

UNIVERSIDAD DE COSTA RICA
SISTEMA DE ESTUDIOS DE POSGRADO

PATRONES DE VOCALIZACIÓN DURANTE INTERACCIONES SOCIALES DE
RHYNCHONYCTERIS NASO (CHIROPTERA: EMBALLONURIDAE) EN COSTA
RICA.

Tesis sometida a la consideración de la Comisión del Programa de Estudios
de Posgrado en Biología para optar al grado y título de Maestría Académica
en Biología

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DEDICATORIA

Para Eva.

Para vos, todo.

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Infinitas gracias a Eli, por escoger siempre la gentileza, el optimismo y la confianza, como sus mejores herramientas para enseñar, y mostrarme que se puede sonreír aún bajo el más recio de los aguaceros tropicales.

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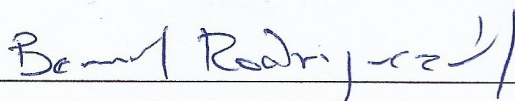
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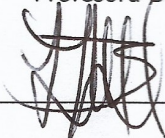
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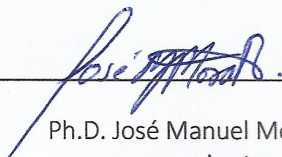


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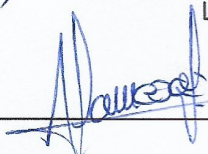
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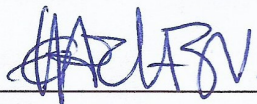
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TABLA DE CONTENIDOS

DEDICATORIA Y AGRADECIMIENTOS.....	ii
HOJA DE APROBACIÓN.....	iii
RESUMEN.....	v
ABSTRACT	vi
LISTA DE FIGURAS	viii
INTRODUCTION.....	1
METHODS	4
Study site	4
Video and sound recording.....	4
Acoustic analysis	6
RESULTS	9
Colony composition	9
Vocalization types.....	9
Statistical analyses	32
Behavioural interactions and associated vocalizations	38
1) Perching:	40
2) Agonistic encounters:	42
3) Mother-pup interactions:	44
4) Courtship:	47
DISCUSSION	51
Vocalization repertoire of R. naso.....	51
Link between vocalizations and behavior	53
R. naso and S. bilineata: comparing elements of the vocal repertoire	58
REFERENCES.....	62

RESUMEN

Las señales vocales en el estudio de la comunicación animal tienen un potencial para transferir información que puede ser evaluado a través de sus características físicas (Kazial y Masters 2004), las cuales convergen en términos de forma y función a través de distintos taxa, según las llamadas reglas de motivación-estructura (MSR) propuestas por Morton (1977). Los murciélagos poseen amplios repertorios vocales de llamadas de ecolocalización, y proveen excelentes oportunidades para estudiar la comunicación y el comportamiento social dadas su diversa taxonomía e historia natural. Una de las documentaciones más completas y llamativas del comportamiento y organización social en conexión con las vocalizaciones en murciélagos se halla en *Saccopteryx bilineata* (Voigt *et al.* 2008). Su pariente, *Rhynchonycteris naso*, posee una organización social distinta y es conocido por sus hábitos de refugio más discretos. El objetivo principal de este estudio fue evaluar el repertorio de comunicación vocal de *R. naso* en términos de su diversidad, uso en distintos contextos de comportamiento, y los factores ecológicos o sociales subyacentes que contribuyeron a su evolución. Como hipótesis, planteé que encontraría diferencias estructurales entre sus llamadas sociales y su ecolocalización, que estas variarían según el contexto de comportamiento, y que las diferencias en repertorio encontradas entre *R. naso* y *S. bilineata* estarían relacionadas con su distinta organización y comportamiento social.

Entre marzo y setiembre de 2006, observé el comportamiento nocturno de una colonia de *R. naso* por 40 noches. Obtuve grabaciones de video y registré la presencia e interacciones entre los miembros del grupo. También grabé las vocalizaciones emitidas por los murciélagos en el refugio con una grabadora prototipo conectada a una computadora personal, que permitía digitalizar los audios y escucharlos en tiempo real. Establecí *a priori* cuatro categorías de comportamiento para el análisis: 1) Individuos perchando, 2) Encuentros agonísticos, 3) Interacciones madre-cría y 4) Cortejo, y seleccioné las secuencias de mejor calidad para el estudio. Categoricé visualmente las llamadas registradas durante las interacciones sociales, agrupando distintos tipos según estudios previos en murciélagos (Behr y Helversen 2004, Bohn *et al.* 2008; Kanwal *et al.* 1994; Kroodsmá 1977) y mis propias contribuciones cuando los datos así lo requerían. Posteriormente, contrasté las categorías de llamadas encontradas en mis grabaciones con resultados publicados en la literatura siguiendo parcialmente los resultados de Behr y Helversen (2004) para *S. bilineata*, a fin de facilitar la comparación entre las especies.

A través del estudio, encontré un total de 15 categorías y 30 sub-categorías de vocalizaciones distintas empleadas por *R. naso* durante sus interacciones sociales. Un tipo de llamadas similares a la ecolocalización fue encontrado con una abundancia abrumadoramente mayor que el resto en todos los contextos de comportamiento. Asimismo, aporté la primera descripción de las llamadas de cortejo y las llamadas de aislamiento de las crías de esta especie. Las otras llamadas encontradas muestran amplia diversidad espectral, con algunas sílabas utilizadas en múltiples contextos.

Esta es la primera descripción del repertorio de comunicación vocal de *R. naso*, y revela una mayor colección de llamadas sociales que la antes esperada para la especie. Determiné ciertas tendencias de asociación vocalización-comportamiento en mis observaciones; en definitiva, algunas llamadas parecen servir distintas funciones sociales dependiendo del contexto en que son utilizadas. Este primer estudio no permitió asignar un contexto de comportamiento específico a cada una de las vocalizaciones encontradas. El repertorio de *R. naso* comparte similitudes estructurales con *S. bilineata*, lo cual sugiere que estos rasgos de su comunicación estaban presentes en su ancestro común. Las diferencias en organización social y hábitos de refugio entre ambas especies pueden haber jugado un papel en la evolución de su comunicación y sistemas sociales. Estudios experimentales posteriores que puedan dar seguimiento a mis hallazgos acerca de la dinámica social y la comunicación vocal de *R. naso* arrojarán más luz sobre los factores que influyen en estos aspectos del comportamiento social en la naturaleza.

ABSTRACT

Vocal signals, as an element to study animal communication, have potential for information transfer that can be assessed through their measurable physical characteristics (Kazial & Masters 2004), which converge in form and function across taxa, according to motivation-structural rules (MSR) (Morton 1977). Bats are known for their rich vocal repertoires in their complex echolocation systems and provide excellent opportunities for studying communication and social behavior given their diverse taxonomy and natural histories. *Saccopteryx bilineata* offers one of the most spectacular and comprehensive such explorations of social behavior and organization linked to vocalizations (review Voigt *et al.* 2008) in bats. The related *Rhynchonycteris naso* exhibits a different social organization and is known to lack conspicuous displays or calling behaviors. The main aim of this study was to assess the vocal communication repertoire of *R. naso* in terms of its repertoire diversity, usage in specific behavioral contexts, and the underlying ecological or social factors contributing to its evolution. I hypothesized I would find structural differences between their social vocalizations and echolocation calls, that they would vary according to varying behavioral contexts, and that the differences in repertoire found between *R. naso* and *S. bilineata* are related to differences in their social organization and behavior.

From March to September 2006, I conducted nighttime behavioral observations in a colony of *R. naso* for a total of 40 nights (17:00 to 06:00). I surveyed the colony with a digital video camera with night vision, recording arrivals, departures, and interactions among group members. I also conducted simultaneous sound recordings of the bats' vocalizations at the roost with a custom-made recorder coupled with a laptop computer, which allowed both for the digitization of the soundbites and for listening to them in real time. I established four behavioral categories *a priori* for analysis: 1) Perching individuals, 2) Agonistic encounters, 3) Mother-pup interactions and 4) Courtship, selecting only high-quality sequences for the study. I visually categorized calls recorded from social interactions into distinct call types following methods documented in previous studies on bat vocalizations (Behr & Helversen 2004, Bohn *et al.* 2008; Kanwal *et al.* 1994; Kroodsmma 1977) and my own contributions when required by the data. I later contrasted the call types found in my sound recordings with published results on social calls, partially following the results of Behr and Helversen (2004) for *S. bilineata*, to facilitate comparison of similar vocal types between the species.

I found a total of 15 categories and 30 sub-categories of distinct vocalizations employed during social interactions throughout the study. One specific type I termed echolocation-like calls was found to greatly outnumber the others across all four behavioral contexts surveyed. I also describe the infant isolation and mating calls of the species for the first time. The other social calls found show great spectral diversity, and distinctly show that some syllables are used in multiple contexts.

This is the first description of the vocal communication repertoire of *R. naso*, and it reveals a richer array of social calls than was previously expected for the species. I was able to determine certain clear trends of call-behavior association based on my observations of the bats at the roost. Certainly, some common call types seem to serve different social functions depending on the context in which they are used. However, this first assessment could not assign a specific behavioral context to every vocalization category encountered. *R. naso*'s vocal repertoire shares several structural similarities with that of the well-studied *S. bilineata*, which suggests these communication traits were already present in their common ancestor. The different social organization and roosting habits of both species might have played a role in the evolution of their communication and social systems. Further experimental studies that follow up from my findings on *R. naso*'s social dynamics and vocal communication will shed more light over the factors influencing these aspects of social behavior in nature.

LISTA DE CUADROS

Table 1. Parameter values measured for echolocation-like calls found in a colony of <i>R. naso</i> during social interactions.	p. 12
Table 2. Parameter values measured for chatter calls found during social interactions in a colony of <i>R. naso</i> .	p. 13
Table 3. Parameter values measured for FM train calls found during social interactions in a colony of <i>R. naso</i> .	p. 14
Table 4. Parameter values measured for u-shaped calls found during social interactions in a colony of <i>R. naso</i> .	p. 15
Table 5. Parameter values measured from complex calls recorded in a colony of <i>R. naso</i> during social interactions.	p. 17
Table 6. Parameter values measured for syllables of crescendo calls found during social interactions in a colony of <i>R. naso</i> .	p. 19
Table 7. Parameter values measured for the three subtypes of down sweep calls found during social interactions in a colony of <i>R. naso</i> .	p. 19
Table 8. Parameter values measured for up sweep calls found during social interactions in a colony of <i>R. naso</i> .	p. 21
Table 9. Parameter values measured for the three subtypes of inverted “v” calls found during social interactions in a colony of <i>R. naso</i> .	p. 23
Table 10. Parameter values measured for two subtypes of low frequency calls found during social interactions in a colony of <i>R. naso</i> .	p. 23
Table 11. Parameter values measured for three subtypes of whines found during social interactions in a colony of <i>R. naso</i> .	p. 26
Table 12. Parameter values measured for three subtypes of ripple calls found during social interactions in a colony of <i>R. naso</i> .	p. 27
Table 13. Parameter values measured for both subtypes of trills found during social interactions in a colony of <i>R. naso</i> .	p. 29
Table 14. Parameter values measured for screech calls recorded during social interactions in a colony of <i>R. naso</i> .	p. 29
Table 15. Parameter values measured for composite calls recorded during social interactions in a colony of <i>R. naso</i> .	p. 31
Table 16. Statistical values for an assessment of model fit of the first 3 discriminant functions (df) of the DFA for all vocalization categories.	p. 32
Table 17. Absolute values of the parameters with the highest standardized canonical discriminant coefficients of the most important discriminant functions (df) for each DFA presented.	p. 35
Table 18. Frequency of occurrence of vocalization categories of <i>Rhynchonycteris naso</i> in specific behavioural contexts, grouped according to five general call types, following Pfalzer and Kusch (2003)– names in italic letters (see Discussion).	p. 39
Table 19. Main vocalization categories found during 4 behavioural contexts analyzed from a colony of <i>R. naso</i> .	p. 50

LISTA DE FIGURAS

Figure 1. Equipment setup for the video and sound recording of behavioural interactions in a colony of <i>R. naso</i> .	p. 6
Figure 2. (A) Monosyllabic call, composite syllable depicting a noisy (n) and tonal (t) component. (B) Frequency modulated (FM) train; (c) depicts the individual syllable that is repeated in a sequence. (C) Multisyllabic call composed of 3 distinct syllables (1, 2, and 3) some of which are repeated several times.	p. 7
Figure 3. Spectrograms and oscillograms of echolocation calls emitted during search flight in 10 emballonurid species in southern Central America in relation to their preferred foraging habitat. Pulse intervals are not scaled. R. n., <i>Rhynchonycteris naso</i> ; C. c., <i>Centronycteris centralis</i> ; S. l., <i>Saccopteryx leptura</i> ; S. b., <i>Saccopteryx bilineata</i> ; C. a., <i>Cyttarops alecto</i> ; C. b., <i>Cormura brevirostris</i> ; B. p., <i>Balantiopteryx plicata</i> ; P. m., <i>Peropteryx macrotis</i> ; P. k., <i>Peropteryx kappleri</i> ; D. a., <i>Diclidurus albus</i> . Taken from Jung <i>et al.</i> 2007.	p. 10
Figure 4. Subtypes of echolocation-like calls found during social interactions in a colony of <i>Rhynchonycteris naso</i> .	p. 11
Figure 5. Two chatter trains recorded from a colony of <i>R. naso</i> during social interactions.	p. 13
Figure 6. One FM train recorded from a colony of <i>R. naso</i> during social interactions.	p. 14
Fig. 7. Two examples of u-shaped calls recorded from a colony of <i>R. naso</i> during social interactions.	p. 15
Fig. 8. Complex call subtypes recorded in a colony of <i>R. naso</i> during social interactions.	p. 16
Fig. 9. Multisyllabic crescendo call recorded from a colony of <i>R. naso</i> during social interactions.	p. 18
Fig. 10. Examples of the three subtypes of down sweep calls recorded from a colony of <i>R. naso</i> during social interactions.	p. 20
Fig. 11. A typical up sweep call recorded from a colony of <i>R. naso</i> during social interactions.	p. 21
Fig. 12. Examples of the three subtypes of inverted “v” calls recorded from a colony of <i>R. naso</i> during social interactions.	p. 22
Fig. 13. Examples of the two subtypes of low frequency calls recorded from a colony of <i>R. naso</i> during social interactions.	p. 24
Fig. 14. Examples of the three subtypes of whines recorded from a colony of <i>R. naso</i> during social interactions.	p. 26
Fig. 15. Examples of the three subtypes of ripple calls recorded from a colony of <i>R. naso</i> during social interactions.	p. 27
Fig. 16. Examples of the two subtypes of trills recorded from a colony of <i>R. naso</i> during social interactions.	p. 28
Fig. 17. One screech recorded from a colony of <i>R. naso</i> during social interactions.	p. 29
Fig. 18. One composite call recorded from a colony of <i>R. naso</i> during social interactions.	p. 30
Fig. 19. Plots of the multi-dimensional signal space created by the acoustic parameters measured for all vocalization categories with more than 2 subtypes, recorded from a colony of <i>R. naso</i> during social interactions: a) echolocation-like calls, b) complex calls, c) down sweeps, d) inverted “v” calls, e) whines, and f) ripple calls.	p. 36
Fig. 20. Plots of the multi-dimensional signal space created by the acoustic	p. 37

parameters measured for two groups of vocalization categories with structural similarities, recorded from a colony of *R. naso* during social interactions: a) chatters, FM trains, echolocation-like calls and crescendos, and b) whines, trills and ripple calls.

