nocturnality, solitary foraging in complex forest environments, kin-related group formation, cooperative infant care in nests, infant parking system with temporal absence of mother) predispose these nocturnal, arboreal primates for the evolution of the acoustic channel for communication (Lehman et al., 2016; Zimmermann, 2016). Indeed, brainstem-evoked response audiometry revealed that the Grey mouse lemur (*Microcebus murinus*) showed a high auditory sensitivity, extending to the ultrasonic range (Schopf et al., 2014). This bioacoustically best known mouse lemur species, the Grey mouse lemur, is highly vocal and exhibits an elaborate vocal repertoire of ten acoustically distinct call types (Zimmermann, 2010) with individual-specific, group-specific, populations-specific, and species-specific signatures (for review see, Leliveld, Scheumann, & Zimmermann, 2011; Zimmermann, Radespiel, Mestre-Francés, & Verdier, 2016). Mouse lemurs were also shown to rely strongly on acoustic signals for prey and predator detection (Fichtel, 2012; Scheumann et al., 2007; Siemers, 2012), social communication and decision-making (Braune, Schmidt, & Zimmermann, 2005; Braune et al., 2008; Kessler, Scheumann, Nash, & Zimmermann, 2012; Scheumann, Linn, & Zimmermann, 2017; Zimmermann, 2016). As vocalizations play a major role in the social life of mouse lemurs, they provide a unique model group for exploring the role of vocal communication in species diversity and evolution. Most mouse lemur species have so far been described solely based on molecular genetics (Andriantompohavana et al., 2006; Louis et al., 2006, 2008; Lutermann, Schmelting, Radespiel, Ehresmann, & Zimmermann, 2006; Olivieri et al., 2007; Radespiel et al., 2002; Radespiel, Reimann, Rahelinirina, & Zimmermann, 2006; Rasoloarison, Weisrock, Yoder, Rakotondravony, & Kappeler, 2013; Yoder et al., 2000; Zimmermann, Cepok, Rakotoarison, Zietemann, & Radespiel, 1998). Information concerning their biology, in particular the significance of vocalizations for their social life, is lacking. Such knowledge is, however, fundamental to assess the role of acoustic signaling for the evolution of primate sociality as well as for primate taxonomy and the relevance of bioacoustics for conservation.

The Claire's mouse lemur (*M. mamiratra*, synonymous to *M. lokobensis* [Olivieri et al., 2007]) was described recently based on phylogenetics (Andriantompohavana et al., 2006). It is limited to humid evergreen forest on the island of Nosy Bé and fragmented forest areas in northern Madagascar (refer to Interriver-system VI in Olivieri et al. [2007]). According to IUCN criteria (IUCN Red List 2017, http://www.iucnredlist.org), the "extent of occurrence (EOO) is estimated to be less than 80 km^2." Thus, this species is considered as critically endangered with a "very restricted and fragmented area, and in decline due to habitat loss and degradation." Nothing is known so far about its biology, example, ecology, predation pressure, home range size, or sociality.

Our study therefore aimed to enhance knowledge about this fairly unknown mouse lemur species by exploring the link between vocal acoustics and behavior and addressing the following hypotheses:

1. In the Claire's mouse lemur, vocalizations classified visually by spectrograms can be assigned to different call types, based on

distinct acoustic features. Comparable to other mouse lemur species, most call types occupy the high frequency/ultrasonic acoustic niche.

2. Comparable to other mouse lemur species, vocalizations of the Claire's mouse lemur are used primarily in social contexts.
3. In competitive social interactions of many species, vocal activity is linked to social rank or body condition and thus argued to represent a honest indicator of fitness ("honest signaling hypothesis"). If acoustic signaling in the Claire's mouse lemur supports the honest signaling hypothesis for a strepsirrhine primate, vocal activity during agonistic conflicts should be linked to social status. Dominant signalers should show a higher vocal activity than subdominant ones.

Findings will be discussed regarding the significance of vocalizations for the diversity and evolution of the mouse lemur's species, the role of vocal asymmetry for honest signaling and promising candidates for vocalization-based non-invasive monitoring for conservation purposes.

2 | METHODS

2.1 | Ethical statement

The objective of the proposed research is consistent with priorities for Malagasy primate conservation: conducting ecological, vocal, and behavioral studies to determine the identity and requirement of endangered populations and species. (Permission No.: 130/16/MEEF/SG/DGF/DAPT/SCBT.Re).

The research further complied with the legal requirements of the country in which the research was conducted, and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates (https://www.asp.org/society/resolutions/EthicalTreatmentOfNonHumanPrimates.cfm).

2.2 | Study site

The study was conducted in low-altitude humid evergreen forest in the protected area of Lokobe National Park (=LNP, S13°23′240″; E48°20′310″; Figure 1) from June 1 to July 31, 2016. The study site was situated around the village of Ampasipohy. LNP covers around 740 ha and includes the last remaining lowland rainforest found on the island (Jenkins, 1987). The climate is characterized by high equable temperatures with a maximum monthly mean temperature of 28 °C in January and February and a minimum temperature of 23 °C in July and August. The mean total annual rainfall is 2356 mm, precipitation is distinctly seasonal, the highest amount (circa 85% of annual total) occurring between November and May (White, 1983).

In the area of LNP, *Microcebus mamiratra* does not live sympatrically with other mouse lemur species, but with the larger-bodied nocturnal lemur species, *Lepilemur tymerlachsoni*, and cathemeral lemur species, *Eulemur macaco*.

