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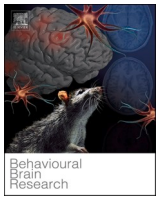
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Research article

A cooperatively breeding mouse shows flexible use of its vocal repertoire according to social context

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ABSTRACT

Mice exchange information using chemical, visual and acoustic signals. Long ignored, mouse ultrasonic communication is now considered to be an important aspect of their social life, transferring information such as individual identity or stress levels. However, whether and how mice modulate their acoustic communications is largely unknown. Here we show that the cooperatively breeding African striped mouse *Rhabdomys pumilio* controls its vocal production both qualitatively and quantitatively, depending on naturally relevant social context. By conducting controlled experiments in captivity, we found a vocal repertoire consisting of seven vocalisation types, which it uses differently depending on different types of social interactions. Familiar individuals of the same or different sex vocalise more than two unfamiliar same-sex individuals. The greatest diversity of vocalisations was recorded during the encounter between an unfamiliar female and male, suggesting that certain vocalisations are mainly used for courtship. Our results highlight that familiar mice may alternate their vocalisations while unfamiliar individuals tend to overlap one another. These observations suggest that African striped mice control the production and temporal dynamics of their vocalisations, addressing targeted information to specific receivers via the acoustic channel.

1. Introduction

In recent decades, our understanding of the importance of vocal communication in mammals in areas such as vocal recognition [1–3], mate choice [4,5], and antagonist interactions [6,7] has increased significantly. However, studies focused on a limited number of mammal groups such as primates and marine mammals [8,9]. Rodents constitute over 40 % of all mammal species [10], but received less attention [11–16]. Our knowledge how rodents exchange vocal information in contexts like aggression, play, and exploration remains rudimentary [11,17,18]. This is partly due to the technical challenge of studying ultrasonic communication. Yet understanding acoustic communication in rodents is crucial for understanding their social life. The subfamily Murinae (old World mice and rats) is especially interesting, due to its biomedical significance [19,20]. Studies regarding the use of ultrasound communication focused so far on laboratory strains of house mice and of brown rats (*Mus musculus* and *Rattus norvegicus*) with marginal consideration of the social contexts faced by animals in their natural environments [21,22]. To address this, an increasing number of studies have been recently conducted in semi-natural and natural environments [23], providing a more naturalistic framework for examining ultrasonic communication. While rodent vocalisations are still widely regarded as mere indicators of emotional states that are stereotypic without variation, ultrasonic vocalisations (USVs) likely hold greater complexity than previously thought [24], suggesting a more dynamic role of USVs [25].

Nevertheless, the extent to which rodents can flexibly control their ultrasonic vocalisations remains unclear [22]. Describing and associating the acoustic characteristics of vocalisations within the social

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contexts in which they are produced might indicate such flexibility. Traditionally, rat vocalisations have been categorized based on frequency and temporal criteria into two categories with some subcategories [26,27]: around 22 kHz (aversive contexts) and around 50 kHz (positive contexts [28–30]), though recent studies found that vocalisations around 31 kHz were emitted in stressful social contexts [31,32]. Laboratory mice also produce a variety of vocalisations, classified according to their acoustic parameters, particularly their frequency shape [33], though it is challenging to attribute clear emotional characteristics to it [18]. Interestingly, recent research has shown variations in vocalisation types as a function of social context, with females producing longer, more complex vocalisations than males [34] in a strain specific way [35].

Ultrasonic vocalisations is part of multi-channel communication, often involving the olfactory channel. For example, male house mice produce more USVs in the presence of female urine than male urine, especially if the female is unfamiliar [36]. In same-sex interactions, males are less vocal in response to other males, and females are more likely to communicate with a familiar than unfamiliar female [36–38]. While these experiments report quantitative changes in USVs, recent studies have begun to focus on the repertoire of wild house mice, showing that variations in frequency modulations can be induced by presenting different individuals behind a Plexiglass cover [39]. In rodents outside the family Murinae, vocalisations also mediate social interactions [40,41]. For instance, spiny mice produce USVs during sexual behaviour and social investigation [42], and various species of voles use USVs to regulate aggressive behaviour [43].

Studying rodent USVs remains challenging. Unlike the discrete vocal repertoire of many bird species that we can easily distinguish acoustically (e.g. zebra finch [44]), the vocal repertoire of mice and rats is graded, with blurred acoustic boundaries between vocalisation categories [45]. Traditionally, authors have used thresholds based on a few acoustic parameters to define vocalisation categories (e.g. average vocalisation duration or frequency [27,33]). Recent advances in artificial intelligence made more objective descriptions of vocal repertoires possible, allowing the exploration of large recording banks [18,46–48]. In the present study, we used machine learning techniques dedicated to describe the vocal repertoire of the house mouse and rat [34,49,50] to understand the complexity of the ultrasound repertoire in a wild rodent.

We studied acoustic communication in the African striped mouse *Rhabdomys pumilio*, a murine rodent closely related to laboratory mice and rats. The striped mouse diverged from the genera *Mus* and *Rattus* 5–6 million years ago [51]. Its social system has been extensively studied in the wild and in the laboratory, making it a key model for exploring the links between environmental variation and social flexibility [51,52]. The African striped mouse exhibits remarkable social flexibility, alternating between solitary living and family groups depending on reproductive competition and population density [53]. Family groups generally comprise one breeding male, 2–4 breeding females, and up to 25 adult offspring of both sexes [54]. Group members can recognize each other and behave amicable towards each other, but aggressive towards mice from other groups [54,55]. This suggests a complex communication system involving chemical, visual and acoustic channels. From a practical point of view, the striped mouse offers the advantage of being diurnal and easy to observe both in captivity and in the field [54,56]. It therefore represents a good model for understanding the evolutionary diversity of vocalisations and acoustic communication in rodents as well as the interactions between social complexity and communication.

Here we tested the hypothesis that the vocalisations produced by African striped mice differ according to the social context, depending on the sex and social familiarity of the interacting individuals. We recorded vocal exchanges between two African striped mice in captivity, reproducing realistic meeting contexts as they exist in the wild when two individuals, familiar or not, meet while they are foraging. We conducted an unsupervised machine learning classification of the vocalisations produced in different social contexts. We also measured the precise timing of acoustic communication to assess the occurrence *versus* avoidance of vocalisation overlap when two mice vocalised, an index that could reflect a propensity to 'turn-take' in these rodents. We address the following questions: 1) What is the extent of the striped mouse vocal repertoire? 2) do striped mice demonstrate flexibility in their vocal repertoire usage depending on social context? 3) are both the qualitative and quantitative aspects of vocal exchanges between individuals influenced by their familiarity and their respective sex?