Fig. 21. Abundance of echolocation-like vocalizations of each subtype recorded from perching bats in a colony of <i>R. naso</i> .	p. 41
Fig. 22. Abundance of non echolocation-like vocalizations of each subtype during perching interactions in a colony of <i>R. naso</i> .	p. 41
Fig. 23. Abundance of echolocation-like vocalizations of each subtype found during agonistic interactions in a colony of <i>R. naso</i> .	p. 42
Fig. 24. Abundance of non echolocation-like vocalizations of each subtype found during agonistic interactions in a colony of <i>R. naso</i> .	p. 43
Fig. 25. Relative abundance of non echolocation-like vocalizations of each subtype found during two extremes (mild vs. strong) of agonistic interactions in a colony of <i>R. naso</i> .	p. 44
Fig. 26. Abundance of echolocation-like vocalizations of each subtype found during mother-pup interactions in a colony of <i>R. naso</i> .	p. 46
Fig. 27. Abundance of non echolocation-like vocalizations of each subtype found during perching interactions in a colony of <i>R. naso</i> .	p. 46
Fig. 28. Abundance of echolocation-like vocalizations of each subtype found during courtship interactions in a colony of <i>R. naso</i> .	p. 48
Fig. 29. Abundance of non echolocation-like vocalizations of each subtype found during courtship interactions in a colony of <i>R. naso</i> .	p. 49



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INTRODUCTION

The study of animal communication requires the observation of the combined action of the different signals exchanged between the individuals involved. It is difficult to understand the role of each of these signals in isolation, whether visual, olfactory or acoustic, since their perception as a whole is key to the regulatory process of communication, in which each individual is looking to influence the other's behavior to its own benefit (Wilson 1980, Fenton 1985, Owings & Morton 1998). However, the vocal part of animal communication has been central to the study of selected vertebrate taxa including bats (Fenton 1985); it constitutes a measurable portion of the multi-signal exchange that is evident to a human observer as a source of information. One of the major challenges is to link distinct vocalizations to other behavioral variables that are needed for the understanding of communication as a whole (Owings & Morton 1998).

A vocal signal's potential for information transfer (or behavior regulation, *sensu* Owings & Morton 1998) can be quantitatively assessed through the signal's measurable physical characteristics. Thus, the vocal signal itself is shaped by natural selection favoring the most suitable combination between signal form and function, in benefit of the communicating individuals' reproductive success (Kazial & Masters 2004).

Despite different evolutionary histories, many animal sounds from different taxa converge in acoustic structure (form) and motivation (function) that their use fulfills (Morton 1977). This trend was summarized by Morton (1977) in the motivation-structural rules (MSR). Those rules propose, in essence, that in a social context birds and mammals produce low-frequency (low-pitched), broadband (harsh) sounds in "hostile" situations, while using high-frequency (high-pitched), narrowband (tonal) sounds in "friendly" or appeasing contexts.

Research on the factors mediating social behavior in birds and mammals has addressed their vocal communication and associated behaviors under the light of the MSR and other evolutionary and ecological questions (August & Anderson 1987; Janik & Slater 1997; Compton *et al.* 2001; Behr *et al.* 2006; Byers & Kroodsma 2009). Among mammals, much research on the topic has focused on primates, cetaceans and, to a lesser extent, bats (reviews in Fenton 1985, Janik & Slater 1997, Boughman & Moss 2003, Wilkinson 2003, Owings & Morton 1998). The rich vocal repertoire of bats has been investigated so far by research mostly in terms of their complex echolocation systems (e.g. Fenton 1984, Schnitzler & Kalko 2001, Denzinger *et al.* 2004). However, bats also provide excellent opportunities for studying communication and social behavior given their species richness, longevity, ample diversity of social structures and ecologies

(e.g., feeding, roosting), the gregarious habits of many species, and their high abundance in many different ecosystems (Fenton 1985; Altringham 2001; Kunz & Fenton 2003).

The main challenges associated with the study of bat communication arise from the difficulties in accessing their roosts without disturbance, the nocturnal activity patterns of most species, and the high frequency (ultrasound) of their vocalizations. All of those factors make it difficult to record their vocal behavior and associate their acoustic social signals with a given behavioral context. This, however, is essential for the inference of the social significance of their acoustic emissions (Kodric-Brown & Brown 1984). Because of the difficulty to work with bats in the field, many studies have used captive colonies, yielding a wealth of valuable results for our understanding of these topics (e.g. Porter 1979; Kanwal *et al.* 1994; Melendez *et al.* 2006; Schmidt-French *et al.* 2006; Carter 2007). However, these studies do not fully account for the environmental variables that may influence the bats' conducts, such as their roosting habits, and therefore direct field observations remain of particular importance for the study of vocal communication. As an example, perhaps one of the most spectacular and comprehensive explorations of the many aspects of social behavior and organization of a bat species associated with elaborate vocalizations and displays is the white-lined bat *Saccopteryx bilineata*. All data have been obtained entirely from free-living colonies in the field (e.g., outside of a laboratory enclosure) (review Voigt *et al.* 2008).

Other sympatric species of the Emballonurid family have received much less attention in this regard, including the proboscis bat *Rhynchonycteris naso*. This small aerial insectivore is known for its high-frequency echolocation calls (96-102 kHz) used to hunt over or next to water (Kalko 1995; Jung *et al.* 2007; pers. obs.). It forms colonies that roost in well-lit, exposed surfaces on trees, boulders or buildings, where they merge visually with their patchy-brown coloration into the background (Bradbury & Vehrencamp 1976a; Plumpton & Jones 1992). In contrast with *S. bilineata*, they do not form harems defended by a single male, but rather groups of both sexes roost together, where one male may show territoriality over the females only during their group hunting, outside of the roost (Bradbury & Vehrencamp 1976a). They have been reported to lack conspicuous displays or calling behaviors like those known for *S. bilineata*'s males, which include hovering flight displays, complex songs and fanning of odors to the harem females (Bradbury & Vehrencamp 1977). *R. naso*'s repertoire of social vocalizations has not been documented so far, nor their specific behavioral interactions studied in detail. The species' high abundance and conspicuous roosting habits make it a good candidate for conducting detailed field research aimed at shedding more light over broader questions on the environmental and social factors

that influence the evolution of vocal communication in bats. Moreover, the possibility of conducting comparative analyses of the acoustic behavior of *R. naso* and the well-studied *S. bilineata* allows evaluating how these factors have played out in these species given their different social or ecological features.

The main aim of this study was to assess the vocal communication repertoire of *Rhynchonycteris naso* in terms of its repertoire diversity, usage in specific behavioral contexts, and the underlying ecological or social factors contributing to its evolution. I hypothesized that there would be structural differences in the social vocalizations of roosting individuals and the echolocation calls of the species. I predicted that the acoustical structure of social vocalizations should be variable to enhance their function as a signal for relevant information exchange between individuals, while that of echolocation calls should be more stereotyped, enhancing the individual's perception of its physical environment and prey capture. I also hypothesized that *R. naso* would employ different social vocalizations in varying behavioral contexts, given the need to exchange distinct information contents and motivations in each case. I predicted the various vocalizations would comply with Morton's (1977) MSR in terms of the relationship between their acoustic structure and their observed/inferred social function. Finally, I hypothesized that the expected differences between the repertoires of *R. naso* and *S. bilineata* are related to differences in their social organization and behavior. I assumed that the repertoire of social calls of *R. naso* would be smaller with less elaborate signal combinations than those known for *S. bilineata*, given its simpler social organization, less pronounced courtship behavior and inconspicuous behavior while roosting.

METHODS

Study site

Behavioural observations and sound recordings were conducted from March to September 2006 in a colony of *R. naso* roosting under the thatched roof of the lodge Centro Neotropico Sarapiquis (CNS) (Costa Rica, Province Heredia, 10°24'N, 84°07'W). The site is bordered by the Sarapiquí river and a natural reserve of mature lowland wet forest (Tirimbina Rainforest Center, 350 ha). The colony was composed of six adult bats at the beginning of the study, when captures were conducted with mist nets. Of these, four adult females and one adult male were successfully captured and marked on the forearm with plastic colour split bands (A.C. Hughes Ltd., Hampton Hill, Middlesex, U.K., size XCS) for individual identification at the roost.

My personal observations of the bats at the roost coincide with those of Bradbury and Emmons (1974), who reported that daily activity tends to be minimal in *R. naso*. Moreover, the groups use the same structures nearby as roosts also during the night in between brief absence periods. Thus, I chose to conduct my behavioural observations during the nights, whenever the bats were present at their night roost and I expected them to be more active. The colony of study offered favourable conditions for conducting the research: since it occupies different points around the lobby and restaurant area of the lodge during the nights, the bats could be observed even under adverse weather conditions, and were constantly exposed to the presence of humans, thus quickly habituated to the observer. Later captures were not attempted throughout the study period to reduce disturbance. All behavioural observations were conducted from 17:00 until 06:00 for a total of 40 nights.

Video and sound recording

The individuals present at the night roost were continuously surveyed with a digital video camera (SONY Digital Handycam DCR-TRV15E, miniDV Sony, EP recording mode) with the night shot option. The camera was installed 3-7 m in front of the roosting group and connected to a recording unit (SONY Video-Walkman GV-D900E PAL) located at least 2 m away in order to change tapes (Sony mini DVs, LP:90 min) without disturbing the bats. Every arrival and departure of an individual, rearrangements of the whole group at the roost site as well as interactions among group members were recorded either with a hand held voice recorder or written in a field

notebook. I recorded the initiator of the behaviour and the recipient, and defined four behavioural categories *a priori* for analysis, described as follows. 1) Perching individuals: bats present in the roost, showing no activity other than occasional rocking and/or grooming behaviours. 2) Agonistic encounters: when one or more individuals showed an evidently aggressive behaviour towards another, like hitting the other with the folded wing with or without achieving contact, crawling or flying towards another bat and shoving it away, beating the other with the folded wing, with or without contact. 3) Mother-pup interactions: these included mother-pup reunions initiated by the solicitation of individual pups, mother-pup separations, and any behaviour in which the pup attempted to approach the mother for nursing or crawling under her wing. 4) Courtship interactions: a behaviour displayed by a male towards a female such as that described by Bradbury and Emmons (1974) as a copulation, in which he attempted to mount her.

All videos were carefully revised and only high quality sequences containing unequivocal examples of the defined behaviours were selected for analysis, in compliance with four conditions: 1) behavioural displays could be clearly assigned to one of the four behavioural categories defined, 2) video quality was good enough to allow for correct identification of individuals and their behaviours, 3) synchronized sound recordings corresponding to the video sequences could be assigned to the individuals involved in the behavioural situation, and 4) signal-to-noise ratio of these sound recordings allowed accurate measurements of the spectral characteristics of the vocalizations; that is, the signal from the bats was at least -20 dB above background noise and thus could be easily characterized.

Parallel to the videos, I recorded the bats' vocalizations at the roost with a custom-made real time recorder (PC-Tape, Animal Physiology, University of Tübingen, Germany) coupled with a laptop computer (Panasonic Toughbook CF-72; Fig. 1). The equipment was set to a sampling rate of 480 kHz and 16 bits resolution for digitization of the recordings (condenser microphone: frequency response +/- 3 dB between 30 and 120 kHz, drop in sensitivity of +/- 6 dB at frequencies below 15 kHz and above 160 kHz). This equipment allowed ultrasound recordings and simultaneous listening to the bats' vocalizations in real time using the heterodyning function, set at a frequency of 90 kHz. This function mixes the incoming signal from a set frequency range (frequency window) with lower, audible frequencies, allowing the observer to listen whenever a high-frequency signal is being detected by the equipment. This does not modify the actual features of the recorded signal and it is only used to be able to trigger the recording of the sound signal in a timely fashion. All recordings of the bats' vocalizations were made by manually

releasing the post-trigger of the recording system 6 s after the onset of a vocalization bout from the bats. The 6 s long sound sequences were read directly from the buffer system onto the hard drive of the computer. Additional recordings were made with the same settings until the vocalizations of the bats ceased. Both video and audio recordings were synchronized by manually resetting the time on the video camera and computer to be equal, at the beginning of each recording session.

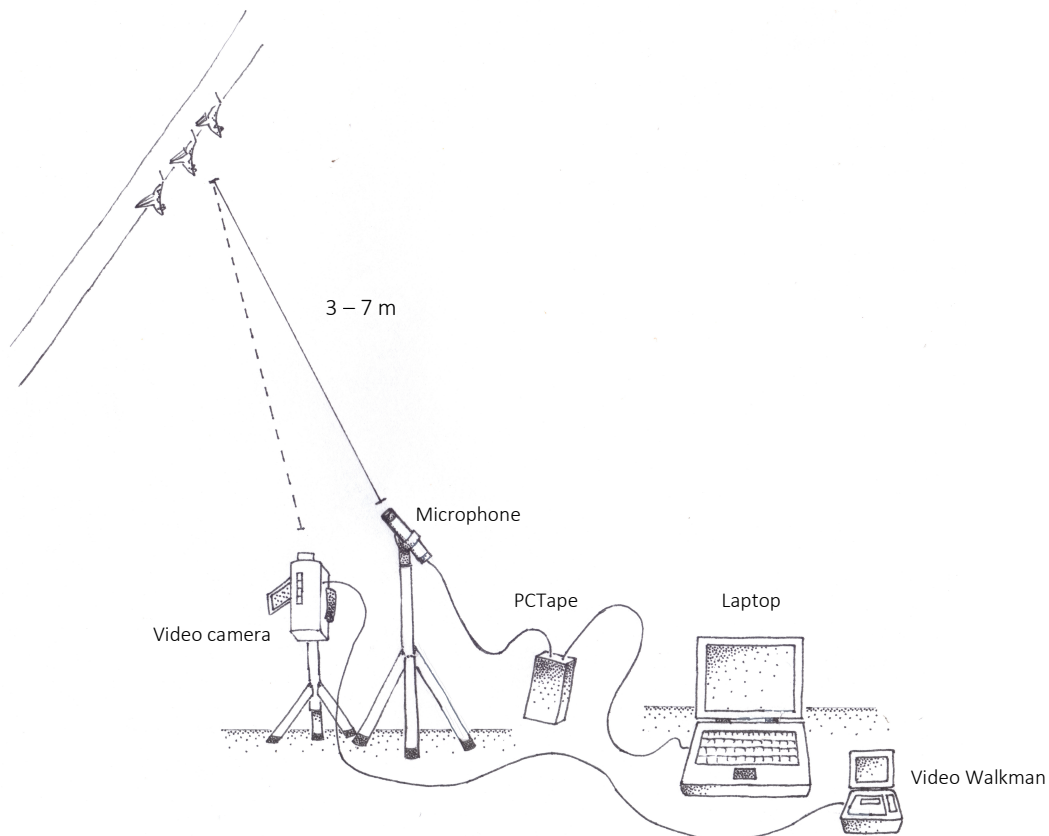


Fig. 1. Equipment setup for the video and sound recording of behavioural interactions in a colony of *R. naso*.