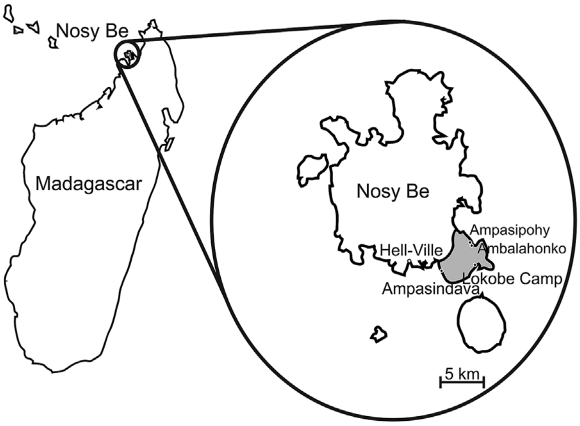

FIGURE 1 Map of Madagascar displaying the Lokobe National Park (in grey) on the island Nosy Be

2.3 | Study subjects

Eighteen males and six females were used for this study, there being a total of six male–female dyads and six male–male dyads. Mouse lemurs were trapped by hand, sexed, checked for reproductive status and weight in accordance with Zimmermann et al. (1998) and Olivieri et al. (2007), the average body weight is shown in Figure 7. The dyad partners were selected based on the criteria of comparable body mass and having been captured as far away as possible from each other, the smallest difference capture points was 370 m, to avoid forming dyads of familiar animals. One animal in each dyad was marked by a fur cut on its tail to distinguish dyad partners during a social encounter experiment.

2.4 | Field housing conditions

The dyad partners were housed together in a cage of about 1 m^3, equipped with wooden bars, and two shelters/sleeping sites. The cage was placed on the ground of the forest close to the research camp at the study site. At the beginning of each night, dyads were fed bananas. Water was provided ad libitum in a water bottle fixed to one side of the cage. Animals had access to arthropod prey that naturally entered their cages during the night.

2.5 | Social encounter paradigm, behavioral, and acoustic data recording

We used a social encounter paradigm to investigate social interactions and vocal behavior in male–female and male–male dyads. From 6 p.m. to 9 p.m., two observers wearing a dimmed head lamp sat motionless at a 2–4 m distance from the front of the cage of a dyad and recorded the behavior using the scan sampling method according to Altmann (1974). In the scan sampling, every 15 s we noted the behavior of the two animals of a dyad using a pre-established ethogram (Table 1). The observer spoke the behaviors on a Dictaphone (SONY ICDPX333.CE7). The audio protocols of the dictaphone were later transferred into Excel tables. Each dyad was

TABLE 1 Ethogram of sound-associated behaviors

Category	Behavior	Definition
Non-social behavior		
Solitary context	Locomotion	The subject changes its position.
	Resting	The subject sits motionless.
	Self-grooming	The subject licks itself.
	Feeding	The subject's tongue comes into contact with the food.
Social interactions		
Affiliative interactions	Allogrooming	The subject licks the fur of the other animal.
	Body contact	The subjects sit together with another animal with direct body contact.
Agonistic interactions	Fighting (A)	The subject bites another animal.
	Chasing (A)	The subject runs quickly after the other, while the other one tries to get out of its way or flees.
	Fleeing (S)	The subjects moves away from the other animal if the other animal chases it.
	Displace (S)	Defined as quick short movement of the subject (aggressor) toward the other animal resulting in a quick retreat of the recipient.
	Avoidance (S)	Defined as quick retreat of the subject as a response to an approach of the partner, who did not show aggressive behaviors.

Definitions for social interactions were made according to Hohenbrink et al. (2015).

studied for six successive nights. After the experiments had finished, the animals were released at the exact site of capture.

Vocalizations were recorded by two ultrasonic microphones (SMX-II weather-proof microphones, Concord, MA; 192 Khz), located at different positions of the cage (see Figure 2). Microphones were connected to a Song Meter (Wildlife Acoustics, Model SM2+, Concord, MA, sampling rate 192 kHz). Vocalizations were saved on SD flash memory cards (Samsung 32 GB SD-Card) and later transferred to hard drives (Transcend).

2.6 | Data analysis

2.6.1 | Analysis of vocal activity

As mouse lemurs vocalize in the ultrasonic range, inaudible for human listeners, we visually scanned the spectrograms of all audio files (216 hr) using Audacity® software 2.1.2 (Audacity team). Based on the contour of the fundamental frequency and the frequency range, calls were visually classified into seven different call types according to the known vocal repertoire of the Grey mouse lemur (Zimmermann, 2010). The presence of call types was then linked to the Excel table containing the behavioral data of the observations. Thus, we noted for each 15-s scan interval whether the respective call type occurred (yes/no counting). Furthermore, we counted the number of calls within a call series. Thereby, a call was defined as a continued sound element having no sound gap (Holy & Guo, 2005). A call series was defined as a series of continuous calls with a respective intercall–interval. The intercall–interval was defined based on measurements of *M. murinus* (Dietz, 2006). Two calls of the same call type were considered as belonging to a series when the duration between the offset of the first call and the onset of the following call was shorter than twice the mean intercall-interval of the respective call types of *M. murinus* (For the call types: Tsak, Croak, and Short Whistle: shorter than 200 ms; for the call types Long Whistle and Trill: shorter than 3,400 ms).

2.6.2 | Acoustic analysis

We cut the detected vocalizations as single calls or call series, saved them as a new file and then transferred them into BatSound Pro 3.31 (Pettersson Elektronik AB, Uppsala, Sweden) to check the acoustic quality. Thus, for further multi-parametric acoustic analysis, we used only calls of high sound quality (no overlap with other sounds, not over-amplified, good signal to noise ratio). Tsak and Grunt calls were uttered with an extremely high call rate compared to the other call types. Therefore, we selected 10 cut files per dyad for multi-parametric sound analysis. For the other call types, we selected all calls which were available.