2. Methods

2.1. Ethical note

Mice were kept in large cages with rich enrichment (tubes, houses, rodents' wheels). Weekly enrichment rotations prevented the manifestation of stereotypical behaviour. Furthermore, mice were reared alongside their parents for a minimum of two months prior to separation, a practice demonstrated to significantly reduce striped mice's stereotypical behaviour in adulthood [57]. Manipulation of an animal (e.g., for cage cleaning or transfer to the experiment room) was executed using small boxes, thereby circumventing direct human handling and minimizing induced stress. To minimize stress, during testing, all experiments were conducted within the same cage model used for housing animals. Video monitoring from outside the room enabled quick intervention and cessation of experiments in cases of severe aggression. However, the most aggressive behaviour observed was chasing, with no instance of physical aggression noted. Following the experiments, animals underwent visual inspection for injuries before being returned to their house cage, and no injury was observed. Finally, animals were closely monitored for a period of two days after the experiment, with particular attention given to observing normal behaviours, especially during social interactions and feeding. All procedures were approved by the Loire Ethic Committee for Animal Experimentation of the University of Saint-Etienne (CEEAL-UJM n°98) under agreement number E422180901, for "Study of ultrasonic vocalisations of African striped mice".

2.2. Subjects

We performed 45 pairwise encounters with a total of 87 African striped mice (3 mice were used in two different encounters). All animals were born in captivity and represents in average the 15th generation descending from wild individuals captured in 2016 in the Goegap Nature Reserve in South Africa. Animals are housed in pairs (unrelated breeding pair) or unisex groups (siblings) in Zolux Neo Panas XL cages (71*41*48 cm). Enrichments (tubes, wooden houses and platforms) are regularly installed, moved and changed in their cage. The mice are kept under a 12/12 h light-dark cycle (lights on at 08:00–20:00), in rooms maintained between 24 and 26°C. The experiments were carried out between 10:00 am and 14:00 pm. Mice were fed 90 minutes before the start of the experiment with 4 g of seeds' mix for rodents (Zolux©), and have access to water *ad libitum* in their housing cage.

2.3. Experimental design

The pairwise encounters were carried out with 2 adult individuals (aged from 4 to 8 months), either familiar or unfamiliar. For each of these categories, we carried out encounters between two males, two females or two individuals of different sex. Familiar encounters between males and females were carried out with unrelated breeding pairs of individuals housed in the same cage for at least 3 weeks and with no dependent offspring. Familiar encounters between individuals of the same sex were carried out with brothers or sisters housed together since birth. In this situation, the familiar individuals were also related. These first two situations mimic what happens in the wild, where the familiar

individuals who share the same community nest are the parental pair and the siblings. Unfamiliar encounters (individuals of the same or different sex) were carried out with two individuals born and housed in two separate rooms, with no possibility of having seen, heard or smelled each other since birth.

For each pairwise trial in each part of the experiment, the two individuals were taken out of their maintenance cage and isolated separately in two other cages, which were placed in separated acoustic chambers for the hour preceding the experiment. The mice were then introduced into an experimental cage placed in another acoustic chamber (SilentBox© with acoustic foam-covered walls). The experimental cage comprised two compartments separated by an opaque, acoustically insulated partition, meaning animals were not able to hear each other before the encounter (one compartment per mouse; Zolux Neo Panas XL cage, 71*41*48 cm). The partition was effective, as no USVs were recorded before the encounter. A trapdoor (with a 6 cm diameter round opening) allowed communication between the two compartments, which opening of the trapdoor was controlled from outside the acoustic chamber, avoiding any disturbance by human intervention. The cage floor was covered with 1 cm of clean bedding (Zolux Chambiose Nature). After a 20-minute habituation period, during which the mice remained in their respective compartments, the trapdoor was opened. Once one of the two mice had joined the other in its compartment, the two individuals remained together for 10 minutes, during which their vocal production was recorded (Fig. 1).

2.4. Acquisition and detection of ultrasonic vocalisations

We recorded the ultrasonic vocalisations of the mice with an Avisoft© Bioacoustics CM16 microphone connected to a sound gate (Avisoft© Ultrasound Gate 416 H, sampling rate = 300 kHz). The microphone was placed above the centre of the experimental cage, at 55 cm above the cage floor. We performed the acoustic analysis using Deepsqueak© v3.0, a MATLAB software dedicated to the automatic detection and analysis of ultrasonic rodent vocalisations [46]. Spectrograms were generated with a 0.0056-s window, 90 % overlap and 0.0056 s NFFT. Two neural networks already trained in Deepsqueak© were used to detect vocalisations (Rat Detector YOLO R1 and Mouse Detector YOLO R2). To decide on the best parametrization to optimize the accuracy of automatic detection by the software, we first visually inspected the spectrograms of three randomly selected encounter experiments. Based on this test phase, we chose to set the tonality (Wiener entropy of the detected vocalisation) and the neural network score thresholds at 0.25 and 0.55 respectively.

We tested the ability of Deepsqueak software to identify the ultrasonic vocalisations of the African striped mouse by comparing the results of automatic analysis with manual analysis. We randomly selected 6 recording sequences (10 minutes each; 1 sequence per encounter type). The evaluation of DeepSqueak's effectiveness was based on the calculation of several metrics:

– *Precision*, corresponding to the proportion of USVs detected (True Positive = TP) relative to the total number of sound events detected by Deepsqueak (TP + False Positive FP):

$$Precision = \frac{TP}{TP + FP}$$

– *Recall*, corresponds to the proportion of USVs detected by Deepsqueak relative to the total *number* of USVs identified manually (TP + False Negative FN):