Acoustic analysis

All calls recorded from social interactions in the roost that were associated with one of the four predetermined behavioural classifications were categorized visually into call types for analysis, based in overall call structure and using the following terminology for their description:

Signals showing a defined fundamental frequency and harmonic structure were termed *tonal*, while signals that lacked these characteristics were called *noisy* (Behr & Helversen 2004). *Syllables* were defined as the smallest acoustic unit and equivalent to one continuous emission separated by silence (Bohn *et al.* 2008; Kanwal *et al.* 1994; Kroodsma 1977). Syllables could be *simple* when composed of a single predominant sound element (e.g., clicks, tonal or noisy), or *composite* if consisting of both noisy and tonal elements without silence in between them (Fig. 2; Behr & Helversen 2004; Kanwal *et al.* 1994). *Calls* were defined as the simplest emission of a vocalization, and could be composed of one (*monosyllabic calls*, Fig 2A & B) or more (*multisyllabic calls*) syllables (*sensu* Bohn *et al.* 2008; Fig. 2C). Finally, a group of calls emitted in a sequence was termed a call (or vocalization) *bout* (*sensu* Bohn *et al.* 2008).

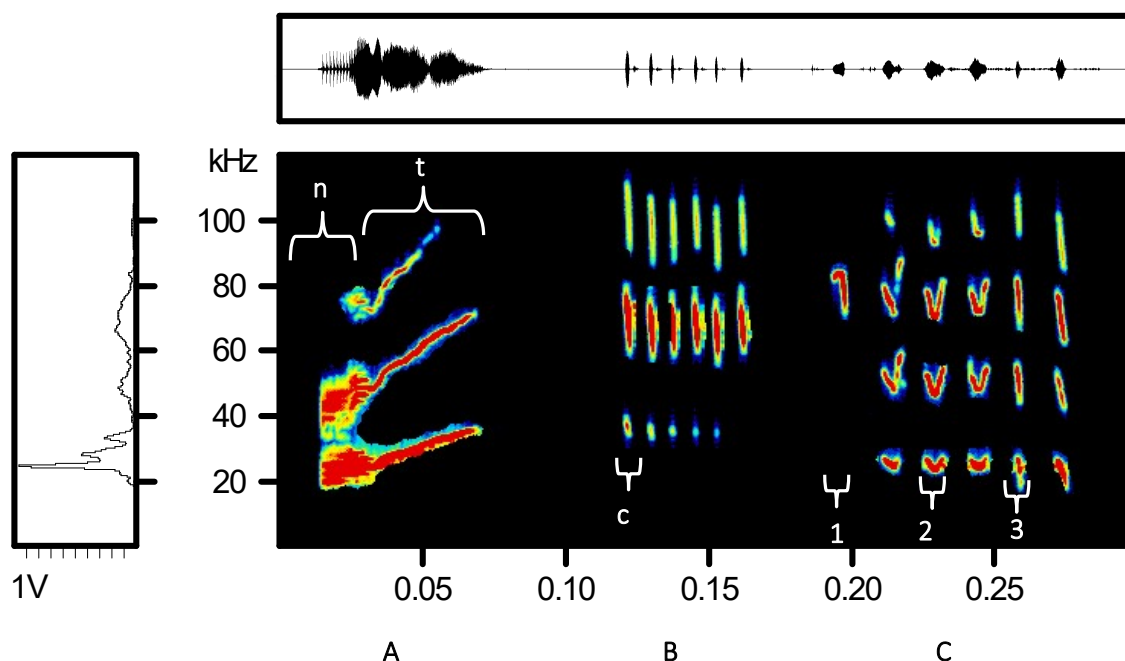


Fig. 2. (A) Monosyllabic call, composite syllable depicting a noisy (n) and tonal (t) component. (B) Frequency modulated (FM) train; (c) depicts the individual syllable that is repeated in a sequence. (C) Multisyllabic call composed of 3 distinct syllables (1, 2, and 3) some of which are repeated several times.

The sound files obtained were visualized with Avisoft SAS-Lab Pro Version 4.40 (R. Specht, Berlin, Germany) for manual parameter extraction. Spectrograms were generated using a Hamming window with a 1024 point FFT and 75% overlap (100% frame size), which resulted in a frequency resolution of 469 Hz (bandwidth 609 Hz) and a time resolution of 0.533 ms. For the quantitative characterization of these vocalization types, I used the “bound cursor” (bound to the frequency

of highest energy in the loudest harmonic) to measure two temporal parameters: syllable and call *duration* and *pulse interval*, the latter measured from the start of one syllable or call to the start of the next. Also, six spectral parameters were taken from each syllable of each call: frequency at *start*, *end*, *maximum*, *minimum*, and *peak* (point of highest energy of the whole syllable or call), and overall syllable or call *bandwidth*. Additional descriptive parameters noted were number of modulations in sinusoidal calls, and number of syllables in multisyllabic calls. In composite calls consisting of two distinct structural parts (noisy and tonal), the measurements were done separately for each part. Duration and pulse interval were measured from the oscillogram, and peak frequency was measured using both oscillogram and spectrogram information. All other parameters were taken from the spectrograms, and their values are reported for the second harmonic (except for screeches and the noisy and tonal components of composite calls), regardless of the energy distribution of the call, to standardize for comparisons among vocalization types.

I performed a discriminant function analysis (DFA) to test my classification of all the vocalization types identified visually. In this analysis, all the acoustic variables measured for all vocal types were introduced simultaneously to create a multi-dimensional signal space in which the vocalization types could be optimally separated and classified accordingly. I also performed additional DFAs to evaluate my classifications of the call subtypes identified in some vocalization categories. Finally, additional DFAs allowed assessing the acoustic separation existing among call types of similar structure in the multi-dimensional signal space created by the parameters measured from them. All statistical tests were conducted using SPSS version 11.5 (SPSS Inc., Chicago, IL, U.S.A.).

Once the call types found in my sound recordings were established, I contrasted them with published results. Echolocation search calls of *R. naso* and their time-frequency characteristics were known from previously published works by Kalko (1995) and Jung *et al.* (2007, Fig. 3). For social calls, since no previous description from this species has been published to date, I partially followed the results of Behr and Helversen (2004) for *S. bilineata*, to facilitate comparison of similar vocal types between the species.

RESULTS

Colony composition

Colony size increased from six adults (two males, four females) to 10 (occasionally 11) individuals throughout the seven-month study period with all five ringed adults remaining in the colony. One of the males did not always return to the roost during the night, while the other one was very frequently perching together with the females throughout the entire study period. Two of the females gave birth to one pup each within a week of each other, at the end of March 2006. They had a second parturition later that year, in the same order as before, in August. The other two females gave birth to their pups in the second and third week of June, respectively. The pups were volant at approximately three weeks of age, and were not seen nursing anymore during the nights as soon as six to seven weeks after birth.

Vocalization types

I analysed vocalisations emitted by non-volant bats at the roost site, hence suggesting their use in a social context. I found a total of 15 vocalization categories, which I first characterized structurally by measuring their temporal and spectral parameters, and named them according to their structure. Unless otherwise mentioned in each case, the average frequencies reported are for the second harmonic, regardless of the energy distribution in the calls.

1) *Echolocation-like (ec-like) calls*- The first category comprises all vocalizations composed of signals that resemble the species' echolocation search calls (Bradbury & Vehrencamp 1976, Kalko 1995, Jung *et al.* 2007). The echolocation signals of *R. naso* are high-frequency signals (95-102 kHz) that start with a slightly upward modulated or straight, shallow QCF component (quasi-constant frequency, signal sweep rate $<400 \text{ kHz ms}^{-1}$, *sensu* Schnitzler & Kalko (2001)), mostly – but not always – followed by a downward FM (frequency-modulated) sweep of variable bandwidth ($>7 \text{ kHz}$, Jung *et al.* 2007, Fig. 3).

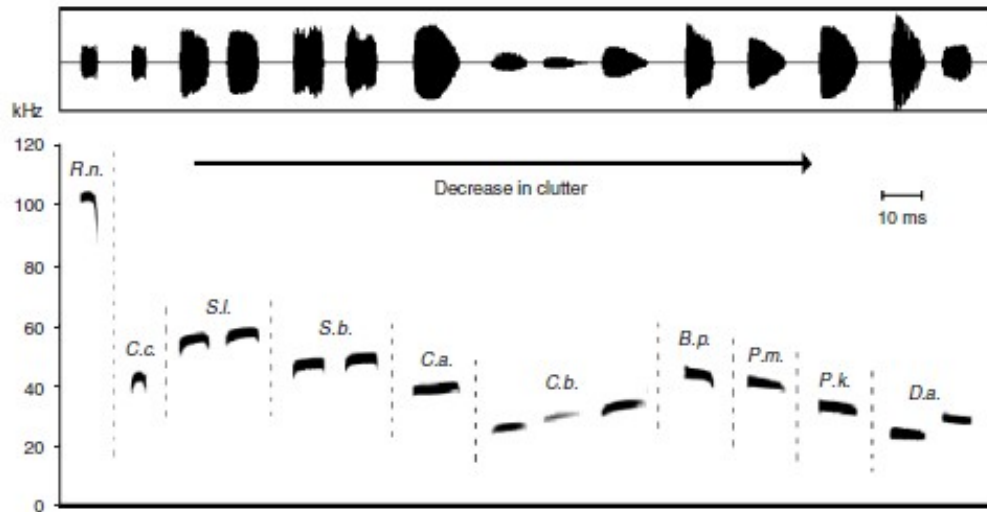


Fig. 3. Spectrograms and oscillograms of echolocation calls emitted during search flight in 10 emballonurid species in southern Central America in relation to their preferred foraging habitat. Pulse intervals are not scaled. R. n., *Rhynchonycteris naso*; C. c., *Centronycteris centralis*; S. l., *Saccopteryx leptura*; S. b., *Saccopteryx bilineata*; C. a., *Cyttarops alecto*; C. b., *Cormura brevirostris*; B. p., *Balantiopteryx plicata*; P. m., *Peropteryx macrotis*; P. k., *Peropteryx kappleri*; D. a., *Diclidurus albus*. Taken from Jung *et al.* 2007.

I identified five subtypes of echolocation-like calls (Fig. 4) that follow this general signal design: a shallow QCF component, in most cases followed by a terminal FM sweep. The subtypes differ in the presence/absence of the FM sweep and the slight modulation observed in the QCF component, as described for each case below. The energy of the ec-like calls was typically concentrated in the 2nd harmonic, though on some call subtypes was occasionally shifted to the 1st harmonic by the bats. I discard this phenomenon to be due to a recording bias caused by a combination of high frequency-calls and the directionality of the bat and the microphone, since the microphone was set to record from a fixed position during each session, allowing many on-axis recordings of the bats' vocalizations. Moreover, comparison between calls recorded before and after the first harmonic-calls make it highly likely that the changes in the distribution of the energy in the calls were attributable to the vocalizing bat(s). As has been noted in other similar studies (Behr & Helversen 2004; Knörnschild 2009) changes in the distribution of energy within or between different harmonics of a call are not caused by the movement of the bat's head, but are part of the call's intrinsic potential variation and are therefore a product of the animal's vocal tract.

Subtype a- Calls of this subtype consist of a pure shallow modulated (QCF) component, with a very short terminal FM sweep. Different from the similar subtype b, pulse interval is not fixed throughout a bout of these calls.

Subtype b- These calls are either pure QCF signals (as type a) or may be followed by an FM sweep. Their distinctive feature is a uniform pulse interval throughout the vocalization bout. In this call subtype, the energy is always concentrated in the 2nd harmonic.

Subtype c- These resemble the typical search phase echolocation calls of the species, with an initial shallow, straight QCF component followed by a terminal FM sweep. As other subtypes, except b, they are emitted at a variable pulse interval throughout the vocalization bout.

Subtype d- These calls resemble subtypes c and d in having a terminal FM sweep, but are distinct from all the other subtypes in having an undulating QCF component. Also, their peak frequency is lower than in other ec-like calls (Table 1).

Subtype e- These calls are characterized by their upward-modulated QCF component, which can be followed by an FM sweep of variable bandwidth.

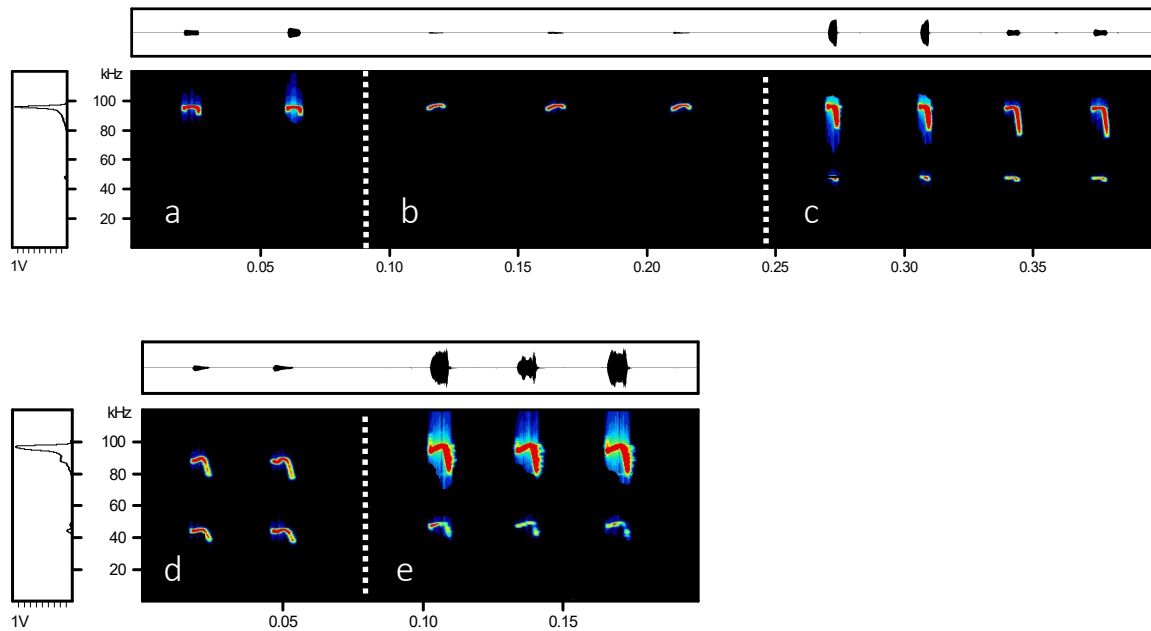


Fig. 4. Subtypes of echolocation-like calls found during social interactions in a colony of *Rhynchonycteris naso*.