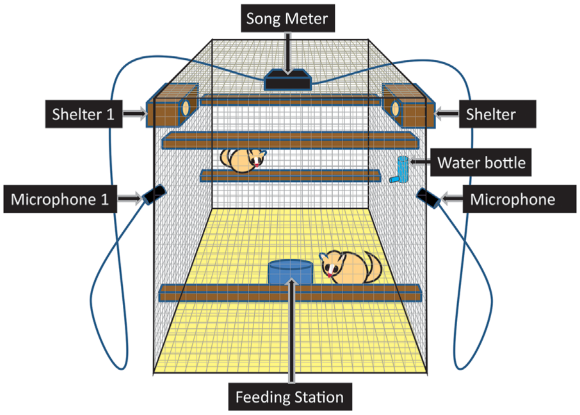

FIGURE 2 Set-up of the social encounter paradigm

For further processing, we band-pass filtered the audio recording using PRAAT (self-written script; http://www.praat.org; Phonetic Sciences, University of Amsterdam, the Netherlands; Boersma (2001); Filter frequency range: 75–60,000 Hz). Then, we time expanded the recording by a factor of 10 using the "override sampling frequency" of PRAAT (oversampling: 19,200 Hz). This results in a 10 times longer file, whereas the frequency values are divided by 10. This was necessary to shift the ultrasonic vocalization into the human hearing range and to improve the efficiency of pitch tracking. In the next step, for each call type we measured the following eight acoustic parameters (Table 2), comparable to our current comparative bioacoustics studies: call duration (DUR), center of gravity (COG), standard deviation of the frequency in the spectrum (SDCOG), Skewness (SKE), and Kurtosis (KUR) of the spectrum, percentage of voiced frames (VOI), Wiener entropy (ENTR), and harmonic-to-noise ratio (HNR). For harmonic calls, we additionally measured five parameters characterizing the contour of the fundamental frequency (F0): minimum F0 (MinF0), maximum F0 (MaxF0), mean F0 (MeanF0), standard deviation of the F0 (SDF0) and calculated the bandwidth (BAND; submenu: "To pitch": min pitch: 75 Hz; max pitch: 6,000 Hz; time steps: 0.01 s). In the last step, we recalculated the time expansion multiplying all frequency values by 10 and dividing all time values by 10.

2.7 | Determination of dominance relationship within dyads

The dominance status of each mouse lemur (dominant/subdominant) within the respective dyad was determined based on the number of won conflicts in accordance with Hohenbrink, Koberstein-Schwarz, Zimmermann, and Radespiel (2015). An animal won a conflict: (1) if this animal showed aggressive behavior toward the interaction partner whereas the interaction partner showed submissive behavior; or (2) if this animal showed no aggressive behavior but the other animal showed submissive behavior (e.g., avoidance). We then counted the number of won conflicts for each interaction partner and tested statistically whether the number of won conflicts differed from the chance level (50%) using a binomial test. If one animal won significantly more conflicts than the other, we defined the conflicts as decided conflict and the animal that won significantly more conflicts was defined as the dominant animal. If there was no significant difference in the number of won conflicts or if no conflicts occurred at all, the dominance relationship between these two dyad partners was defined as undecided.

2.8 | Statistical analysis

For the vocal activity analysis, we calculated the call rate and call occurrence for each call type and each dyad. Call rate was defined as the total number of recorded calls per hour. Thereby, the sum of each call type uttered by both individuals of a dyad was divided by the analyzed observation time (call/hour). Call occurrence was defined as the percentage of scan intervals which contained calls divided by the total number of scan intervals. In five dyads, technical problems occurred, leading to a damaged audio file which could not been opened by the software. For these dyads, the total number of scan intervals was adjusted accordingly. As data were not normally distributed, we used non-parametric statistical tests to check for differences between groups. Differences in call rate and call occurrence between call types were tested using the Friedman Test followed by pairwise comparison using the Wilcoxon sign rank test and the Bonferroni–Holm procedure to control for multiple testing. Difference in call occurrence between male–male and male–female dyads was tested using the Mann-Whitney U Test.

To confirm the appropriateness of the call type classification, a statistical analysis of the acoustic measurements was performed for the three most frequent tonal call types: Tsak, Long Whistle, and Short Whistle. In the first step, we performed univariate ANOVAs using the dyad as random factor to investigate which acoustic parameters

TABLE 2 Description of acoustic parameters measured in PRAAT

Parameters	Unit	Definition
DUR	ms	Duration between the onset and the offset of a call.
COG	kHz	Center of gravity—Mean of the frequency of the spectrum of a call.
SDCOG	kHz	Standard deviation of the center of gravity of a call.
SKE		Skewness—Difference between the spectral distribution below the COG and the spectral distribution above the COG of a call.
KUR		Kurtosis—Difference between the spectral distributions around the COG from a Gaussian distribution of a call.
VOI	%	Percentage of voiced frames of a call.
HNR	db	Harmonic-to-noise ratio—Ratio of the harmonic to the atonal energy of a call.
ENTR		Wiener entropy—Ratio of the geometric to the arithmetic mean energy of a call.
MinF0	kHz	Minimum fundamental frequency of a call.
MaxF0	kHz	Maximum fundamental frequency of a call.
BAND	kHz	Difference between MaxF0 and MinF0 of a call.
MeanF0	kHz	Mean fundamental frequency of a call.
SDF0	kHz	Standard deviation of the fundamental frequency of a call.

differed significantly between the three call types. To control for multiple testing, we performed the Fisher–Omnibus test (Haccou & Melis, 1994). In the second step, a step-wise discriminant function analysis (DFA) was performed with all measured acoustic parameters using the one-leave out cross-validation. We tested whether classification accuracy for each call type was above chance level by using Binomial tests. Classification agreement was measured using the Kappa test. To optimally balance our data set for the DFA analysis, we selected a maximum of 10 calls per dyad randomly from different recording files, if possible.