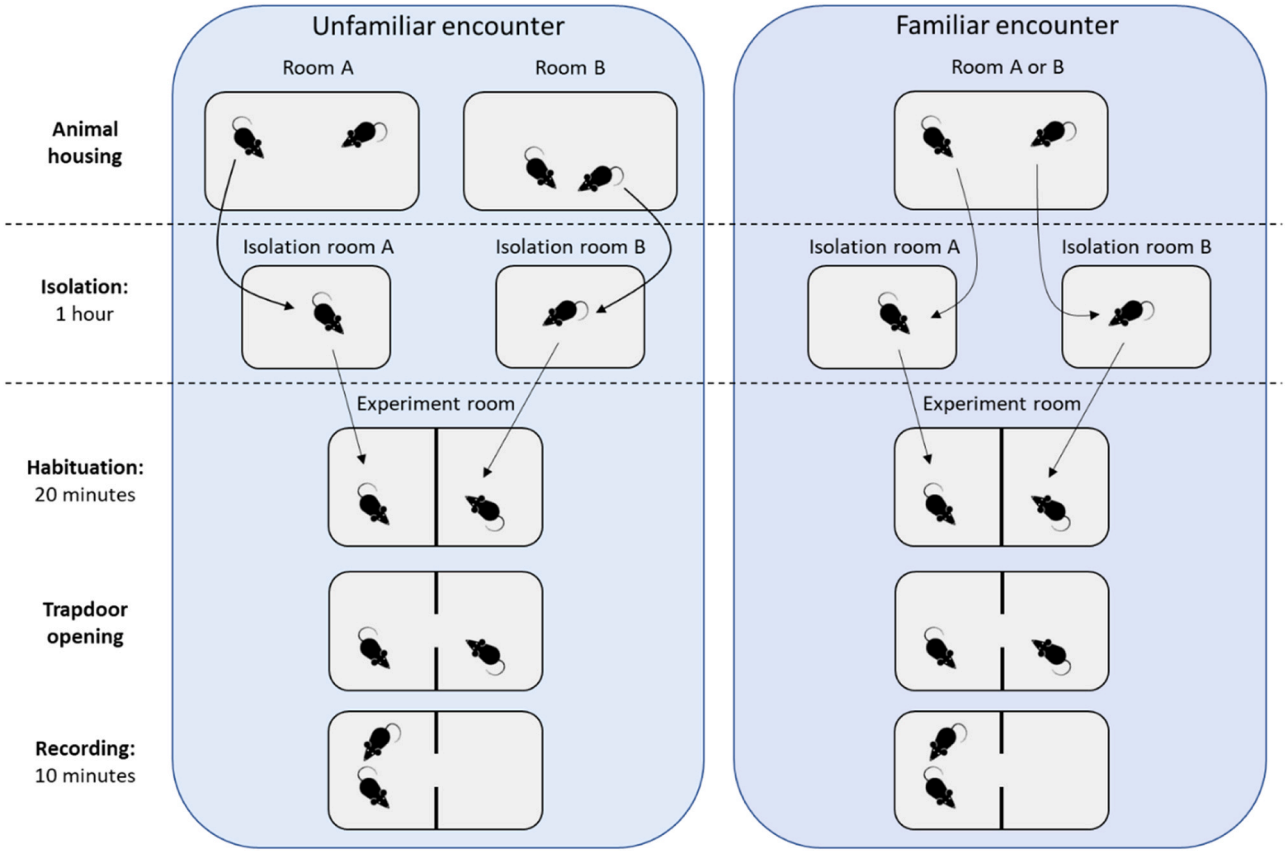


Fig. 1. Encounter experiments. Left panel: encounter of unfamiliar individuals (housed in different rooms). Right panel: encounter of familiar individuals (housed in the same cage).

$$Recall = \frac{TP}{TP + FN}$$

– *F1-Score*: score of correct USV detection (score representative of the performance of the model, by penalizing large disparities between precision and recall), calculated as follows:

$$F1score = 2 \times \frac{Precision \times Recall}{Precision + Recall}$$

– *Missed USVs rate: proportion of missed vocalisations over all vocalisations.*
– *False USVs rate: proportion of sound events detected by Deepsqueak© which are not USV over all sound events detected.*

The comparison of automatic and manual analysis shows that the two approaches give almost identical results, confirming that Deepsqueak is a suitable tool for the analysis of the African striped mouse's vocalisations (Supplementary Table 1).

2.5. Classification of vocalisations

When vocalising, mice generally emitted a series of vocalisations separated by silences. Using Deepsqueak© software, we isolated and analysed each vocalisation produced during each recording (average: 159 ± 112 vocalisations per minute of recording). Each vocalisation was described by a set of 9 acoustic descriptors representing its spectro-temporal characteristics (frequency contour, duration and average frequency of vocalisations; Table 1).

We then classified these vocalisations according to the 9 acoustic descriptors, using Deepsqueak's unsupervised k-means clustering method (*kmeans_opt* functions in Deepsqueak package). The maximum number of clusters was set to 100 in order to achieve the most accurate clustering possible, with 10 replicates. Elbow method was used to determine the optimal number of clusters. The cut-off was set at 27 clusters which were then visually inspected. Clusters of vocalisations with a similar frequency contour were then merged. Clusters containing vocalisations or noise that overlapped in time were excluded. This resulted in the 7 clusters presented in the results section (see below). For this classification, we chose to double the weights given to the parameters describing the frequency contour (maximum amplitude for each time point in the spectrogram), compared with the weight for vocalisation duration and mean frequency. We adopted this method emphasizing spectral features because frequency modulation is expected to be particularly significant in mammalian vocal communication [58], and after extensive testing of the clustering results with different weights combined with pilot evaluations based on manual examination of the calls.

Table 1
Acoustic parameters used to describe the mice vocalisations. The frequency parameters are measured on the frequency contour, which is the frequency pattern over time (see Supplementary Figure 1).

Acoustic feature	Description
Vocalisation Length (s)	Duration of the vocalisation
Principle Frequency (kHz)	Median frequency of the vocalisation contour
Lowest Frequency (kHz)	Lowest frequency of the vocalisation contour
Highest Frequency (kHz)	Highest frequency of the vocalisation contour
Frequency Bandwith (kHz)	Total frequency modulation of the vocalisation contour
Frequency Standard Deviation (kHz)	Standard deviation of the frequency of the vocalisation contour
Slope (kHz/s)	Mean slope of the vocalisation contour
Tonality	Wiener entropy of the vocalisation contour
Sinuosity	Length between the first and last points of the vocalisation contour divided by the Euclidean distance between the first and last points

2.6. Quantifying the temporal overlap between vocalisations

We defined vocalisations as overlapping when the spectrogram presented two different frequencies at the same time. Because Deepsqueak detected overlapping vocalisations as one single vocalisation, we first used the software's unsupervised classification which assigned most of these paired vocalisations to a novel cluster, different than non-overlapping vocalisations. We then visually reviewed vocalisations of this novel cluster to exclude non-overlapping ones that had been included due to classification errors.

2.7. Visualization of data and statistics

To visualize mouse vocalisations in a two-dimensional acoustic space, we applied the UMAP algorithm (a non-linear algorithm of dimension reduction) on the 9 acoustic predictors used to classify vocalisations using "uwot" package [59].

For statistical analyses of the effect of social context on the number, temporal dynamics (number of vocalisations / minutes) and overlapping patterns of vocalisations, we used Bayesian multilevel models fitted with the "brms" R package with default priors [60]. Posterior distributions of fitted values were discussed using their medians and 95 % credible intervals (CIs). Differences were considered credible when the 95 % CI of the difference between posterior distribution of the median between two conditions did not include the null value.

3. Results

3.1. Vocal production depends on familiarity and sex

Fig. 2 shows the average number of vocalisations recorded over 10 minutes for each type of encounter (66,137 vocalisations for all 45 trials). Mice made significantly fewer vocalisations during encounters between same-sex unfamiliar individuals compared to the other types of contexts. Compared to other conditions, they produced on average 1157 less vocalisations over 10 minutes (95 % CI [-2241; −142]) for two unfamiliar females and 1259 less (95 % CI [-2350; −354]) for two unfamiliar males (see Supplementary Table 2 for all differences between conditions). The number of vocalisations emitted was not significantly different between all other conditions, i.e. all encounters between familiar individuals, whether of the same sex or not, and encounters between unfamiliar individuals of the opposite sex.