Table 1. Parameter values measured for echolocation-like calls found in a colony of *R. naso* during social interactions.

Parameters	All (n = 49)			ec a (n = 10)			ec b (n = 10)			
	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	
(kHz)	freq start	94,3	2,5	6,0	95,2	0,8	0,6	95,8	1,1	1,1
	freq end	84,5	7,1	49,8	94,0	1,6	2,6	87,9	5,6	31,4
	freq peak	93,8	3,1	9,5	95,9	1,0	1,0	95,6	2,5	6,3
	freq max	95,3	2,4	5,8	96,3	1,1	1,1	96,8	0,9	0,8
	freq min	84,6	6,9	47,4	93,7	1,6	2,4	88,0	5,6	31,6
	bandwidth	10,8	6,1	37,3	2,6	1,3	1,8	8,8	6,1	37,6
(ms)	duration calls	7,3	3,4	11,48	6,9	0,5	0,2	6,7	1,1	$1,2 \times 10^{-6}$
	interval calls	77,8	40,0	1599,8	110,3	46,6	2167,5	54,1	14,2	$2,0 \times 10^{-4}$
Parameters	ec c (n = 10)			ec d (n = 9)			ed e (n = 10)			
	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	
(kHz)	freq start	94,8	3,3	11,1	92,5	2,9	8,6	93,1	1,8	3,2
	freq end	80,1	3,7	13,5	78,2	2,6	6,8	81,6	5,4	28,6
	freq peak	93,4	3,7	13,7	91,4	2,7	7,3	92,4	2,6	6,9
	freq max	95,4	3,3	10,6	93,2	3,0	8,8	94,9	1,5	2,2
	freq min	80,2	3,5	12,4	78,6	2,6	6,8	81,6	5,4	28,8
	bandwidth	15,1	2,8	8,1	14,5	3,3	10,8	13,2	4,6	21,3
(ms)	duration calls	6,5	0,8	$6,0 \times 10^{-7}$	7,2	0,7	$4,6 \times 10^{-7}$	9,1	7,3	$5,4 \times 10^{-5}$
	interval calls	60,1	25,9	1000	70,8	10,3	$1,0 \times 10^{-4}$	92,8	54,4	$3,0 \times 10^{-3}$

2) **Chatter**- Individual chatters resemble ec-like vocalizations subtype *e* for their upward-modulated start (Fig. 5). However, in contrast to these, - which are also emitted in sequences -, chatter calls are emitted in trains of up to seven, with regular pulse intervals within a train, shorter than those between consecutive ones (Table 2). As in ec-like calls, the main energy is typically in the 2nd harmonic, and is shifted to the 1st on occasion. Bandwidth of the calls may vary within the same train. Usually more than two chatter units are emitted at a time, and they may appear as transition calls to trills (vocalization category 13).

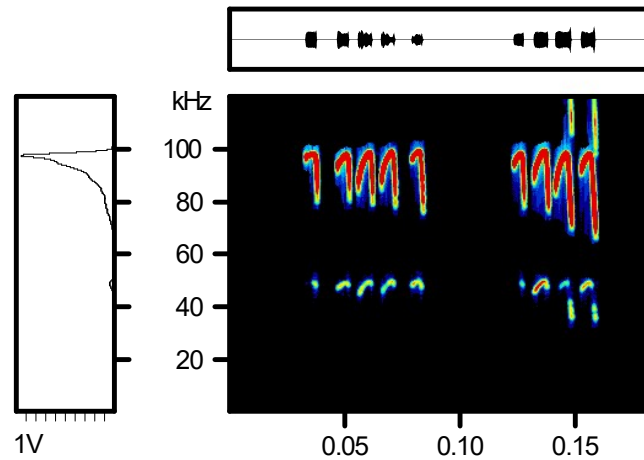


Fig. 5. Two chatter trains recorded from a colony of *R. naso* during social interactions.

Table 2. Parameter values measured for chatter calls found during social interactions in a colony of *R. naso*.

n=10	Parameter	Average	Std. Dev.	Variance
(kHz)	freq start	92,9	2,4	5,6
	freq end	77,4	6,4	40,7
	freq peak	90,5	6,3	39,9
	freq max	97,6	1,5	2,2
	freq min	20,3	5,6	31,3
	bandwidth	77,5	6,6	43,1
(ms)	duration call	6,0	0,9	870,2
	interval call	10,9	1,8	1767,2
	duration group	40,1	4,0	3990,6
	interval group	35,7	3,5	3528,3

3) FM trains- Downward-modulated, pure FM sweeps (no QCF component) of very short duration (Table 3), tightly emitted in trains (4-11 calls) with short pulse intervals between them (Fig. 6). FM trains are usually immediately preceded (and followed) by ec-like calls (subtype c), and in contrast to chatters, they are emitted singly and not consecutively.

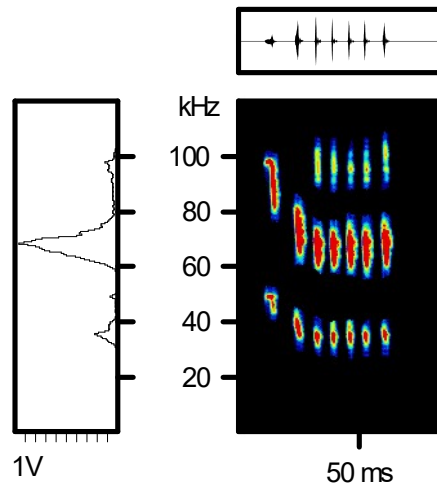


Fig. 6. One FM train recorded from a colony of *R. naso* during social interactions.

Table 3. Parameter values measured for FM train calls found during social interactions in a colony of *R. naso*.

n=10	Parameters	Average	Std. Dev.	Variance
(kHz)	freq start	71,6	3,6	13,1
	freq end	58,7	2,7	7,2
	freq peak	67,9	3,1	9,5
	freq max	76,3	3,5	12,0
	freq min	58,9	2,7	7,2
	bandwidth	17,5	3,7	14,0
(ms)	duration call	4,2	7,1	$5,0 \times 10^{-5}$
	interval call	15,3	24,2	1000
	duration group	100,5	152,8	23000

4) U-shaped call- As FM trains, u-shaped calls are also emitted in groups (2-8 calls) with regular pulse intervals between the individual calls (Table 4). They start with a downward modulated sweep and end in a steep upwardly modulated portion (Fig. 7). Their main energy can be in the 1st, 2nd or 3rd harmonic, and up to five harmonics can be visible in the call trains recorded. U-shaped calls also appear as syllables of complex calls subtypes *a* and *c* (vocalization category 5).

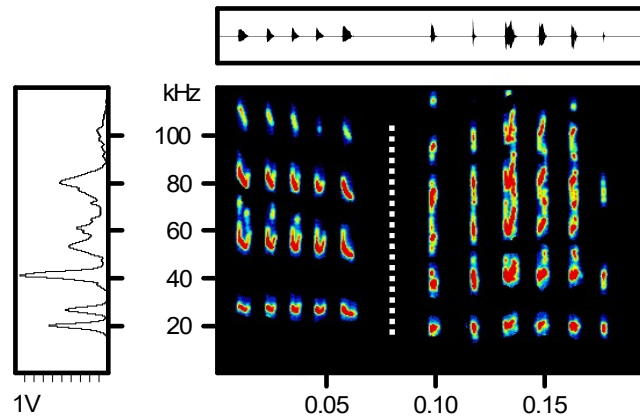


Fig. 7. Two examples of u-shaped calls recorded from a colony of *R. naso* during social interactions.

Table 4. Parameter values measured for u-shaped calls found during social interactions in a colony of *R. naso*.

n=7	Parameters	Average	Std. Dev.	Variance
(kHz)	freq start	52,7	7,9	62,3
	freq end	51,8	7,7	58,9
	freq peak	48,0	8,3	68,6
	freq max	55,6	8,4	70,1
	freq min	45,2	6,9	47,4
	bandwidth	10,4	3,7	13,9
(ms)	duration calls	5,6	1,7	$3,0 \times 10^{-6}$
	interval calls	16,3	4,7	$2,2 \times 10^{-5}$
	duration group	63,3	23,5	1,0

5) Complex call- These multisyllabic calls are composed of two parts, which are emitted in the same order: the first part is composed of either upward modulated or QCF syllables, while the second part is composed of u-shaped syllables and/or downward modulated FM-sweeps (Fig. 8). The first syllable is usually emitted only once, but may be repeated up to three times. The second part can have up to 6 syllables of either – or both – syllable type. Pulse interval between syllables is uniform within each part of the call, and the main energy may shift from the second to the first harmonic along the call (Table 5).

Subtype a- The first syllable of this call has an upward modulated component that ends in a downward sweep, which gives it the shape of an “inverted v” (vocalization category 9, subtype a). One to three of these syllables make up the first part of the call. The second part consists of 2-

6 syllables: u-shaped signals of up to four visible harmonics, sometimes interspersed with short, downward modulated FM sweeps.

Subtype b- Different from subtype *a*, this call starts with a syllable resembling ec-like calls, composed of a pure QCF signal that may have a terminal FM down sweep. U-shaped syllables are never present in the second part of the call, which is only formed by downward-modulated, short sweeps with typically three visible harmonics.

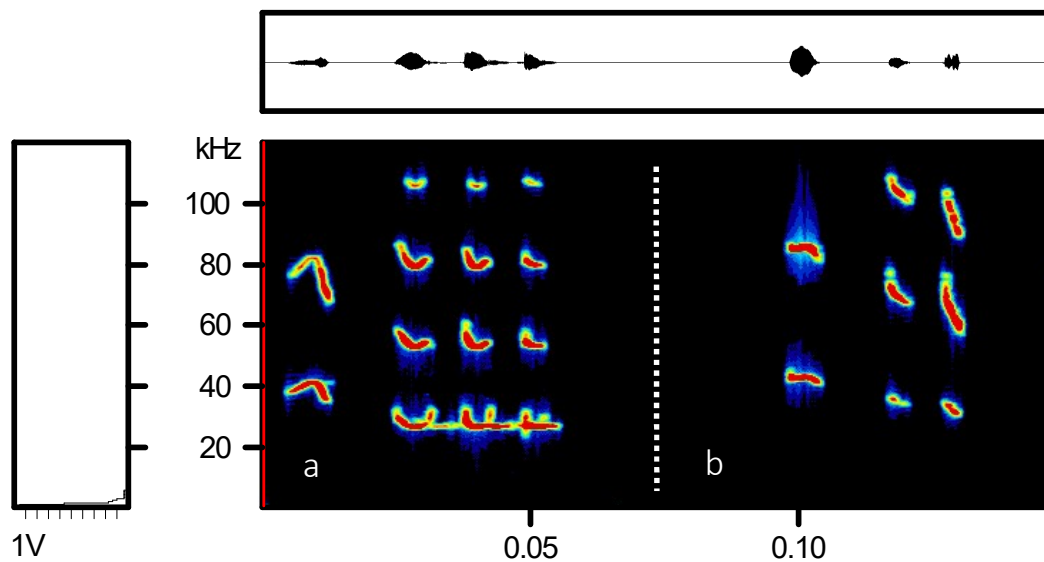


Fig. 8. Complex call subtypes recorded in a colony of *R. naso* during social interactions.

Table 5. Parameter values measured from complex calls recorded in a colony of *R. naso* during social interactions.

		COMPLEX A			1° Syllable Inverted v a (n=10)			2° Syllable u-shaped (n=10)			3° Syllable downsweep (n=7)		
Parameters		Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance			
(kHz)	freq start	80,3	9,9	97,1	59,7	5,7	32,2	61,1	6,3	40,0			
	freq end	73,9	3,9	14,9	59,5	6,9	47,0	52,6	4,8	22,9			
	freq peak	81,1	8,7	75,2	56,4	6,1	37,2	58,3	4,6	20,8			
	freq max	84,2	7,3	53,2	63,0	7,0	48,7	63,6	5,3	27,6			
	freq min	71,9	6,1	37,5	53,2	6,1	36,9	51,8	4,9	24,4			
	bandwidth	12,3	2,3	5,2	9,8	3,6	12,8	10,7	3,0	8,9			
(ms)	duration calls	7,4	2,0	$4,0 \times 10^{-6}$	5,3	1,0	$9,7 \times 10^{-7}$	2,7	0,6	$4,1 \times 10^{-7}$			
	interval calls	73,7	36,8	$1,4 \times 10^{-3}$	15,2	2,3	$5,4 \times 10^{-6}$	11,2	3,8	$1,4 \times 10^{-5}$			

		COMPLEX B			2° Syllable downsweep (n=10)			All (n = 47)		
Parameters		Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance
(kHz)	freq start	75,8	14,7	215	61,7	7,7	59,9	68,2	12,7	162
	freq end	69,9	7,5	56,9	51,3	8,1	65,6	62,0	11,1	123
	freq peak	77,8	13,2	175	55,8	8,5	71,9	66,4	14,3	201
	freq max	80,2	8,9	79,8	63,1	7,9	62,2	71,3	12,0	143
	freq min	67,1	11,5	132	50,3	8,0	64,4	59,3	11,7	138
	bandwidth	13,1	4,2	17,9	12,5	4,5	20,0	11,7	3,7	13,7
(ms)	duration calls	8,1	3,7	$1,3 \times 10^{-5}$	3,9	1,4	$2,0 \times 10^{-6}$	5,7	2,8	$8,0 \times 10^{-6}$
	interval calls	78,4	17,8	$3,2 \times 10^{-4}$	15,0	5,0	$2,5 \times 10^{-5}$	25,4	26,6	$7,1 \times 10^{-4}$

6) **Crescendo-** Multisyllabic call consisting of a series of slightly upward modulated, QCF syllables which start with their main energy at a lower frequency (below 20 kHz), and progress in frequency and structure until the last ones resemble echolocation pulses, containing both QCF and FM components (Fig. 9). The first low frequency syllables of the call are of two types (Table 6): very brief pulses without a defined structural shape, or longer, more defined upward modulated signals. In either case, the main energy of the first syllables is in the 1st harmonic, while subsequent syllables that resemble echolocation-like calls, have two discernible harmonics with the energy shifted to the 2nd harmonic. The total number of syllables in the call is variable (4-13), and it may occur alone or followed by other echolocation-like calls, which sometimes obscures the limits between both vocalization types. Thus, for the purposes of analysis, we arbitrarily defined that a crescendo call followed by an ec-like call bout ends with the first element whose peak frequency exceeds that of the echolocation search calls of the species (95.1 kHz).