To understand the relation between vocal activity and social interactions, we calculated the call occurrence for four context categories: Non-social behavior, Social interaction, Agonistic social interaction, and Affiliative social interaction (Table 1). We calculated call occurrence per context category per dyad dividing the number of scan intervals containing calls associated with the respective context category by the total number of scan intervals of the respective context category. Furthermore, we tested differences in call occurrence between context categories (Non-social vs. Social, Agonistic vs. Affiliative) using the Wilcoxon sign rank test.

For all dyads with clear determined dominant-subdominant relationships, we calculated the call occurrence for each interaction partner. This was achieved by dividing the number of scan intervals containing a call of the dominant/subdominant subject by the total number of scans containing calls of both interaction partners. However, it should be noted that due to the ultrasonic character of the mouse lemur calls, not all vocalizations could be assigned to a specific interaction partner. Consequently, unassigned vocalizations were excluded from this analysis. Differences in call occurrence between the dominant and subdominant social partners were explored using the Wilcoxon sign rank test.

The software SPSS statistics 24.0 (IBM corporation) was used for the analyses. The Bonferroni-Holm correction and the Fisher Omnibus test were calculated by using Excel. The level of significance was set to $p \le 0.05$.

3 | RESULTS

3.1 | Vocal activity: Call rate and call occurence

Based on the spectrographic structure, vocalizations were assigned to seven different call types: Tsak, Grunt, Croak, Long Whistle, Short Whistle, Trill, and Zip (see Figure 3).

Tsak calls were recorded in all dyads, Grunt calls in ten dyads and Croak calls in six dyads (four male–female and two male–male). Long Whistle calls were recorded in four, Short Whistle calls in three male–male dyads and Trill calls in only one male–male dyad. Zip calls occurred only once and were only recorded in one male–female dyad. Tsak calls (mean = 56.41 ± SD 71.1 calls/hr) showed a significantly higher call rate than the other call types (Figure 4a, Friedman: X2 = 51.75, df = 6, $N = 12$, $p < 0.001$; Wilcoxon test: $Z \le -3.06$, $N = 12$, $p \le 0.002$, $p_{corr} \le 0.046$ for Tsak v. Grunt/Croak/LongWhistle/Trill/Zip) except for Short Whistle calls where the significance did not persist after Bonferroni–Holm correction (Wilcoxon test: $Z = -2.43$, $N = 12$, $p = 0.015$, $p_{corr} = 0.180$). On analyzing the call occurrence, a similar result was obtained. Tsak calls (mean 1.27 ± SD 1.33%) occurred in significantly more scan intervals than the other call types (Figure 4b, Friedman: X2 = 51.84, df = 6, N = 12, $p < 0.001$; Wilcoxon test: $Z \le -2.981$, $N = 12$, $p \le 0.003$, $p_{corr} \le 0.046$ for all pairwise comparisons). Thereby, Tsak calls were recorded with a significantly higher probability in male–female compared to male–male dyads (Mann-Whitney U: $U = 4$, $N_m = 6$, $N_f = 6$, $p = 0.025$).

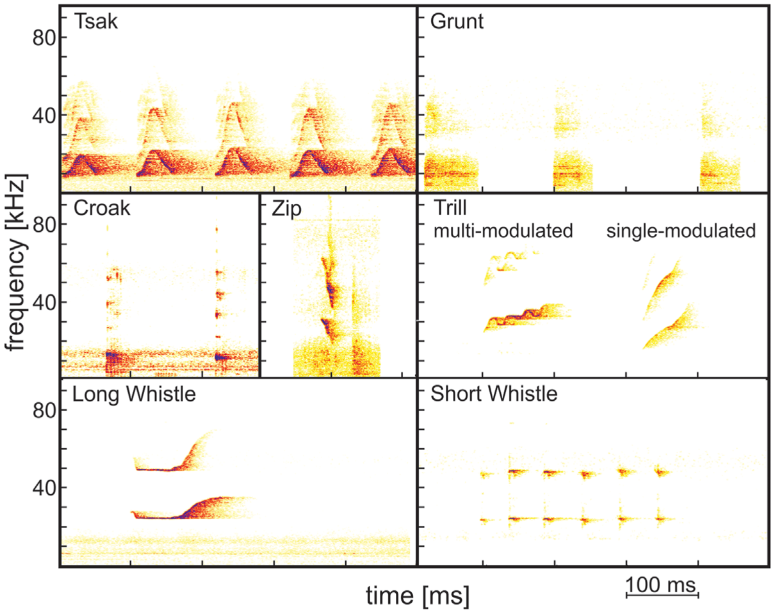

FIGURE 3 Representative spectrograms for each of the seven call types

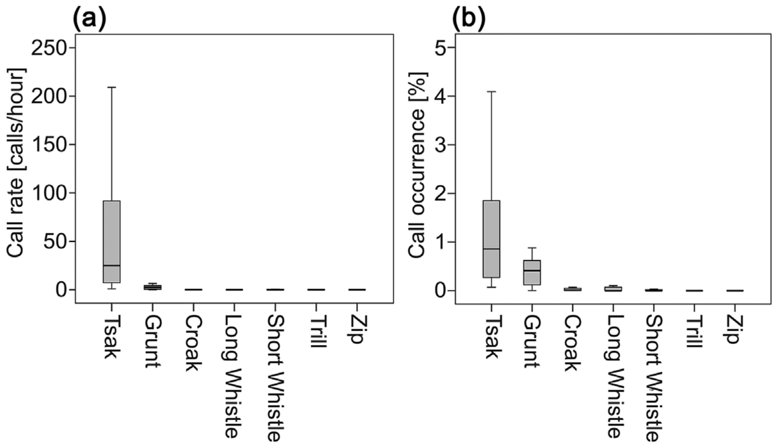

FIGURE 4 Vocal activity for each call type; (a) Call rate, number of calls per hour; (b) Call occurrence, percentage of the number of 15 s intervals which contain vocalizations; Black line, Median; Grey box, 25–75% quartiles; Whiskers, minimum –maximum values

3.2 | Acoustic structure

The Tsak call (Figure 3, Table 3) can be recognized by an inverse U-shaped frequency contour, a harmonic, and broadband structure (mean bandwidth = 5 ± SD 3 kHz) in the high frequency range (about 15–19 kHz), and a mean call duration of 27 ± SD 9 ms. Calls are almost always given in series (mean = 3 ± SD 3 calls per series), of up to 76 calls per series.