3.2. The African striped mouse vocal repertoire

We detected and categorized recorded vocalisations using Deepsqueak© software. We performed a k-means classification based on the frequency contour and duration of the vocalisations. This unsupervised method separated the vocalisations into seven clusters, i.e. corresponding to 7 different types of vocalisations, characterized by particular spectro-temporal parameters (Fig. 3). Table 2 summarizes the mean values of these acoustic parameters for each cluster. Most mouse vocalisations were characterized by narrow frequency bands, with varying degrees of frequency modulation. For five of the clusters, frequency modulation was either zero ("flat" cluster), rising ("up" cluster), falling ("down" and "longdown" clusters) or S-shaped ("modulated" cluster). The "trill" and "longdown-trill" clusters were distinguished from the others by a rapid, pronounced sinusoidal frequency modulation, which characterizes all or part of the signal.

3.3. Social context drives the use of vocal repertoire

As illustrated in Fig. 4, the vocal repertoire deployed by the mice depended on the sex and familiarity of the individuals in contact. The

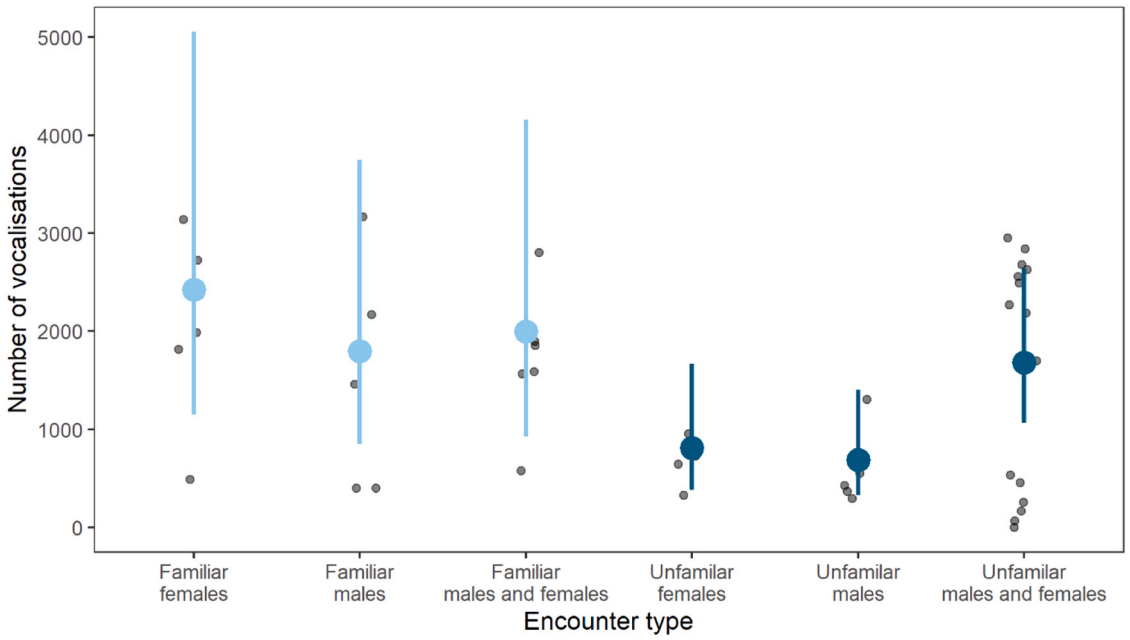


Fig. 2. Mice vocal production depends on social context. Solid disks represent the medians of the posterior distributions of the mean and bars represent 95 % CI of the data fitted using the Bayesian model *Percentage of overlapping vocalisations* ~ *Encounter type* (gaussian distribution). Points represent the number of vocalisations emitted by a pair of mice during ten-minute encounters between two individuals, familiar or unfamiliar, of the same or different sex (n = 15 for unfamiliar males and females encounter, and n = 6 for other encounter types). We recorded on average more vocalisations when the two individuals, female or male, were already living together ("familiar" contexts) than if they had never met before ("Unfamiliar" contexts), unless when the two unfamiliar individuals were of different sexes. In the latter case, the distribution of vocalisations was bimodal: there were either a high number of vocalisations (between 2000 and 3000), or a low number (between 0 and 500).

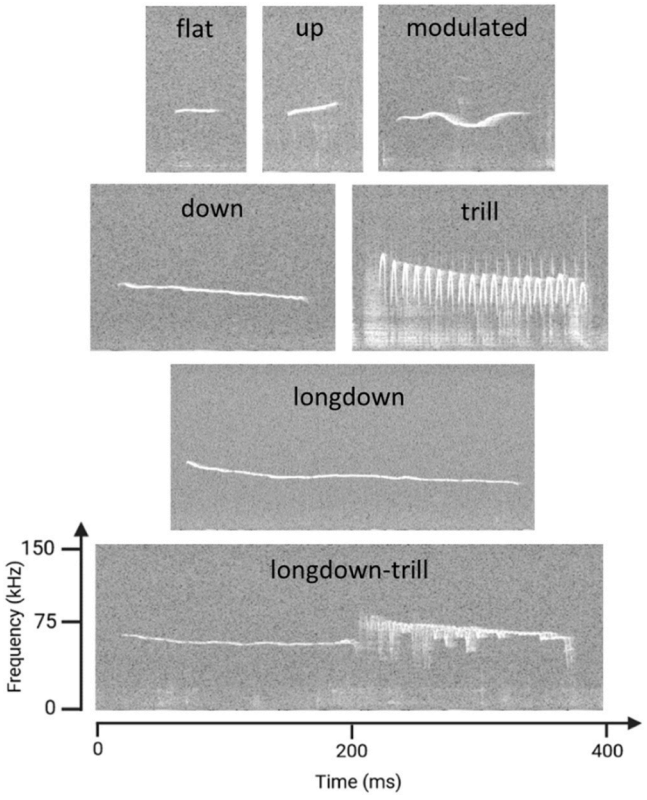


Fig. 3. The vocal repertoire of the African striped mouse. Unsupervised K-means clustering on frequency contours of 63,694 recorded vocalisations led to a repertoire of seven acoustic clusters. The acoustic characteristics of these clusters are detailed in Table 2.

mice emitted "flat" vocalisations in all contexts (shown in red in Fig. 5), and these vocalisations account for most of the vocalisations emitted when two unfamiliar males meet (94.8 %). In other contexts, mice used a more varied repertoire. This variation was particularly true during encounters between unfamiliar females and males. In this context, the mice produced 63.1 % "flat" vocalisations (other contexts: 71–94.8 %), but compared to all other contexts more "down" vocalisations (6.6 % vs. 0.1–3.8 %), more "longdown" vocalisations (2.7 %, vs. 0.0–1.5 %), more trills (6.6 % vs.0.0–0.2 %) and more longdown trills (0.8 % vs. 0.0 %). The mice also used a diversified repertoire when familiar females and males met, with more "down" vocalisations (3.8 %), "longdown" (1.5 %) and a few trills (0.2 %), than when unfamiliar individuals of the same sex met. Modulated vocalisations were emitted in greater proportion during encounters between individuals of the opposite sex, whether unfamiliar (10.5 %) or familiar (7.3 %), than during encounters between same-sex individuals. However, the proportion of modulated vocalisations was higher when the individuals are of the same sex but familiar than when they have never met (4.5 % for familiar males and 5 % for familiar females vs. 0.3 % and 1.2 % for unfamiliar individuals, respectively for each sex). In encounters between familiar females, there was a significant proportion of "up" vocalisations (22.3 %) compared to other encounters (see Supplementary Table 3 for all comparisons).