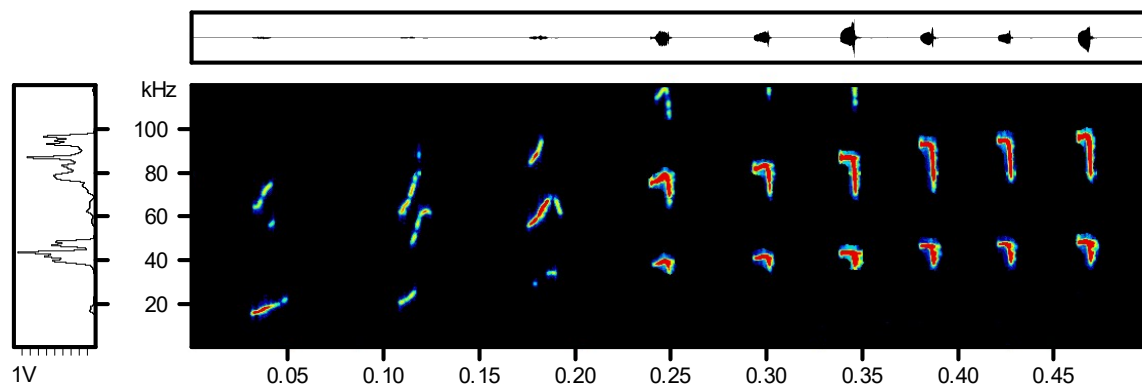


Fig. 9. Multisyllabic crescendo call recorded from a colony of *R. naso* during social interactions.

Table 6. Parameter values measured for syllables of crescendo calls found during social interactions in a colony of *R. naso*.

Parameters	All (n = 19)			Syllable upward mod. (n=9)			Syllable ec-like (n=10)			
	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	
(kHz)	freq start	76,9	20,0	400	59,3	15,3	233	92,8	2,2	4,6
	freq end	72,2	13,6	184	63,1	15,1	229	80,3	3,1	9,4
	freq peak	78,5	18,6	348	63,2	16,6	277	92,3	2,1	4,3
	freq max	81,3	17,5	307	67,1	15,9	253	94,2	2,0	4,0
	freq min	69,6	16,0	255	57,4	15,7	245	80,6	3,2	10,5
	bandwidth	10,7	4,3	18,4	8,0	3,7	14,0	13,2	3,2	10,1
(ms)	duration syll.	9,0	2,7	$7,1 \times 10^{-6}$	11,0	2,4	$5,8 \times 10^{-6}$	7,2	1,3	$1,7 \times 10^{-6}$
	interval syll.	57,7	17,5	$3,1 \times 10^{-4}$	66,3	19,9	$4,0 \times 10^{-4}$	49,9	10,8	$1,2 \times 10^{-4}$

Table 7. Parameter values measured for the three subtypes of down sweep calls found during social interactions in a colony of *R. naso*.

Parameters	All (n = 26)			down a (n = 10)			down b (n = 10)			down c (n = 6)			
	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	
(kHz)	freq start	83,4	10,9	118	76,0	12,0	145	92,0	5,4	29,3	81,7	3,7	13,9
	freq end	67,9	12,3	151	57,0	11,9	141	78,0	5,7	32,9	69,1	1,3	1,7
	freq peak	78,2	13,0	170	66,6	12,6	158	88,6	6,1	37,0	80,2	2,8	8,1
	freq max	84,5	11,2	126	76,9	12,6	158	93,3	5,7	32,3	82,5	3,2	10,1
	freq min	67,6	12,0	143	56,7	11,0	120	77,6	5,6	31,8	69,2	1,2	1,5
	bandwidth	16,9	5,1	26,1	20,2	5,5	30,1	15,7	4,1	16,8	13,3	2,4	5,8
(ms)	duration call	3,6	2,1	$4,2 \times 10^{-6}$	3,4	1,3	$1,6 \times 10^{-6}$	2,1	0,3	$1,2 \times 10^{-7}$	6,6	1,8	$3,1 \times 10^{-6}$
	interval call	47,7	27,3	$7,4 \times 10^{-4}$	---	---	---	31,5	7,6	$5,8 \times 10^{-5}$	74,9	26,8	$7,1 \times 10^{-4}$

7) Down sweep- Calls are distinctly downward modulated FM sweeps (Fig. 10), that may appear singly or in groups, usually interspersed with other vocalization types. Three subtypes are distinguished:

Subtype a- These are individual elements of an FM train that are typically emitted singly or in groups of up to 4 calls. These pure FM sweeps have a very short duration (Table 7), a steep downward modulation and a larger bandwidth (20.2 ± 5.5 kHz; N=10) than the other two call types in this category.

Subtype b- Also composed only of an FM downward sweep; these have a shorter duration and a narrower bandwidth (15.7 ± 4.1 kHz; N=10) than down sweeps subtype *a*, as well as a higher peak frequency (Table 7). They may appear singly or in groups.

Subtype c- These downward sweeps have a slower modulation rate than the previous types, with the main energy in the 1st harmonic. The calls are slightly longer in duration than subtypes *a* and *b* (Table 7), and are the only type of down sweep that typically appears in a sequence.

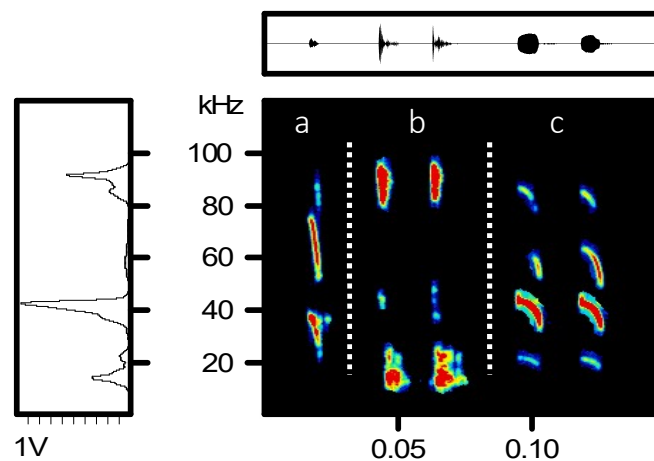


Fig. 10. Examples of the three subtypes of down sweep calls recorded from a colony of *R. naso* during social interactions.

8) Up sweep- Calls consisting of an upward-modulated FM component, that can also be found as one of the transition syllables between the low and high frequency ends of a crescendo. However, not all crescendos have these elements, and when they do, they have a shorter average duration and lower peak frequency (Tables 6 and 8). This vocalization category represents the cases when these calls appear either singly or in groups of up to three, not as part of a crescendo (Fig. 11).

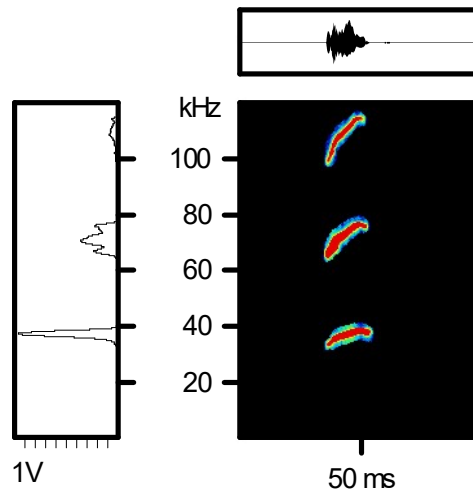


Fig. 11. A typical up sweep call recorded from a colony of *R. naso* during social interactions.

Table 8. Parameter values measured for up sweep calls found during social interactions in a colony of *R. naso*.

n=10	Parameters	Average	Std. Dev.	Variance
	freq start	64,5	10,0	100
	freq end	75,5	8,2	66,8
(kHz)	freq peak	70,8	8,1	66,0
	freq max	76,4	8,6	74,6
	freq min	63,0	8,7	75,0
	bandwidth	13,3	2,7	7,2
(s)	duration calls	18,3	9,5	$8,95 \times 10^{-5}$
	interval calls	114,0	42,0	$1,8 \times 10^{-3}$

9) Inverted “v”- Hook-like calls composed of upward and downward modulated FM sweeps joined by a sharp inflection point in the middle of the call (Fig. 12). Peak frequency differs in the three subtypes identified:

Subtype a- The signal is modulated upwards from 74.0 ± 4.0 kHz (N=6) on average to a maximum below 85 kHz, and after a sharp inflection sweeps down to a variable end frequency of 70.2 ± 6.2 kHz (N=6) on average (Table 9). The main energy may be concentrated in both 1st and 2nd harmonics. This element is the first part of a complex call, but it has been granted an own category because it also occurs individually.

Subtype b- The inflection point, or frequency maxima, of these hook-shaped calls is similar to subtype *a* (Table 9) but differs in being shallower with similar bandwidth between its start and end FM components.

Subtype c- These calls are similar in structure to subtype *a*, but their FM portions have a smaller bandwidth and their peak frequencies are much higher (Table 9). However, it was only found to occur once during the sequences analysed.

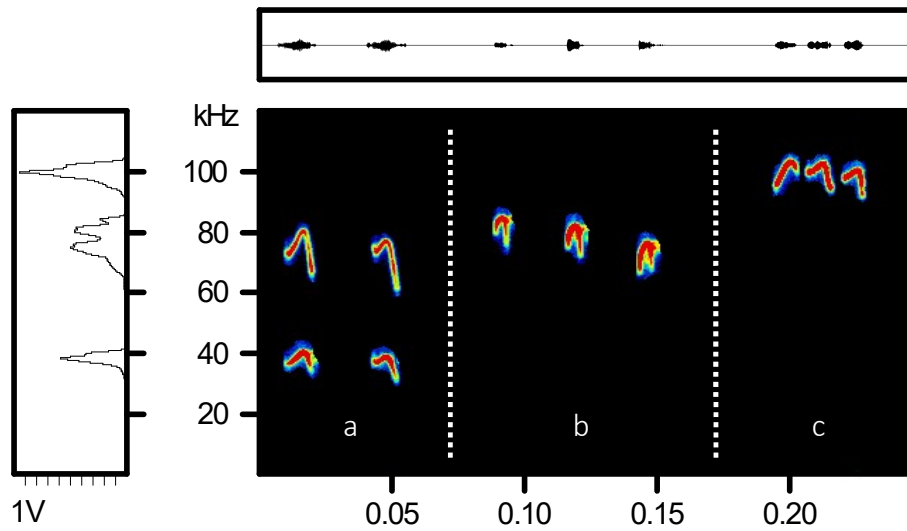


Fig. 12. Examples of the three subtypes of inverted “v” calls recorded from a colony of *R. naso* during social interactions.

Table 9. Parameter values measured for the three subtypes of inverted “v” calls found during social interactions in a colony of *R. naso*.

Parameters	All (n = 15)			Inverted a (n = 6)			Inverted b (n = 8)			Inverted c (n = 1)			
	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Var.	
(kHz)	freq start	76,2	7,2	51,4	74,1	4,0	16,0	75,1	4,5	20,6	97,6	---	---
	freq end	73,6	8,3	69,7	70,1	6,2	38,0	73,3	4,5	20,5	97,5	---	---
	freq peak	79,7	6,5	41,9	78,3	2,7	7,4	78,3	4,2	17,6	99,7	---	---
	freq max	82,8	6,5	42,8	84,1	2,3	5,4	79,5	4,0	16,3	101,7	---	---
	freq min	71,5	7,7	59,5	68,4	4,1	16,7	70,9	4,1	16,9	95,4	---	---
	bandwidth	11,3	5,0	25,0	15,8	4,5	20,0	8,6	2,6	6,7	6,3	---	---
(ms)	duration calls	6,2	4,0	$1,6 \times 10^{-5}$	9,7	4,0	$1,6 \times 10^{-5}$	3,5	0,9	$8,3 \times 10^{-7}$	7,3	---	---
	interval calls	56,5	44,0	$1,9 \times 10^{-3}$	97,2	45,3	$2,0 \times 10^{-3}$	30,2	5,8	$3,4 \times 10^{-5}$	21,9	---	---
	duration group	236,3	131,5	$1,7 \times 10^{-2}$	273,6	149,0	$2,2 \times 10^{-2}$	193,3	115,7	$1,4 \times 10^{-2}$	356,4	---	---

Table 10. Parameter values measured for two subtypes of low frequency calls found during social interactions in a colony of *R. naso*.

Parameters	All (n = 18)			low a (n = 10)			low b (n = 18)			
	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	
(kHz)	freq start	36,7	6,7	44,9	36,8	7,5	56,2	36,5	6,1	36,8
	freq end	38,5	7,1	51,1	38,2	8,5	73,1	38,8	5,5	30,0
	freq peak	39,5	6,7	45,1	38,9	7,4	54,3	40,3	6,2	38,4
	freq max	43,0	6,7	45,4	43,4	7,5	57,0	42,5	6,0	36,4
	freq min	33,0	6,2	38,9	32,4	7,1	50,2	33,7	5,4	28,9
	bandwidth	10,0	2,8	7,8	11,0	2,1	4,3	8,7	3,2	10,1
(ms)	duration calls	2,7	0,9	$8,6 \times 10^{-7}$	2,2	0,5	$2,6 \times 10^{-7}$	3,4	1,0	$9,7 \times 10^{-7}$
	interval calls	29,2	6,2	$3,8 \times 10^{-5}$	27,4	6,1	$3,7 \times 10^{-5}$	31,4	5,9	$3,5 \times 10^{-5}$
	duration group	182,0	68,8	$4,7 \times 10^{-3}$	205,4	72,0	$5,2 \times 10^{-3}$	152,7	55,3	$3,1 \times 10^{-3}$

10) Low frequency pulse- These calls are all in the lower frequency range and have the main energy predominantly in the 1st harmonic. Two subtypes are identified (Fig. 13):

Subtype a- Extremely short pulses (Table 10) without any discernible structure, with first-harmonic peak frequencies ranging from 10.7 to 39.8 kHz (N=10).