The high frequency Croak call may represent a variation of the Tsak call as it often occurs at the beginning of a Tsak call series with a slightly lower fundamental frequency and a shorter duration.

The ultrasonic Short Whistle call (Figure 3, Table 3) is a short (mean duration = 12 ± SD 3 ms) and almost constant frequency call with a mean bandwidth of 1 ± 2 kHz. It is also always given in a series of on average 6 calls ± SD 4 per series, of up to 28 calls.

The ultrasonic Long Whistle call (Figure 3, Table 3) has similar frequency characteristics as the former call type, but an approximately 10-fold higher duration (mean duration = 117 ± SD 26 ms). It may be given as a single call or uttered in a series.

Two very distinct, but rare call types were also found. The ultrasonic Zip call (Figure 3, Table 3), a downward frequency modulated call with a bandwidth of about 8 kHz. Furthermore, two

TABLE 3 Acoustic features of the measured call types

					Trill		
	Tsak	Croak	Long Whistle	Short Whistle	Multi	Single	Zip
No. of calls	167	11	14	30	1	1	1
No. of dyads	10	4	4	3	1	1	1
DUR [ms]	27.0 ± 9.3	18.8 ± 8.2	117.3 ± 26.0	12.39 ± 2.95	79.9	55.3	15.8
COG [kHz]	22.9 ± 9.7	19.4 ± 6.2	30.2 ± 1.8	34.4 ± 4.1	31.7	26.6	40.3
SDCOG [kHz]	8.3 ± 3.2	10.4 ± 3.0	6.4 ± 2.7	9.6 ± 4.1	5.2	16.3	9.5
SKE	1.8 ± 2.5	1.8 ± 1.4	0.6 ± 2.5	−0.77 ± 3.5	−1.6	0.3	−1.2
KUR	12.7 ± 32.0	5.2 ± 8.1	15.7 ± 15.3	15.3 ± 36.7	13.4	−1.0	0.9
VOI [%]	91.6 ± 18.0	67.8 ± 44.8	98.5 ± 2.8	99.33 ± 3.7	98.7	100.0	100.0
HNR [db]	6.8 ± 2.3	5.5 ± 4.0	16.1 ± 3.1	16.4 ± 3.9	11.5	6.6	9.6
ENTR	−1.6 ± 0.6	−1.4 ± 0.5	−3.0 ± 0.6	−3.5 ± 0.8	−2.7	−1.4	−2.0
MinF0 [kHz]	13.9 ± 3.8	14.6 ± 1.1	27.0 ± 2.64	26.3 ± 3.3	25.8	16.0	22.6
MaxF0 [kHz]	19.0 ± 4.5	16.7 ± 1.3	33.3 ± 3.3	27.6 ± 3.6	35.2	28.6	30.2
BAND [kHz]	5.1 ± 2.7	2.03 ± 0.9	6.4 ± 2.0	1.23 ± 1.54	9.4	12.6	7.6
MeanF0 [kHz]	16.9 ± 4.1	15.9 ± 1.2	28.9 ± 2.7	27.0 ± 3.3	31.4	23.6	26.4
SDF0 [kHz]	1.7 ± 0.9	7.4 ± 0.4	1.9 ± 0.7	0.5 ± 0.6	2.2	3.8	3.0

No., number; DUR, duration; MinF0, minimum fundamental frequency; MaxF0, maximum fundamental frequency; BAND, Bandwidth; MeanF0, mean fundamental frequency; COG, center of gravity; SDCOG, standard deviation of center of gravity; SKE, skewness; KUR, Kurtosis; VOI, percentage of voiced frames; HNR, Harmonic-to-noise ratio; ENTR, Wiener entropy; Multi, multi-modulated, Single, single-modulated.
Mean and standard deviation for each measured acoustic parameter is displayed.

variants of trill-like calls were recorded: an ultrasonic Trill call (Figure 3, Table 3) with multiple frequency modulations, a bandwidth of 9 kHz, and a relatively long duration of 80 ms, and a high frequency/ultrasonic Trill call (Figure 3, Table 3) with a single upward frequency modulation and a bandwidth of 13 kHz.

The Grunt call (Figure 3) is almost always given in series and has a noisy, low-frequency structure. Due to the fact that our recording system did not cover the low frequency range appropriately, only temporal features could be described. Therefore for Grunt calls ($N = 9$, $n = 59$), no description of acoustic parameters is presented except for the duration which lasted around 32 ms ± SD 11 ms.

To validate the visual classification for the three most frequent harmonic call types: Tsak, Short Whistle, and Long Whistle, we performed a univariate ANOVA using dyad as a random factor. Five of the 13 parameters showed significant differences between the three call types ($F \geq 5.82$, $N = 102$, df = 2, $p \leq 0.036$ for DUR, MinF0, MaxF0, BAND, KUR; Fisher Omnibustest: X2 = 80.74, df = 26, $p \leq 0.001$). The step-wise discriminant function analysis selected four acoustic parameters out of the 13 parameters for model calculation (DUR, MinF0, ENTR, SDCOG) to calculate two discriminant functions. Based on these functions, 97.1% of the calls could be correctly assigned to the respective call type (cross-validation: 97.1%; Kappa = 0.94-almost perfect agreement). Thus, 98.5% of the Tsak, 90% of the Short Whistle, and 100% of the Long Whistle calls were correctly assigned to the respective call type, significantly more than expected by chance (Binomial: $p < 0.001$). Thereby, misclassifications occurred only between Tsak and Short Whistle calls for which transitions from one to the other call type within a calling bout could be observed. The first DFA correlated most strongly with call duration ($r = 0.781$), whereas the second DFA function showed additional strong correlations with the spectral and tonality-related parameters ($r \geq |0.499|$ for DUR, MinF0, HNR, ENTR). Thus, Long Whistle calls could be separated from Short Whistle and Tsak calls regarding the call duration, whereas the Short Whistle calls could be separated from Tsak calls for spectral and tonality-related parameters (see Figure 5).