3.4. Number of vocalisations and proportion between vocalisation types do not change over time

We measured the number of vocalisations and their distribution between the different vocalisation types during the 10 minutes of recording, for each of the six types of encounters (Fig. 6). In all contexts, we observed a short adaptation time: during the first minutes, the mice emitted few vocalisations, but their rate of vocal production reached its regular level as early as the third or fourth minute. The rate of vocal production remained stable over time (On average, 12 % of the total vocalisations in an encounter were produced per minute between the

Table 2
Spectro-temporal features of the African striped mouse vocalisations. Values are the mean of acoustic measurements for each vocalisation type ± standard deviation (extracted from 63,694 vocalisations).

Vocalisation type	*Number of vocalisations*	*Duration (ms)*	*Main Frequency (kHz)*	*Lowest Frequency (kHz)*	*Highest Frequency (kHz)*	*Frequency Bandwith (kHz)*
flat	41,713	25.5 ± 1.2	59.6 ± 5.1	57.9 ± 5.4	61.8 ± 5.3	3.9 ± 3.0
up	8437	36.5 ± 1.2	59.1 ± 2.5	57.3 ± 2.8	64.1 ± 2.9	6.7 ± 3.0
modulated	6455	69.8 ± 1.6	58.1 ± 3.0	55.7 ± 3.2	61.1 ± 3.6	5.4 ± 3.3
down	3174	128.5 ± 2.5	54.9 ± 4.5	51.1 ± 5.2	60.5 ± 5.2	9.3 ± 4.7
trill	2435	77.3 ± 4.5	74.3 ± 8.4	64.8 ± 10.8	83.1 ± 8.0	18.3 ± 10.4
longdown	1203	266.1 ± 11.9	56.6 ± 6.6	50.1 ± 6.7	68.1 ± 10.1	18.0 ± 10.5
longdown-trill	277	249.9 ± 9.7	64.7 ± 7.7	50.8 ± 6.9	78.0 ± 7.0	27.2 ± 8.2

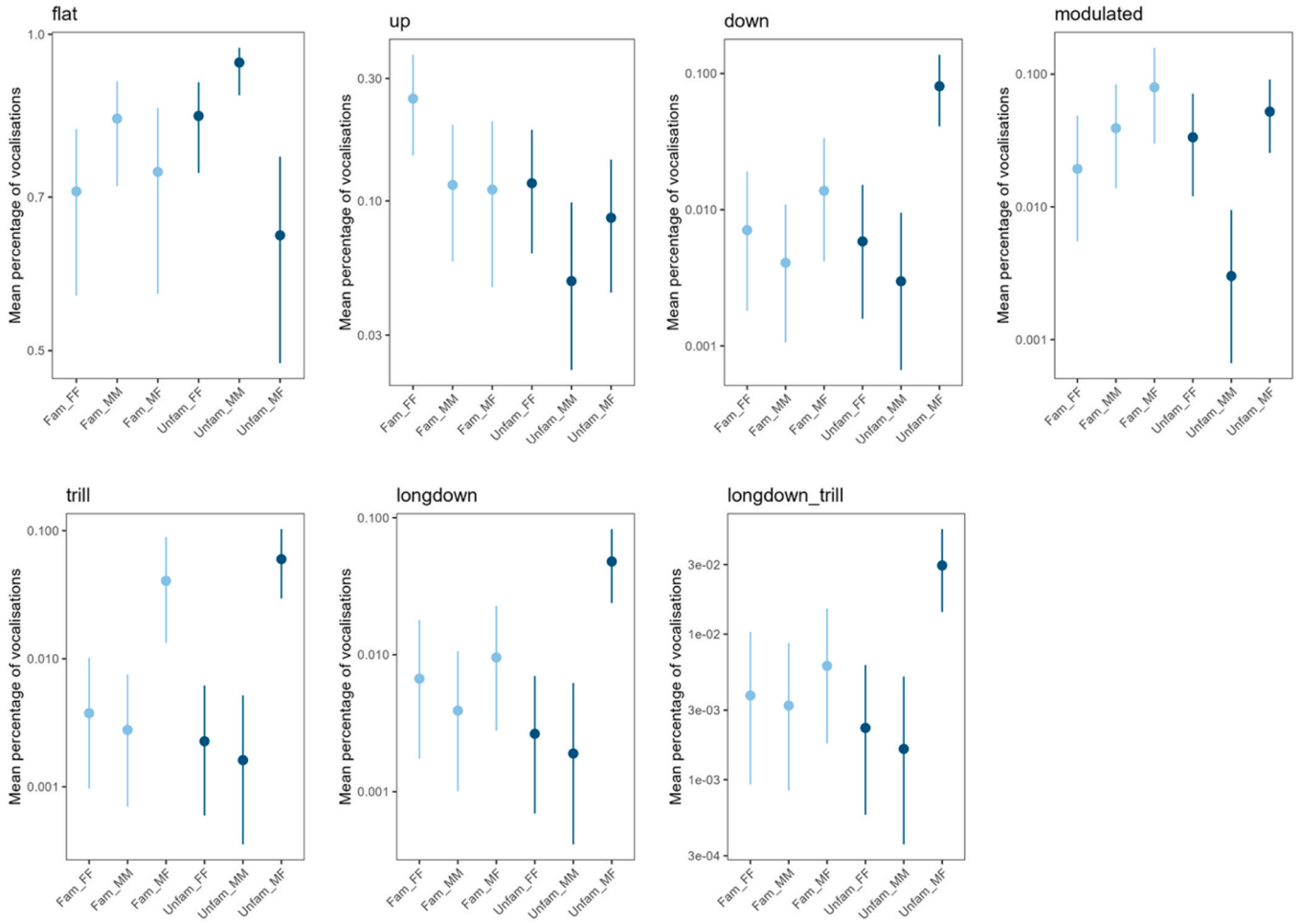


Fig. 4. The relative proportion of vocalisation types depends on social context. Fam_FF**:** familiar females; Fam_MM: familiar males; Unfam_FF: unfamiliar females; Unfam_MM: unfamiliar males; Unfam_MF: unfamiliar female and male. Solid disks represent the medians of the posterior distributions and bars represent 95 % CI of the data fitted using the Bayesian model *Percentage of vocalisations ~ Encounter type*. Model fitted using a Dirichlet distribution.

third and final minute, with a standard deviation of 4 %). As illustrated in Fig. 6, the relative proportion of the different types of vocalisations is characteristic of each social context (Bayesian model: percentage of vocalisations ~ Time * Type of vocalisation + (1 | Identity of animals). The African striped mouse therefore modulates the use of its vocal repertoire according to the type of social interaction.