Subtype b- Slightly longer than type a, these are still short calls (Table 10), with an inverted horseshoe shape. Peak frequency is similar, averaging 20.2 ± 3.1 kHz (N=8) in the first harmonic.

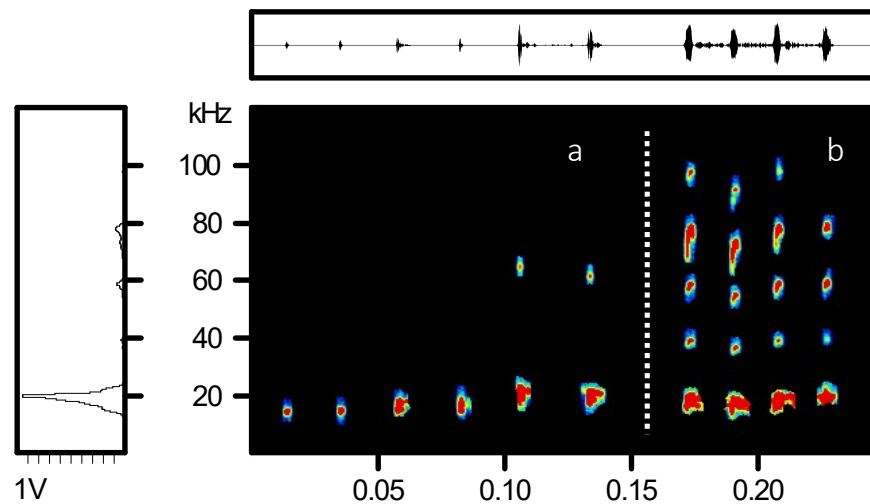


Fig. 13. Examples of the two subtypes of low frequency calls recorded from a colony of *R. naso* during social interactions.

11) Whine- Long calls (Table 11) that show a prominent narrowband component (Fig. 14), not present as such in any other vocalization category found. Peak frequency is typically in the 1st harmonic, and three subtypes are identified:

Subtype a- The call starts with a downward modulated FM-sweep (average bandwidth 11.0 ± 5.4 kHz; N=5) that leads into the long QCF component (34 ± 9 ms; N=5). One or two harmonics can be present.

Subtype b- The call starts with the long QCF component (18 ± 6 ms; N=5) that may or may not be followed by an FM sweep (14.3 ± 5.5 kHz; N=5). Normally two harmonics are present.

Subtype c- In contrast to subtypes *a* and *b*, the call starts with a slight upward modulation that leads into the long QCF component. This is the least common of the three whine subtypes.

12) Ripple- These calls are long (Table 12) and highly variable in frequency and structure. Their distinctive characteristic is to contain several down- and upward modulations, of irregular bandwidth (Fig. 15). They appeared singly or, rarely, in groups of up to three calls across the same recording sequence (6 s). Typically, three or more harmonics are visible, and the energy distribution in them varies throughout the call.

Subtype a- Peak frequency in this subtype is higher in average than in the other two (Table 12). The call spans over a bandwidth of 16.1 ± 10.4 kHz (N=4) in average. It has 3 to 7 frequency modulation peaks (average: 5 ± 1.8 ; N=4), more than those found in subtypes *b* and *c*.

Subtype b- Though similar to subtype *a*, its average peak frequency is lower (Table 12). While it has less frequency modulations than subtype *a* (range: 2-6; average: 3.5 ± 1.5 ; N=6), it spans over a larger bandwidth (21.0 ± 19.7 kHz; N=6).

Subtype c- The last subtype includes upward modulated calls which also show ripple modulations (less than 3). Peak frequency is intermediate between the other two subtypes (Table 12), and they have the smallest bandwidth of the three (14.3 ± 3.4 kHz; N=6). These calls may be emitted as the beginning syllables of crescendo calls, instead of up sweeps or low frequency pulses.

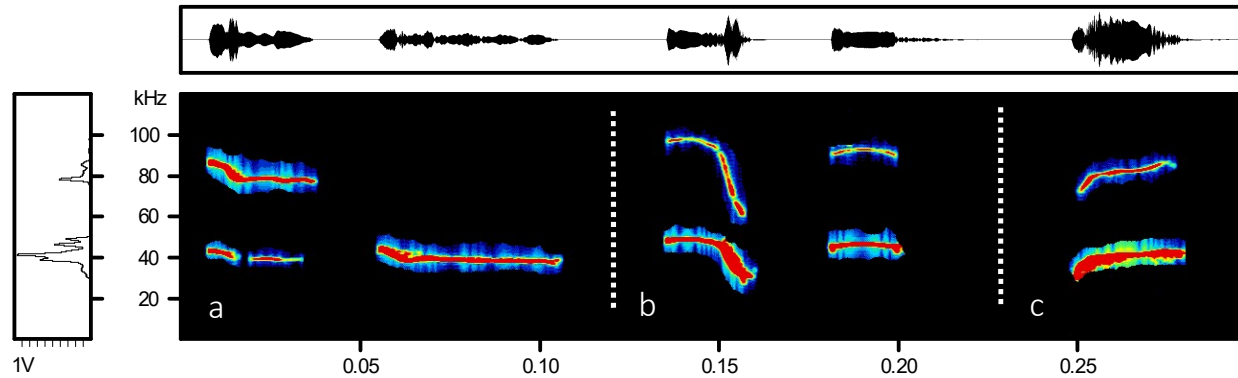


Fig. 14. Examples of the three subtypes of whines recorded from a colony of *R. naso* during social interactions.

Table 11. Parameter values measured for three subtypes of whines found during social interactions in a colony of *R. naso*.

Parameters	All (n = 12)			whine a (n = 5)			whine b (n = 5)			whine c (n = 2)			
	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	
(kHz)	freq start	74,1	22,5	508	86,0	9,4	88,9	78,8	15,5	241	32,8	6,0	36,1
	freq end	66,4	15,8	250	77,3	6,7	44,4	65,1	13,9	193	42,0	0,5	0,2
	freq peak	71,9	17,4	302	80,3	7,7	58,9	76,4	12,2	149	39,9	0,5	0,3
	freq max	77,6	19,1	364	86,8	8,8	77,9	81,9	14,9	223	43,8	1,7	2,9
	freq min	64,0	18,2	331	75,2	7,9	62,2	65,3	13,8	190	32,8	6,0	36,1
	bandwidth	10,7	4,2	17,9	11,6	5,2	26,8	9,6	3,9	15,3	11,1	4,3	18,6
(ms)	duration												
	calls	31,0	10,8	$1,2 \times 10^{-4}$	39,8	8,2	$6,7 \times 10^{-5}$	22,4	7,8	$6,1 \times 10^{-5}$	30,3	2,4	$5,9 \times 10^{-6}$
	interval calls	102,4	21,4	$4,6 \times 10^{-4}$	118,4	12,8	$1,6 \times 10^{-4}$	79,3	5,8	$3,3 \times 10^{-5}$	107,7	---	---
duration group	347,9	221,3	$4,9 \times 10^{-2}$	459,9	245,1	$6,0 \times 10^{-2}$	268,6	157,1	$2,5 \times 10^{-2}$	137,6	---	---	

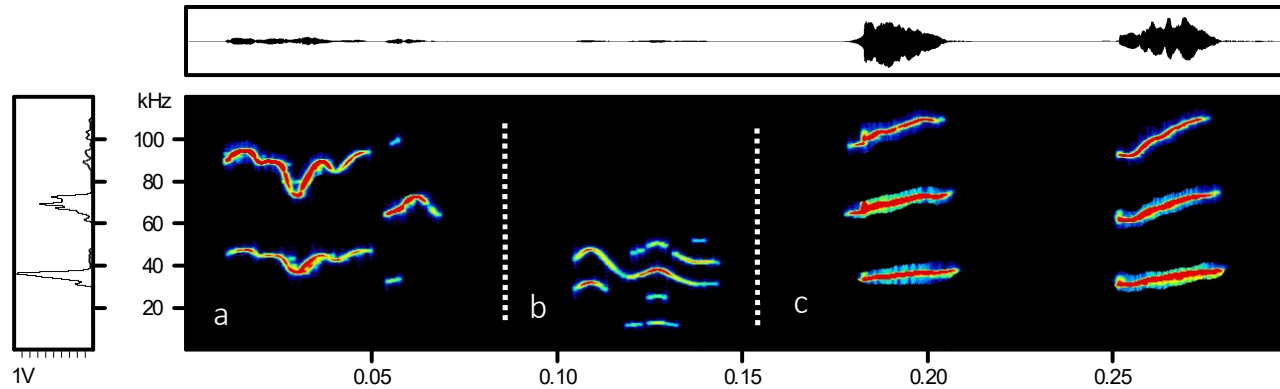


Fig. 15. Examples of the three subtypes of ripple calls recorded from a colony of *R. naso* during social interactions.

Table 12. Parameter values measured for three subtypes of ripple calls found during social interactions in a colony of *R. naso*.

Parameters	All (n = 16)			ripple a (n = 4)			ripple b (n = 6)			ripple c (n = 6)			
	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	Avg.	Std. Dev.	Variance	
(kHz)	freq start	53,9	23,5	551	70,1	28,4	805	47,6	26,9	721	49,5	13,0	169
	freq end	53,9	21,8	475	64,5	24,5	599	40,6	22,1	487	60,0	15,2	232
	freq peak	54,1	20,1	404	66,7	20,4	416	45,4	21,9	478	54,5	16,3	266
	freq max	62,5	24,6	604	74,2	28,0	786	56,1	31,4	984	61,1	14,0	195
	freq min	45,3	17,0	290	58,1	17,8	317	35,2	13,6	185	46,8	15,4	237
	bandwidth	17,2	12,8	164	16,1	10,4	108	21,0	19,7	389	14,3	3,5	11,9
(ms)	duration calls	28,8	6,0	$3,6 \times 10^{-5}$	30,5	9,4	$8,9 \times 10^{-5}$	30,4	2,6	$6,9 \times 10^{-6}$	26,5	5,1	$2,6 \times 10^{-6}$

13) Trill- These calls also consist of rippled modulations of the sound. They differ from ripple calls in that two or three of their modulations show similar bandwidths. They are typically preceded by an echolocation-like call, and the subsequent modulations resemble a series of echolocation-like pulses (subtype c) emitted without silence in between them, but instead connected from the end FM-sweep of one to the QCF start of the next one (Fig. 16). The main energy may appear in the 1st or 2nd harmonic.

Two subtypes are distinguished:

Subtype a- Higher in frequency (Table 13), the downward sweeps cover a narrower bandwidth (22.4 ± 8.1 kHz; N=8) than in subtype *b*. The minima of the modulations have sharper points of inflection than the maxima, which are shallower in shape. There are between five and up to 14 modulations in a single call, throughout a similar duration in both subtypes.

Subtype b- The maximum frequency of the modulations typically decreases across the call, thus, the average peak frequency of the call is lower (Table 13). The bandwidth is broader than in subtype *a* (50.6 ± 16.6 kHz; N=10), and the total number of modulations ranges from 4 to 9.

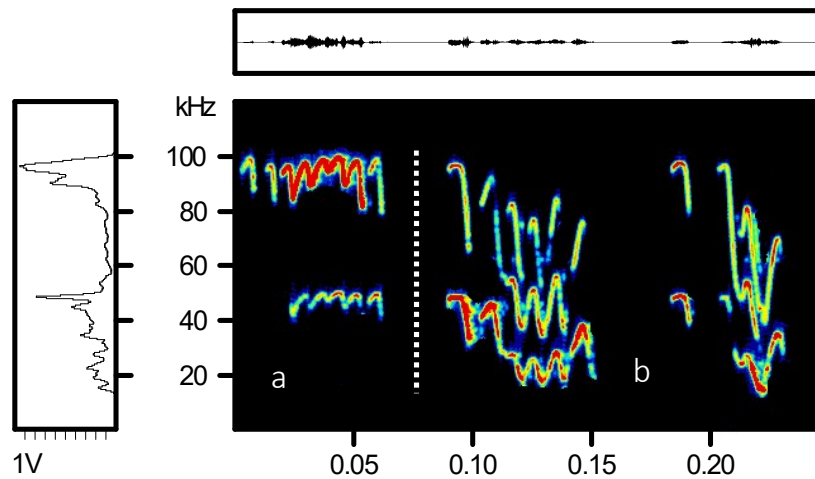


Fig. 16. Examples of the two subtypes of trills recorded from a colony of *R. naso* during social interactions.

Table 13. Parameter values measured for both subtypes of trills found during social interactions in a colony of *R. naso*.

Parameters	All (n = 18)			trill a (n = 8)			trill b (n = 10)			
	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	
(kHz)	freq start	91,5	4,8	23,5	92,6	2,5	6,3	90,7	6,1	37,6
	freq end	61,9	20,5	421	76,4	7,3	52,6	50,3	20,5	419
	freq peak	80,7	13,4	180	93,2	3,9	15,4	70,7	8,9	79,1
	freq max	97,7	2,5	6,2	98,9	1,1	1,2	96,8	2,9	8,5
	freq min	59,6	21,0	443	76,5	7,7	58,9	46,1	18,3	334
	bandwidth	38,1	19,5	382	22,4	8,1	65,2	50,7	16,6	276
(ms)	duration									
	calls	33,6	8,5	$7,3 \times 10^{-5}$	34,6	8,2	$6,7 \times 10^{-5}$	32,9	9,2	$8,4 \times 10^{-5}$

14) Screech- In this call type, the sound energy is distributed across a broad range of frequencies (Table 14) and when distinguishable, several harmonics are present. It is audible to the human ear as a harsh noise, with its low peak frequencies (19.9 ± 2.6 kHz; N=9). Sometimes, a series of successive click-like elements are visible towards the end of the call, a feature which only appears in this vocalization category (Fig. 17).

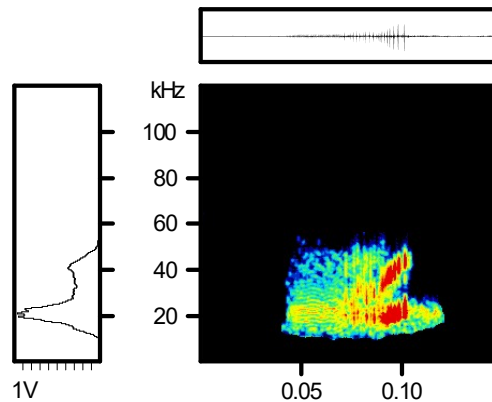


Fig. 17. One screech recorded from a colony of *R. naso* during social interactions.