3.3 | Sound-associated context related to vocal activity

We focused our analysis on the two call types, Tsak and Grunt, as both occurred in almost all dyads. Both call types occurred significantly more often during social interactions versus non-social behavior (Wilcoxon: $Z \leq -2.80$, $N = 12$, $p < 0.005$ for both call types). In the social context, Tsak and Grunt calls occurred most often during agonistic compared to affiliative social interactions (Wilcoxon: $Z \leq -2.66$, $N = 11$, $p < 0.008$ for both call types).

3.4 | Vocal activity and social status

All six females were dominant over all males, whereas only three male–male dyads showed decided conflicts (Table 4). Thereby, the dominant interaction partner had a significantly higher probability to produce Tsak calls ($N_{\text{dominant}} = 205$, $N_{subdominant} = 39$) and Grunt calls ($N_{subdominant} = 27$, $N_{\text{dominant}} = 92$) than the subdominant one (Wilcoxon: $Z = -2.52$, $N = 9$, $p = 0.012$ for both call types; Figure 6).

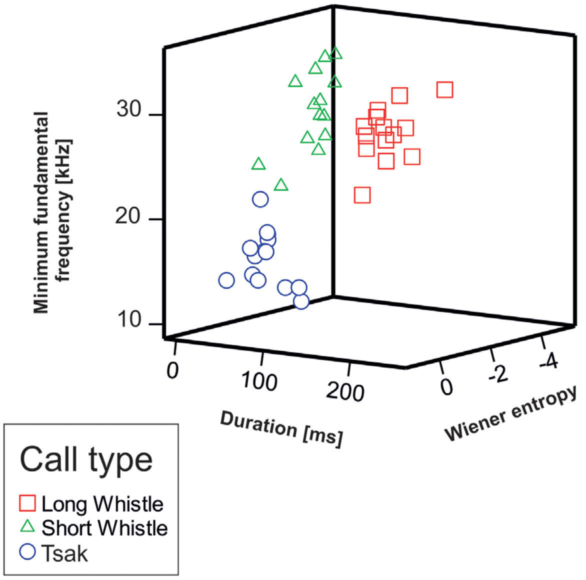

FIGURE 5 3D-Scatter-plot representing the three most discriminating acoustic parameters separating the call types, the Tsak ($N = 68$), the Short Whistle ($N = 20$), and the Long Whistle call ($N = 14$) were used for the DFA analysis

4 | DISCUSSION

Our study revealed that Claire's mouse lemur vocalizations occur primarily in the high frequency and ultrasonic acoustic space. Seven different call types were discriminated, based on a combination of harmonicity, fundamental frequency variation, call duration, and degree of tonality. Vocalizations are predominantly given in a social context. In agonistic conflicts, vocal activity of the dominant interaction partner is significantly higher than in the subdominant.

Mouse lemurs belong to the taxonomic family Cheirogaleidae, in which small-bodied species were found to use the high frequency/ultrasonic range for communication (Zimmermann, 2018). Findings, presented in this study, supported such a high frequency/ultrasonic window for the Claire's mouse lemur as well. In contrast to other small-bodied mouse lemurs studied bioacoustically, even three of the seven call types were found to occur exclusively in the ultrasonic range (MeanF0 > 20 kHz; see Figure 7). Thus, Claire's mouse lemur is the species with the highest and most cryptic vocal communication range among all bioacoustically studied mouse lemur species. As in the other studied mouse lemur species, small body size and high predation pressure may contribute to the high frequency/ultrasonic acoustic communication niche.

The vocal repertoire of Claire's mouse lemur consists of at least seven acoustically distinct call types, and is thus comparable to those of other small-bodied mouse lemur species, such as the Grey mouse lemur (e.g., Zimmermann, 2016), Goodmann's mouse lemur

TABLE 4 Social dominance in *M. mamiratra*

Category	Dyads	Number of decided conflicts	Ind. 1	Ind. 2[a]	*p*-value	Dominant subject	Weight difference[b] [g]
Male–Female							
	1	203	5	198	**<0.001**	Female	−14
	2	42	1	41	**<0.001**	Female	+2
	3	65	4	61	**<0.001**	Female	+2
	4	81	4	77	**<0.001**	Female	0
	5	266	3	263	**<0.001**	Female	−6
	6	120	9	111	**<0.001**	Female	+3
Male1–Male2							
	7	79	2	77	**<0.001**	Male 2	+4
	8	0	0	0		Undecided	+1
	9	61	8	53	**<0.001**	Male 2	−15
	10	7	2	5	0.453	Undecided	+1
	11	15	13	2	**0.007**	Male 1	+16
	12	17	12	5	0.143	Undecided	4

Displayed are the number of won conflicts per individual (Ind.) of the respective dyad.

[a] In male–female dyads individual 2 is always female.

[b] Negative value, Ind. 1 lighter than Ind. 2; positive value, Ind. 1 heavier than Ind. 2.

p-value reflects the results of the Binomial test.

Bold values $p < 0.05$

(Braune, Schmidt, & Zimmermann, 2008; Zimmermann, Vorobieva, Wrogemann, & Hafen, 2000), Madame Berthe's mouse lemur (Zietemann, 2000), the Golden-brown mouse lemur (Braune et al., 2008; Zietemann, Rasoamampianina, & Zimmermann, 2000), and the Sambirano mouse lemur (Hending, Holderied, & McCabe, 2017).