3.5. Familiar males and females display fewer overlapping vocalisations

We measured the number and proportion of temporally overlapping vocalisations in each recording context. The results show that overlaps between vocalisations were rarest during encounters between familiar females and males compare to encounters between unfamiliar females and males (-3.68 % [-7.32 %; −2.03 %], Fig. 7). No differences were observed between familiar same-sex males and females encounter, nor between unfamiliar same-sex ones (see Supplementary Table 4 for all comparisons). The comparison across familiarity is not relevant here, as familiar and unfamiliar same-sex animals show differences of number of vocalisations and time spent vocalising, therefore diminishing the likelihood of observing vocal overlap (Fig. 1; supplementary Figure 2).

4. Discussion

Here we reveal how the striped mouse uses its diverse vocal repertoire according to social context, in a both quantitatively and qualitatively flexible way. The content of vocal exchanges between two striped mice differed according to whether they were familiar with each other (sisters, brothers or a paired female and male), or not (from different

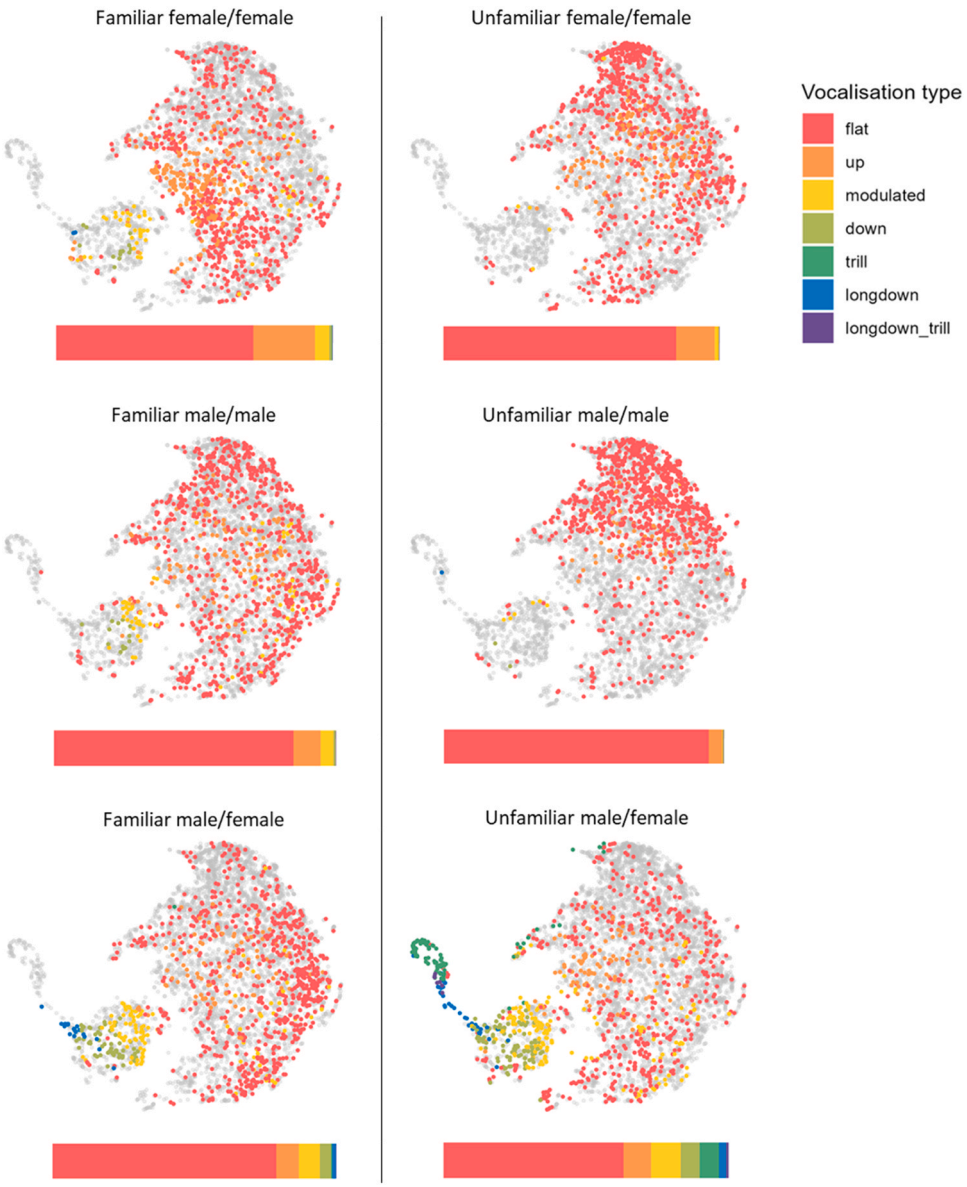


Fig. 5. The use of the vocal repertoire by the African striped mouse is context-dependent. Each panel is an acoustic space constructed using UMAP algorithm of dimension reduction applied on nine acoustic parameters extracted with Deepsqueak software. Each dot represents one vocalisation (for clarity, only 1500 vocalisations randomly selected among all vocalisations detected within an encounter type are represented). The coloured labels correspond to the vocal repertoire illustrated in Fig. 3. In each of the panels, the vocalisations recorded in the corresponding social context are represented in colour. The grey dots represent the vocalisations from other contexts. Bar charts under the UMAP representation show the distribution of vocalisations for each type of encounter. The longdown, the longdown trill, the trill, the modulated and the down vocalisations types make a cluster (including sub-clusters for each of these vocalisations types) distinct from another cluster made of flat and up vocalisations.

family groups). Although our experimental setup involved interactions between animals kept in a confined space, our results highlight the complexity of acoustic exchanges in this highly social rodent of wild origin. Together with a few other species like voles [41] and the African gerbil [61], the African striped mouse highlights the diversity of vocal exchanges within Muridae [62].

Our methodological approach allowed us to analyse vocalisations at the dyad level, providing valuable insights into social interactions. While precisely identifying the emitter remains a technical challenge due to the absence of visible indicators during vocalisation and the proximity of individuals, recent technical developments [63,64] promise to resolve this identification question [11], which will enable exploration of temporal syllable sequences and testing for syntactic rules in this species. Our study establishes a solid foundation for these future investigations and already demonstrates that African striped mice possess a complex ultrasonic vocal repertoire comprising at least seven distinct call forms. Our results reveal that these rodents control their vocal production both qualitatively and quantitatively depending on social context, notably distinguishing between group members and strangers. Communication becomes particularly intensive between unrelated male-female pairs, suggesting a crucial role in courtship.