Table 14. Parameter values measured for screech calls recorded during social interactions in a colony of *R. naso*.

n=9	Parameters	Average	Std. Dev.	Variance
(kHz)	freq peak	19,9	2,6	6,9
	freq max	60,3	14,2	201
	freq min	14,3	1,8	3,1
	bandwidth	46,0	13,5	182
(ms)	duration calls	82,6	49,4	$2,4 \times 10^{-3}$

15) **Composite call**- This is the least common vocalization category found in the repertoire described. Composite calls are monosyllabic, but show two distinct parts (Fig. 18): a noisy, broadband start (bandwidth 22.5 ± 8.9 kHz; N=3) and a tonal end which is upward modulated, of narrower bandwidth (17.7 ± 16 kHz; N=3), and slightly longer duration (Table 15). Most of the call's energy is concentrated in the lower frequency range, so that it can be perceived by the human ear as a high shriek.

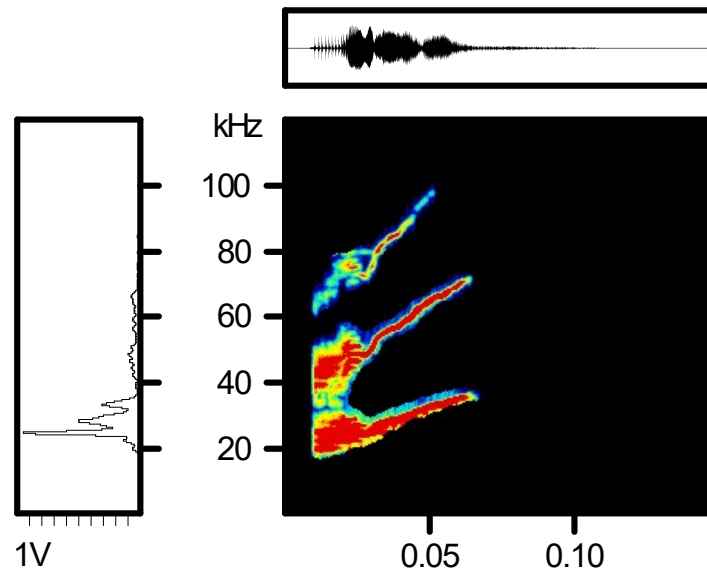


Fig. 18. One composite call recorded from a colony of *R. naso* during social interactions.

Table 15. Parameter values measured for composite calls recorded during social interactions in a colony of *R. naso*.

Parameters	All (n = 6)			Noisy part (n = 3)			Tonal part (n = 3)			
	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	Average	Std. Dev.	Variance	
(kHz)	freq start	25,8	7,2	52,3	20,6	3,7	13,7	31,0	6,0	35,4
	freq end	38,3	14,8	219	27,5	1,8	3,2	49,2	13,8	191
	freq peak	37,4	18,6	348	27,9	5,1	25,7	46,9	24,0	574
	freq max	39,9	21,5	460	27,9	5,1	25,7	51,8	26,4	696
	freq min	28,0	12,9	165	16,5	1,2	1,4	39,5	4,2	17,7
	bandwidth	20,1	11,9	141	22,5	8,9	79,3	17,7	16,0	255
(ms)	duration calls	22,1	9,7	$9,5 \times 10^{-5}$	19,2	5,1	$2,5 \times 10^{-5}$	25,1	13,6	$1,9 \times 10^{-4}$

Statistical analyses

The first DFA performed included all the parameters measured simultaneously for all 15 vocalization categories (n= 272). The first three discriminant functions generated had a cumulative eigenvalue of 91.8%, and correctly classified 56.3% of the calls, which is significantly better than expected by a random classification (6.66%). Thus, the categories established visually were confirmed statistically. For a detailed assessment of model fit, see Table 16. A stepwise DFA with the same data yielded the exact same results, and showed that bandwidth, followed by duration and peak frequency, were the most important parameters for the classification.

Table 16. Statistical values for an assessment of model fit of the first 3 discriminant functions (df) of the DFA for all vocalization categories.

Parameter	df1	df2	df3
eigenvalue	5,46	5,11	1,96
explained variance [%]	40,00	37,40	14,40
Wilk's Lambda	0,003	0,220	0,134
Chi-Square	1480,43	994,47	523,14
P	<0,0001	<0,0001	<0,0001

Additional DFAs were done for each vocalization category that has two or more subtypes. The standardized canonical coefficients of the variables that most prominently contributed to the 1st and 2nd discriminant functions in each case can be found in Table 17.

- *a) Echolocation-like calls:* The first three discriminant functions had a cumulative eigenvalue of 99.0%. The DFA with 49 call groups correctly separated the ec-like subtypes with 71.4% of classification success, significantly better than expected by a random classification (20%). Subtypes *a* and *b* are best separated from each other and from the other three, which remain relatively clustered together in signal space (Fig. 19a). The most important parameters for separating these subtypes were end and minimum frequency, which are highly correlated variables given the structure of these calls.
- *b) Complex calls:* the first three discriminant functions had a cumulative eigenvalue of 97.8%. The DFA separated the five syllables composing the three subtypes (n= 47) with a classification success of 66.6%, which is higher than the 20% expected from a random classification. The closer distance reflected in signal space between the centroids of the syllables “down FM sweep” (*d*) and “inverted v” (*r*) measured from the different call subtypes, reflects their acoustic similarity (Fig. 19b). Peak and

maximum frequency contributed mostly to the separation of these syllables and subtypes, followed by end frequency.

- *c) Crescendo*: The first discriminant function had an eigenvalue of 100%. With a classification success of 94.7%, significantly higher than expected by randomness (50%), the analysis could correctly differentiate and classify statistically both syllable types composing the call (n= 19). Of the parameters measured, maximum frequency and start frequency were the most important for the discrimination.
- *d) Down sweeps*: The three subtypes grouped in this vocalization category are well separated in signal space by means of the acoustic parameters measured, most importantly by their minimum and end frequencies (Fig. 19c). The first two discriminant functions had a cumulative eigenvalue of 100%, and the DFA had a significantly higher classification success (96.2%) than was expected by a random classification (33.3%).
- *e) Inverted “v” calls*: The first two discriminant functions had a cumulative eigenvalue of 100%. Using data from 18 call groups of the three subtypes identified, the DFA had a classification success of 80%, significantly higher than what was expected from a random classification (33.3%). Subtypes *a* and *b* are well separated in signal space (Fig. 19d), with peak frequency and maximum frequency as the most prominent parameters for the separation. However, since there was only one example of subtype *c* included in the analysis, I cannot draw definite conclusions about its separation with respect to the others.
- *f) Low frequency pulses*: Using 18 call groups of both low frequency pulse subtypes, the first discriminant function already accounted for all the variance of the original data set (eigenvalue of 100%). Even though the DFA achieved a significantly higher classification success than expected by chance (61.3% vs. 50%), the quite low rate indicates that both call subtypes are, at the least, not as distinguishable by the parameters I measured as they are visually. The most important parameters contributing to the main discriminant functions that classified these subtypes were maximum and peak frequency.
- *g) Whines*: The first two discriminant functions had a cumulative eigenvalue of 100%. The DFA (n= 12) correctly separated the subtypes with 66.7% classification success, a rate greater than expected by chance (33.3%). As in inverted “v” calls, the three subtypes of whines are well separated in signal space (Fig. 19e), but there were only two examples of whines subtype *c* included in the analysis, due to their rarity in the data set. The most important parameters for the discrimination of the subtypes were maximum and peak frequency.

- *h) Ripple calls:* The first two discriminant functions had a cumulative eigenvalue of 100%, and were most prominently influenced by the peak and maximum frequency of the calls. However, the classification success of the DFA (n= 16) was almost equal to chance (37.5% vs. 33.3%). Thus, the parameters measured are not sufficient to accurately separate the three subtypes of this category. The high internal variability of the calls reflected on their scattered pattern in signal space (Fig. 19f) may be one reason for the difficulty of a correct statistical classification.
- *i) Trills:* As in ripple calls, the first discriminant function of the DFA had an eigenvalue of 100% (n= 18). The analysis separated the two subtypes of trills with a classification success of 83.3%, a rate significantly higher than the 50% expected by chance. Different from ripples, the parameters measured, mainly end and minimum frequency, did supply sufficient data for a more successful statistical separation of this frequency modulated calls, though a larger sample size could have rendered higher classification accuracy to the analysis.
- *j) Composite calls:* The first discriminant function had an eigenvalue of 100%, and was mostly correlated with the minimum frequency and duration of the two distinct call components. The DFA could correctly classify both parts of this call with a success rate of 83.3%, which is significantly higher than expected by random (50%). However, the rarity of this vocalization category within the repertoire rendered a rather low sample size available for analysis (n= 6); a larger sample would have probably raised the classification success rate obtained.

Finally, two groups of vocalization categories with similar structural characteristics were screened for their distinctiveness. A DFA including chatters, FM trains, ec-like calls and crescendos (n= 88) created three discriminant functions with a cumulative eigenvalue of 100% (canonical standardized coefficients in Table 17). The analysis had a higher classification success than expected by chance (83% vs. 25%), and the plotting of the calls in the multi-dimensional signal space shows that chatter and FM trains are well separated from each other and the other call types, mainly by their minimum frequency and bandwidth. On the other hand, ec-like calls and crescendos appear closer together (Fig. 20a), and thus have greater acoustical similarities.

The second group of vocalization categories explored included the call types with longer durations and frequency modulations of the sound: whines, trills and ripples. The first two discriminant functions had a cumulative eigenvalue of 100% (n= 46), while the analysis managed a classification success of 76.1%, which is significantly higher than expected from a random classification (33.3%). The high internal variability of the calls in all three categories is evident in their scattered distribution in signal space,

though their centroids appear rather well separated from each other based on the acoustical parameters included in the analysis. The most important acoustic parameters contributing to the main discriminant functions were maximum frequency and bandwidth.

Table 17. Absolute values of the parameters with the highest standardized canonical discriminant coefficients of the most important discriminant functions (df) for each DFA presented.

Vocalization category	Parameters	df1	df2	df3
Ec-like calls	freq end	2.589	5.231	
	freq min	2.021	4.228	4.244
	freq start			4.260
Complex calls	freq max	1.072	3.939	
	freq peak	1.733		3.606
	freq end		2.129	
	freq min			3.570
Crescendo	freq max	10.546		
	freq start	5.887		
Down sweeps	freq min	6.483	5.324	
	freq end	5.475	4.188	
Inverted "v"	freq peak	7.794		
	freq max	5.090		
	duration group		1.632	
	interval call		1.240	
Low frequency pulses	freq max	8.480		
	freq peak	8.279		
Whines	freq max	15.679	9.907	
	freq peak	12.126		
	freq start		8.539	
Ripple calls	freq peak	4.579	5.673	
	freq end	2.633		
	freq max		7.098	
Trills	freq end	1.626		
	freq min	1.266		
Composite calls	freq min	2.242		
	duration component	1.667		
Chatters, FM trains, ec-like calls, crescendos	freq min	3.041	4.283	8.914
	freq peak	2.483		
	bandwidth		2.420	
	freq max			8.321
Whines, trills, ripples	freq max	5.060	3.957	
	freq min	4.150		
	bandwidth		3.462	

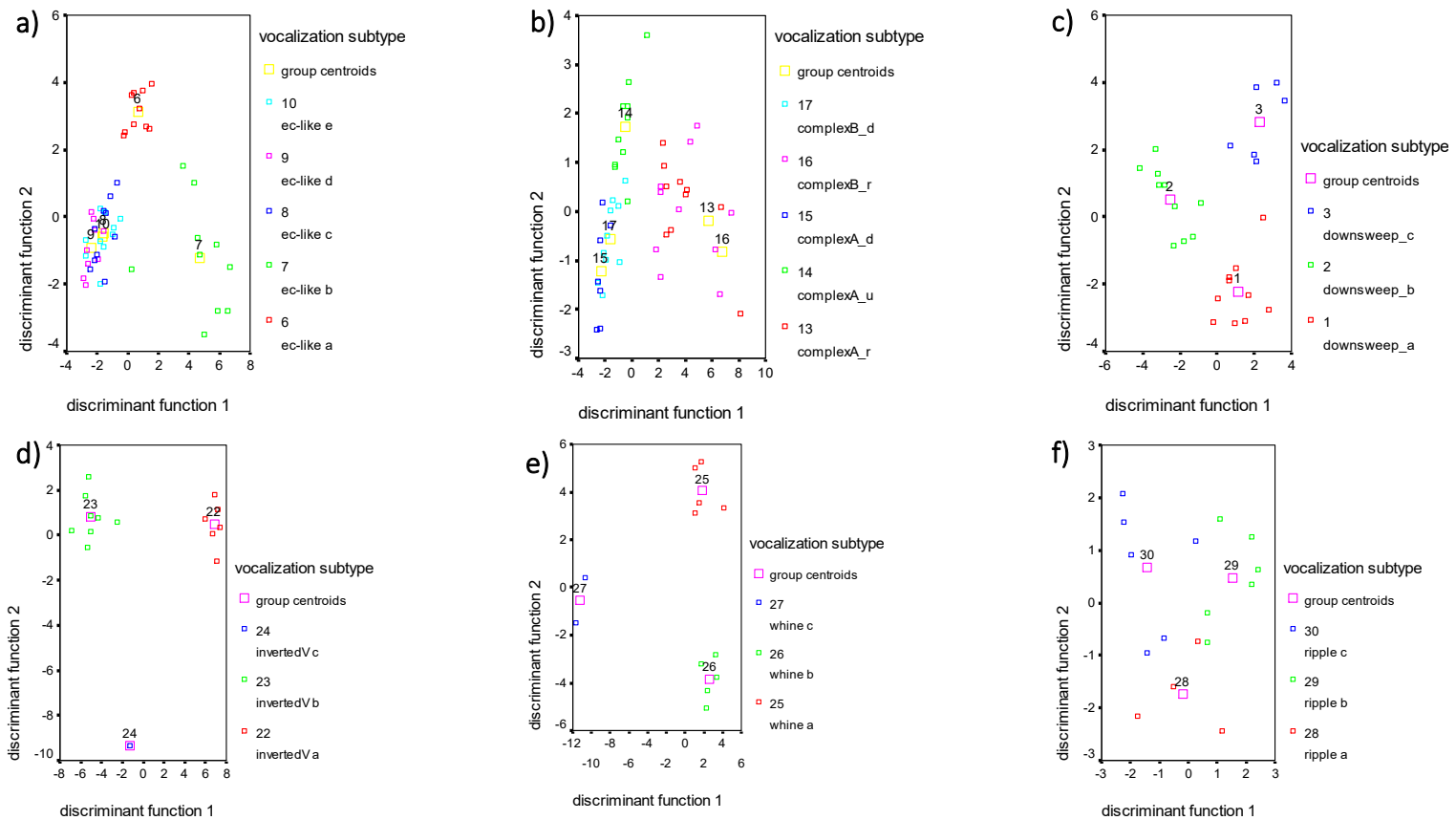


Fig. 19. Plots of the multi-dimensional signal space created by the acoustic parameters measured for all vocalization categories with more than 2 subtypes, recorded from a colony of *R. naso* during social interactions: **a)** echolocation-like calls, **b)** complex calls, **c)** down sweeps, **d)** inverted "v" calls, **e)** whines, and **f)** ripple calls. The distance between group centroids in signal space reflects acoustic distance between the subtypes. For details on the parameters correlated with the discriminant functions in each case, see text.