Noisy Grunt calls given during agonistic conflicts were also recorded in the Grey, the Golden-Brown and the Goodman's mouse lemur, as are harmonic high-frequency/ultrasonic Short Whistle calls, given during disturbances and in alarm situations, and high frequency Long Whistle calls given spontaneously, often at the beginning of the activity period. The rare occurrence of the Trill and the Zip call in this study may be explained by the fact that studied females showed no sign of estrous. However, most males had large testis, as typical for the mating season (Rina Evasoa et al., accepted), and we cannot rule out that an estrous female from outside visited one male dyad provoking Trill calls. In the Grey, the Golden-Brown and the Goodman's mouse lemur, these two call types are recorded primarily during the mating season. The Tsak call is the most common call type, used in agonistic conflicts in all mouse lemur species. In all studied species, these calls reveal a uniform, inverse U-shaped frequency contour, suggesting a conservative mechanism in voice production. Motivation-structural (MS) rules, put forth by Morton (2017), predict these contours for motivations conveying conflicting intentions of fear and aggression. Indeed, this acoustic contour is found in vocalizations given during

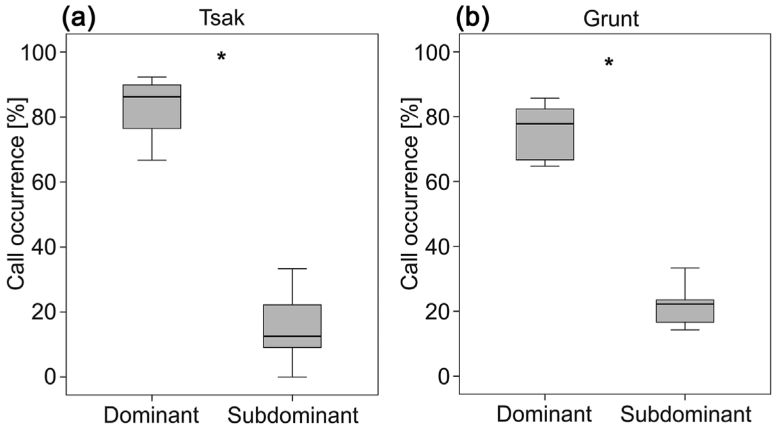

FIGURE 6 Call occurrence for the dominant and subdominant interaction partners for (a) Tsak calls and (b) Grunt calls; Black line, Median; Grey box, 25–75% quartiles; whiskers, minimum–maximum values; *Wilcoxon Test: $p < 0.05$

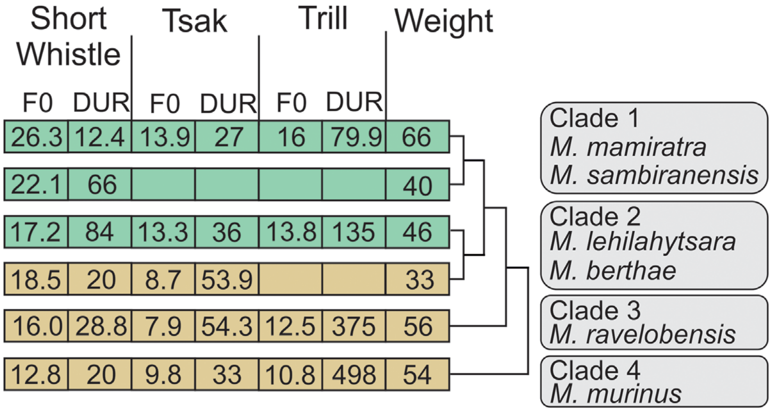

FIGURE 7 Acoustic characteristics of the Short Whistle, the Tsak, and the Trill call for the six bioacoustically studied mouse lemur species: *M. mamiratra*, *M. sambiranensis*, *M. lehilahytsara*, *M. berthae*, *M. ravelobensis*, and *M. murinus*. Phylogenetic relatedness is based on Hotaling et al. (2016) and Olivieri et al. (2007); ecology is based on Du Puy and Moat (1996): Green, evergreen humid forest; Brown, deciduous dry forest species. Acoustic data and body weight data are based on: this study for *M. mamiratra*; Hending et al. (2017) (referring to Whistle Type 3, study site: Anabohazo forest) and Olivieri et al. (2007) (body weight) for *M. sambiranensis*; Zimmermann et al. (2000) (Short Whistle), Braune et al. (2008) (Trill), and unpublished data (Tsak) and Zimmermann et al. (1998) (body weight) for *M. lehilahytsara* (origin: Andasibe region, eastern Madagascar); on Zietemann (2000) for *M. berthae* (study site: Kirindy, western Madagascar); on Zietemann (2000) (Short Whistle and Tsak), Braune et al. (2008) (Trill), and Zimmermann et al. (1998) (body weight) for *M. ravelobensis* (study site: Ampijoroa, northwestern Madagascar); on Zimmermann (2018) and Zimmermann et al. (1998) (body weight) for *M. murinus* (study site: Ampijoroa, northwestern Madagascar); F0, minimum fundamental frequency [kHz]; DUR, call duration [ms]; F0, DUR; and body weight values are represented by mean except for Trill of *M. ravelobensis* and *M. lehilahytsara* and Short Whistle of *M. sambiranensis*, where the median is represented

agonistic conflicts in a high number of bird and mammalian vocalizations (Fitch, 2010; Hauser, 1996; Morton, 2017), providing some support for Morton's rules.