African striped mice vocalised least during encounters between unfamiliar same-sex individuals, mainly emitting flat vocalisations. The mice appear to establish vocal contact during the first few minutes of the encounter, with a marked increase in the number of vocalisations emitted, before rapidly decreasing it. In the field, encounters between two African striped mice from different groups results in short lasting agonistic interactions, after which the animals rapidly move away from each other [54,65]. Our results are congruent with findings in female house mice *Mus musculus*, where two unfamiliar females vocalised less

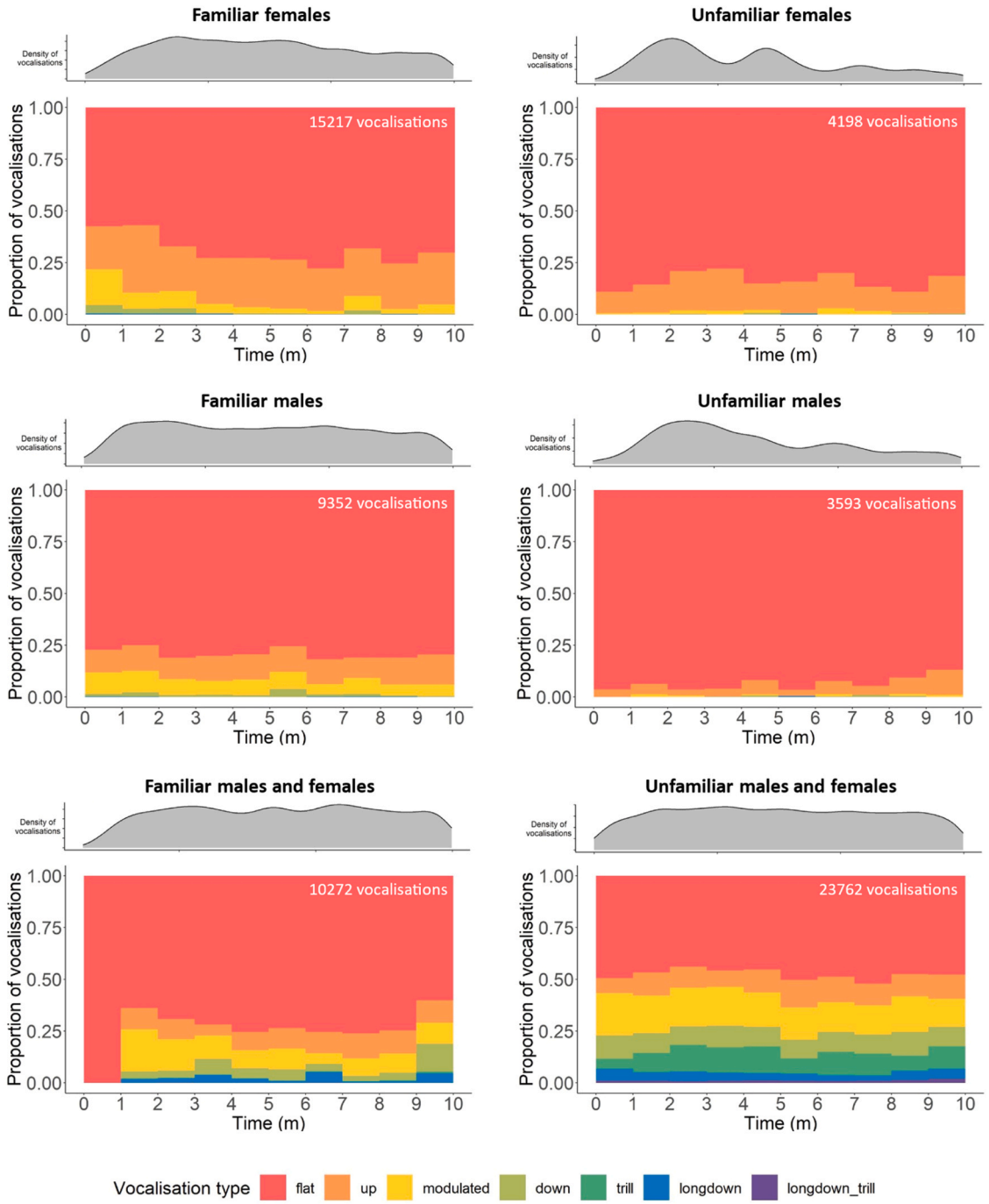


Fig. 6. Temporal dynamic of vocalisations as a function of social context. The grey curves represent the evolution of the number of vocalisations per minute over the ten minutes of recording. Coloured bar graphs represent the average percentage of each type of vocalisations.

during the first night of contact compared to the second night [37]. In such contexts, the olfactory channel may become rapidly dominant over the acoustic channel [66].

In encounters of unfamiliar striped mice of opposite sexes, a bimodal pattern emerged: either very low or very high vocal activity. This bimodality may be attributed to variations in sexual motivation. Male house mice, for instance, produce more vocalisations when presented with receptive females [38], and high USVs production correlates with sexual behaviour in spiny mice [42]. In striped mice, the rate of vocal production remained high throughout the encounter, and the vocalisations were diverse, using particularly modulated vocalisations and trills. The oestrus cycle in striped mice spans 11 days, with five days in oestrus [67], potentially explaining the bimodal distribution, as approximately 45 % of females might be in oestrus by chance. Additionally, individuals brought into contact may or may not be attracted to each other. In our laboratory breeding facilities, some mouse pairs reproduce easily, while others do not, possibly due to a lack of mutual attraction. No bimodal pattern was observed in same-sex encounters or between familiar individuals.

When familiar individuals reunited after separation, their vocal production increased rapidly and remained high throughout the encounter. This mirrors observation in the wild, when African striped mice emerge from the nest at first sunlight and interact for about 30 minutes [54,55]. The vocal repertoire in these encounters was diverse and similar between females and between males. The only minor difference was the “up” vocalisation that was more present during

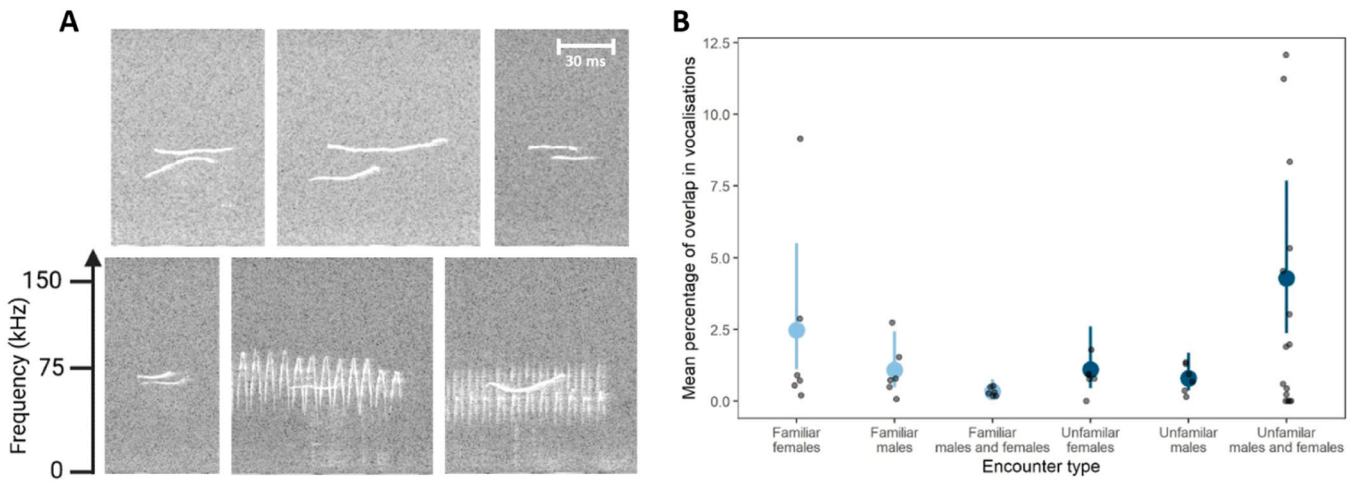


Fig. 7. Vocal overlapping during mice encounters. **A.** Examples of overlapping vocalisations. **B.** Proportion of overlapping vocalisations for each encounter type. The highest proportion of overlap is observed in encounters between an unfamiliar female and an unfamiliar male. Solid disks represent the medians of the posterior distributions and bars represent 95 % CI of the data fitted using the Bayesian model *Percentage of overlapping vocalisations* ~ *Encounter type* (hurdle gamma distribution).

encounters between familiar females. The richest vocal repertoire was observed in familiar female-male encounters, with a high production of modulated vocalisations. Notably, trills were nearly absent, contrasting with their prevalence in unfamiliar female-male interactions, where the repertoire was most diverse. This suggests that different information is communicated in these contexts.

Overall, these results demonstrate that African striped mice possess the ability to discriminate between the sexes and between familiar and unfamiliar conspecifics. Behavioural studies in the field already showed that striped mice can recognize individuals, showing a preference for specific group members with which they interact more upon their return after an experimental removal for one day [55]. In rodents, the olfactory channel also allows the identification of sex and status [68]. While the similarity of vocal repertoire used across same-sex encounters suggests the absence of sexual vocal differences, individual recognition via vocal signatures, as described for prairie voles [69], is still a possibility.

In our study, encounters between familiar female and male were at the same time encounters between brothers and sisters, confounding familiarity and relatedness [70]. Our experimental setup mimicked natural conditions, where members of one group are both familiar with each other and close kin [52]. Apart from the breeding male, no outsider ever joins a family group. Additionally, all mice in our laboratory share a strong genetic background, descending from the same South African population. This genetic proximity does not diminish the generalizability of our results to unrelated individuals, as a study on house mice [71] has shown that familiar unrelated individuals and familiar related individuals display the same social behaviours towards each other.

Understanding how exactly African striped mice use USVs for social communication requires further studies where one can identify individual vocal contributions during interactions. The present work already revealed that the vocal repertoire of the African striped mouse forms an acoustic continuum, with the exception of the trill, which has distinct acoustic features. This acoustic gradation could encode dynamic information, related to short-term fluctuations in the sender's physiological and psychological states [2,72,73]. Graded vocal signals are common in social species where individuals exchange subtle dynamic information [74]. For example, the five most common tonal vocalisations of the bonobo *Pan paniscus* form an acoustic continuum reflecting the sender's arousal level [2]. In the African striped mouse, the up, modulated and down vocalisations define an acoustic continuum around the flat vocalisation, potentially enabling mice to encode dynamic information (level of arousal and/or valence). This is supported by the context-dependent use of these vocalisations. The use of up, modulated and down vocalisations in female-male encounter contexts may reflect a high arousal level. Moreover, these modulated vocalisations may allow animals to produce more complex, less redundant patterns, increasing the likelihood that these vocalisations contain more information (cf. Shannon on the Mathematical Theory of Communication [75]). This hypothesis is reinforced by the fact that most trills are recorded in the female-male contexts - particularly when the individuals are unfamiliar. Trills may therefore play a role in courtship, potentially indicating the quality of the animals. Therefore, it would be valuable to determine whether both males and females produce trills and to correlate their production with body condition and fitness.

African striped mice adjust the timing of their vocalisations based on their interaction partner, generally avoiding overlap with a neighbour's vocalisations. The incidence of overlapping declines from 5 % in unfamiliar male/female pairs to less than 1 % in familiar male/female pairs. Avoiding overlap may facilitate information exchange. This seems to be the case in great apes [76] and cetaceans [77,78]. In birds, overlapping often occurs during territorial interactions as a marker of aggression [79]. Here we described for the first time such control over interactive timing in a murid rodent, suggesting the possibility of "intentionality" ("capacity to act with, and understand, communicative intentions" [80–82]) and rhythm adjustments [83].

Since our study has been limited to dyadic interactions, the vocal repertoire presented here may not be exhaustive. In interactions involving more individuals, especially when of different ages and statuses, other vocalisations may be identified. In this respect, the interactions between pups and adults of different classes (breeders and helpers) deserves to be explored. Furthermore, laboratory rodents are known to vocalise in frequencies audible to humans when handled or when in an agonistic context (squeaks, [84]). We have had occasion to hear such vocalisations in African striped mice when handling them [85], but not when the animals were interacting in their cages, nor during our field observations. It could be that the significant risk of predation faced by striped mice in their natural environment causes them to avoid using audible sounds.

African striped mice display a diverse ultrasound communication system, in line with the social complexity hypothesis [86]. These animals demonstrate the ability to optimise communication efficiency by controlling the emission of USVs based on the social context, and by adjusting their timing to avoid overlap when interacting with familiar individuals. Additionally, these mice adapt their repertoire use between group members and strangers in their ultrasound communication, with the most intensive interactions occurring between unrelated

male-female pairs. By comparing acoustic communication between rodents and taking advantage of the unique social structure of striped mice, future research can certainly deepen our understanding of how vocal communication is shaped by social complexity.

CRediT authorship contribution statement

de Witasse Thézy Aude: Validation, Investigation, Formal analysis, Data curation. **Perrier Léo:** Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Levréro Florence:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Mathevon Nicolas:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Greenfield Michael D.:** Writing – review & editing, Supervision. **Schradin Carsten:** Writing – review & editing, Resources. **Pradeau Aurélie:** Resources.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.bbr.2025.115575.

Data Availability

There is a link in the manuscript, and data will be available on GitHub in case of publication.

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