A further interesting finding emerging from our study was that acoustically governed agonistic conflicts were significantly enhanced in male–female compared to male–male dyads and that dominant interaction partners differed significantly in vocal activity from subdominants. As found in this study, all conflicts in male–female-dyads were exclusively decided for females supporting that the Claire's mouse lemur exhibits female dominance. Female social dominance over males is a rare trait in mammals, but reported so far for six diurnal, four nocturnal, and seven cathemeral lemur species (Dammhahn & Kappeler, 2010; Eichmüller, Thorén, & Radespiel, 2013; Génin, 2012; Ramanankirahina, Joly, & Zimmermann, 2011). An exclusive female dominance pattern is so far only known for the Grey mouse lemur, both in the laboratory and in the field (Génin, 2003; Radespiel & Zimmermann, 2001), whereas the Golden-Brown mouse lemur lacks female dominance (Eichmüller et al., 2013) and the Goodman's mouse lemur showed only moderate female dominance (Hohenbrink et al., 2016). More information on the biology of the Claire's mouse lemur is urgently needed to interpret this finding.

In acoustically governed and decided social conflicts of the Claire's mouse lemur, dominance in both sexes was associated with a higher probability to vocalize. Thus, social dominance seems to constrain the ability to vocalize. Vocal signaling in competitive situations in mammalian societies is known to bear energetic and predatory costs for the signaler, but also to avoid injuries by costly fighting via social assessment (Morton, 2017). In various sound-producing species, from animal to humans, it was found that body condition/health status/dominance may constrain the ability to vocalize in competitive interactions, making vocal activity to be an honest indicator of fitness (Fitch, 2010). Our study on the Claire's mouse lemur with the found link between dominance status and vocal activity coincides with these findings and suggests that vocal signaling may be decisive for conflict resolution, even in a primate with a less complex social system than in monkeys and apes.

By comparing bioacoustic findings of the Claire's mouse lemur to those of five further mouse lemur species, studied in comparable behavioral contexts, we revealed a striking variation in the acoustic features between species. The following five species were bioacoustically studied: *M. sambiranensis*, *M. lehilahytsara* (until 2005 lumped together with *M. rufus*), *M. berthae* (until 2000 termed *M. myoxinus*), *M. ravelobensis* and *M. murinus*. Interestingly, three species are distributed in the humid evergreen forest (*M. mamiratra*, *M. sambiranensis*, *M. lehilahytsara*) and three in the deciduous dry forest (*M. berthae*, *M. ravelobensis*, and *M. murinus*), two of them even share the same habitat (*M. berthae* and *M. murinus* in western Madagascar [Kirindy], *M. ravelobensis* and *M. murinus* in northwestern Madagascar [Ampijoroa]). According to recently published phylogenies of mouse lemurs (Hotaling et al., 2016; Olivieri et al., 2007) the studied species can be assigned to four phylogenetically defined clades (Figure 7): (1) *M. mamiratra*—*M. sambiranensis*; (2) *M. berthae*—*M. lehilahytsara*; (3) *M. ravelobensis*; and (4) *M. murinus* is member of a clade most distantly related to the former three clades and less closely related to the other five species than the three clades among themselves (Hotaling et al., 2016; Rina

Evasoa et al., submitted). This situation provides the unique opportunity to explore to what extent there are links among habitat/ecology, phylogenetic relatedness and acoustic diversification between species. Due to lacking comparable data, comparisons could only be made so far for three call types: Tsak, Short Whistle and Trill.

If habitat affects acoustic divergence between species, as the habitat adaptation hypothesis (HAH) predicts (Morton, 1975; Richards & Wiley, 1980; Waser & Brown, 1986) deciduous dry forest-dwelling species should be more similar to each other than to evergreen humid forest-dwelling species. For the Short Whistle calls, data are available for all six species. Whereas two evergreen humid forest-dwelling species showed high F0, the third rainforest species showed values in the lower frequency range of the three deciduous dry forest-dwelling species. Concerning call duration, two evergreen humid forest-dwelling species showed the longest call duration, whereas one evergreen humid species showed the shortest call duration among the studied mouse lemur species. For the Tsak and Trill call, comparative data are available for five or four species, respectively. For all deciduous dry forest-dwelling species the fundamental frequency was lower than for the evergreen humid forest-dwelling species. For call duration, however, data are mixed. Thus, altogether, comparative bioacoustics findings provided no conclusive support for the HAH.

A comparison of acoustic divergence between the studied mouse lemur species with phylogenetic distances provided a promising phylogenetic signal. Considering the fundamental frequency, these four clades differed substantially for the call types Short Whistle and Trill. Thus, clade 1 had the highest, clade 2 a medium, clade 3 a lower, and clade 4 the lowest fundamental frequency for both call types. The results for duration were not as clear as for the Short Whistle call. However, for the Trill, clade 1 had the shortest duration, clade 2 a medium, clade 3 a longer duration, and clade 4 the longest duration. The findings for the Tsak call did not provide the same strong phylogenetic signal for fundamental frequency and call duration as in both other call types, as the variation of clade 2 may overlap with the other clades. Differences in fundamental frequency did not seem to be linked to body mass as the smallest bodied species (*M. berthae*) showed a lower fundamental frequency than the largest bodied species (*M. mamiratra*) in our sample.

Our findings have to be treated cautiously as only a few of the phylogenetically characterized mouse lemur species are acoustically phenotyped. Nevertheless, comparative bioacoustics, using standardized acoustic recording and analysis approaches, along with standardized behavioral paradigms to investigate sound-associated behaviors allow first insights into the complex interplay among ecological and phylogenetic factors, and acoustic diversification in primate acoustic communication.

The fact that not only vocalizations involved in mating, differ species-specifically (Braune et al., 2008; Zimmermann, 2016), but also vocalizations given in alarm situations and in agonistic conflicts (Zimmermann, 2016), emphasize the significance of these vocalizations for tracking species diversity and for identifying promising candidates for vocalization-based non-invasive monitoring of mouse lemurs for conservation purposes.

All in all, this study provides first bioacoustic and social information on a critically endangered, and fairly unknown nocturnal primate species. It represents the first step toward a fundamental framework in understanding the role of vocalization for primate species diversity and evolution.

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