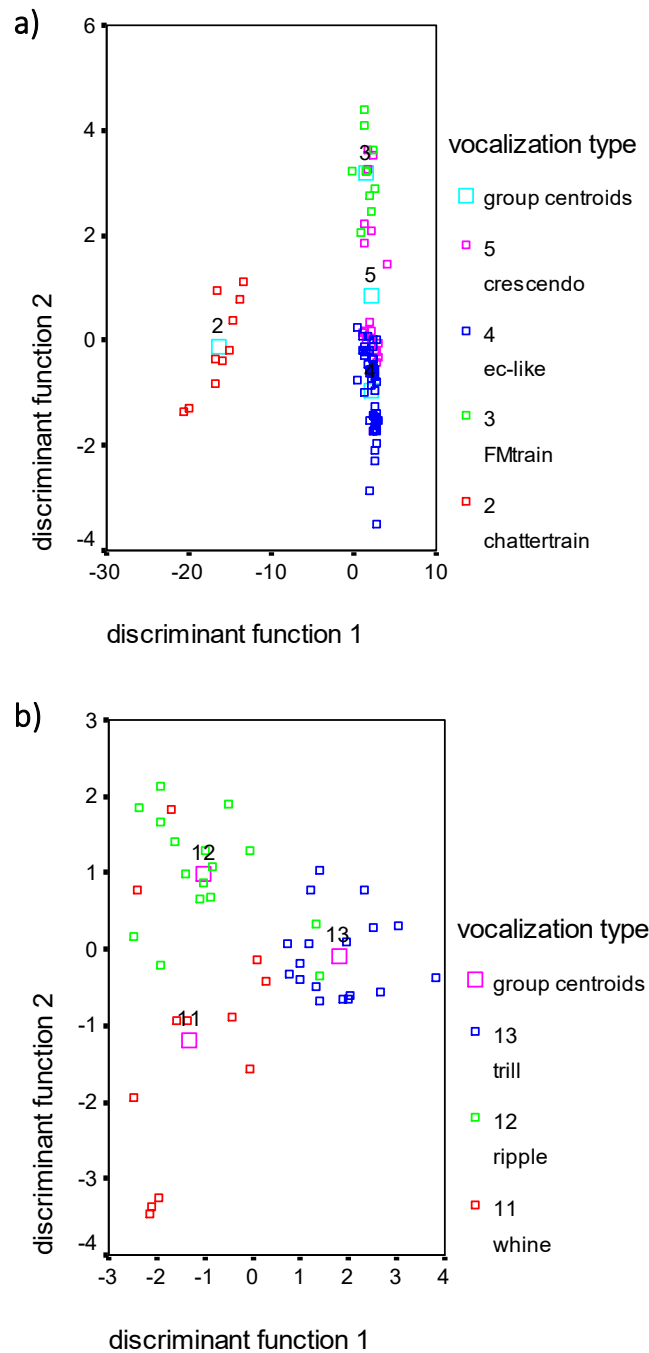


Fig. 20. Plots of the multi-dimensional signal space created by the acoustic parameters measured for two groups of vocalization categories with structural similarities, recorded from a colony of *R. naso* during social interactions: **a)** chatters, FM trains, echolocation-like calls and crescendos, and **b)** whines, trills and ripple calls. The distance between group centroids in signal space reflects acoustic distance between the subtypes. For details on the parameters correlated with the discriminant functions in each case, see text.

Behavioural interactions and associated vocalizations

I obtained over 382 h of video recordings. High quality video recordings of the behaviors selected encompassed 4:01:27 h. Since the sound recording set up did not allow assigning specific vocalizations to individual bats, there was usually uncertainty about which bat uttered which vocalization. Thus, the temporal synchrony of the video and sound recordings and the direct observations conducted on site were used to relate the vocalizations recorded to the individuals observed in the roost at any given moment. When possible, specific signals could be assigned to individuals when they were accompanied by evident movements from them.

A total of 24 645 sound files were obtained throughout the study period. With 6 s per sound recording, this corresponded to more than 41 hours (2 464.5 min) in real time. The behavioural sequences selected for analysis from the videos were related to a total of 1:38:00 h real time of sound recordings (979 files = 5874 s). All interactions among the roosting bats were predominantly accompanied by ec-like vocalizations. Due to their extremely high abundance, only a sample of ca. 20% of the files containing these call types for each behavioural context was analysed and classified according to each of the five subtypes observed. Thus, results from ec-like calls are discussed separately from other non ec-like call types. Table 18 summarizes the frequency of occurrence of the different vocalization types across the behavioural sequences analysed.

Table 18. Frequency of occurrence of vocalization categories of *Rhynchonycteris naso* in specific behavioural contexts, grouped according to five general call types, following Pfalzer and Kusch (2003)– names in italic letters (see Discussion). Percentages demonstrate relative abundance of each call type within each context. Bold numbers mark the most frequent vocalization type in each behavioural category, numbers in italic mark the behaviour with highest relative abundance of each vocalization type.

Category	Vocalization type	Behavioral context							
		Perching	%	Agonistic	%	Mother-young	%	Courtship	%
	N files	453		111		302		106	
<i>Ec-like</i>	Ec-like	432	95,4	106	95,5	277	91,7	105	99,06
	Files sampled	92	20,3	111	100,0	65	21,5	106	100,00
	ec a	24	26,1	20	18,0	42	64,6	42	39,6
	ec b	47	51,1					78	73,6
	ec c	18	19,6	80	72,1	53	81,5	36	34,0
	ec d					10	15,4	2	1,9
	ec e	38	41,3	48	43,2	64	98,5	43	40,6
<i>Repeated</i>	Chatter	17	3,8	19	17,1	9	3,0	2	1,9
	FM train	7	1,5	14	12,6	47	15,6	4	3,8
	U-shaped call	5	1,1			8	2,6	1	0,9
<i>Complex</i>	Complex								
	complex a	9	2,0	9	8,1	84	27,8		
	complex b	4	0,9	6	5,4	33	10,9	1	0,9
	Crescendo	26	5,7	38	34,2	33	10,9	8	7,5
<i>Modulated (curved)</i>	Down sweep								
	down sweep a	1	0,2	2	1,8			1	0,9
	down sweep b	3	0,7	21	18,9	6	2,0	1	0,9
	down sweep c	1	0,2			3	1,0	1	0,9
	Up sweep	11	2,4			22	7,3	2	1,9
	Inverted v								
	inverted a	3	0,7	1	0,9	12	4,0		
	inverted b	1	0,2	23	20,7	5	1,7	2	1,9
	inverted c			1	0,9				
	Whine								
	whine a			4	3,6				
	whine b	1	0,2	1	0,9	1	0,3	1	0,9
	whine c			1	0,9				
	Ripple								
	ripple a			1	0,9	1	0,3		
ripple b	1	0,2	2	1,8	5	1,7			
ripple c	2	0,4	1	0,9	11	3,6			
Low freq pulse									
low a			15	13,5	12	4,0	1	0,9	
low b	4	0,9	2	1,8	5	1,7			
Trill									
trill a	1	0,2	1	0,9	11	3,6			
trill b	7	1,5	10	9,0	10	3,3			
<i>Harsh (squawk)</i>	Screech	5	1,1	11	9,9	7	2,3		
	Composite			1	0,9	1	0,3		

1) Perching:

A total of 33 sequences (1:22:45 h) of bats perching in their roost were selected for analysis, from the whole observation period. In these, at least one and up to 10 bats of both sexes were present, not visibly interacting with each other (except for mother and pup pairs). The bats would be completely immobile, or would engage in behaviours such as: general grooming of their fur, wings, and feet, rocking sideways (swaying) or bouncing, stretching their wings or, on occasion, non-volant pups would be seen flipping their wings while hanging from their feet as if practicing flight. Additionally, individuals in this context were seen crawling a few centimetres from their roosting position towards to or away from other individuals nearby, without physical contact or overt physical reactions from the others. Usually, one bat in the group would start grooming or rocking and other members would follow; however, this was not always the case. On 20 of the cases analysed, there were pups present in the roost, either suckling (nine sequences) or simply perching together with the group; the remaining sequences show only adult bats. Also, 11 of the sequences include one to three bats flying out of their position in the roost, whether momentarily or for longer periods of time.

Vocalizations were recorded during each one of these sequences (453 sound files, 2718 s), coming from one or several bats, though it was not always possible to visualize which individuals were emitting the signals. Echolocation-like calls were found in 432 of the files (95.4%), of which 92 (21.3%) were revised to further classify them into the corresponding subtypes (Fig. 21). Not all call subtypes appeared equally abundant in the files ($\chi^2 = 52.2$, $df = 4$, $p < 0.001$). The most common calls emitted were ec-like subtypes *b*, *e* and *a*, while there was no occurrence of subtype *d*. The only other behavioural context where ec-like subtype *b* occurred was courtship.

There was a significant difference in the abundances of non ec-like calls in the sound files recorded from perching bats ($\chi^2 = 140.2$, $df = 19$, $p < 0.001$). From these, six vocalization categories comprised 70% of the call types found (crescendo, chatter, up sweep, complex a, trill b and FM train) (Fig. 22).

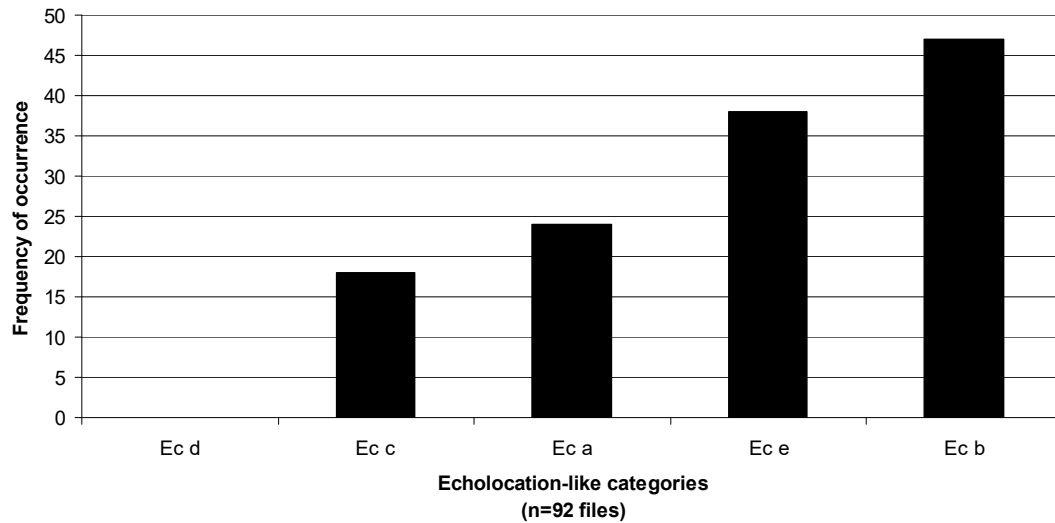


Fig. 21. Abundance of echolocation-like vocalizations of each subtype recorded from perching bats in a colony of *R. naso*. The graph shows the number of times each vocalization subtype was encountered in the files reviewed.

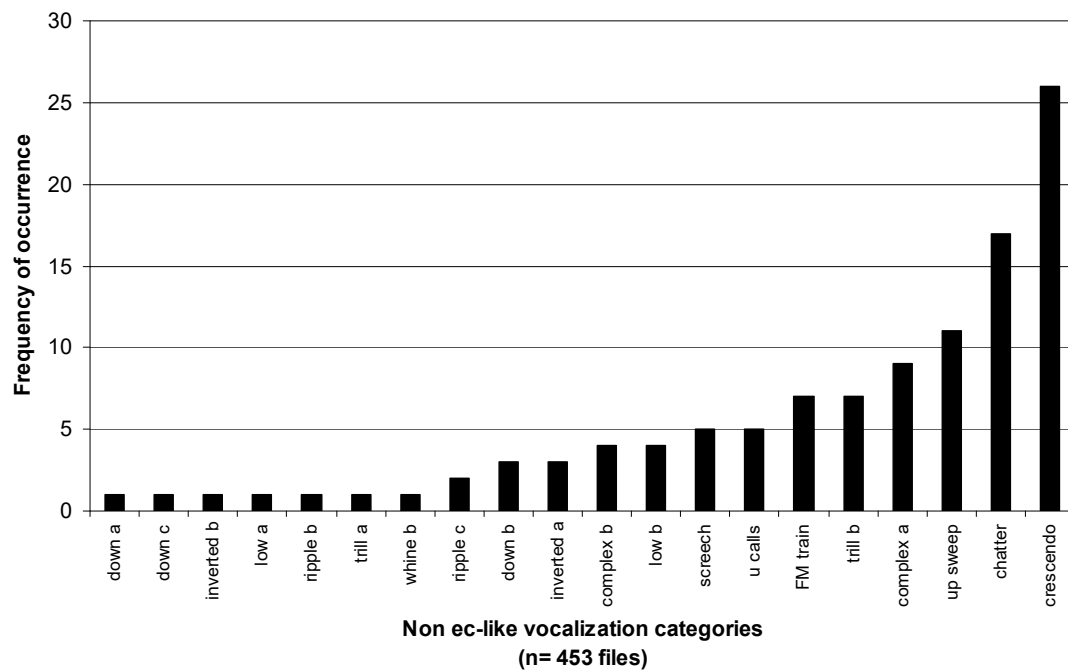


Fig. 22. Abundance of non echolocation-like vocalizations of each subtype during perching interactions in a colony of *R. naso*. The graph shows the number of times each vocalization subtype was encountered during this behavioural context.

2) Agonistic encounters:

Good quality aggressive interactions between two or more individuals of the colony were recorded 27 times during the observation period. These showed a range of observable aggressive actions; those considered *mild* aggressions included short crawling persecutions from one individual without equal reaction from the other, and folded-wing poking between individuals. Normally, these were the shortest ones and were somehow resolved without much physical contact between the individuals involved. On the other side, those considered *strong* aggressions lasted longer and always included repeated physical contact, such as folded-wing swaps between individuals, one bat flying towards and directly landing on top of another bat, and evident pulling or poking towards sensitive tissues like the patagium and ears with the thumb claw.

The 27 sequences (0:18:28 h) were associated with 111 sound files (666 s). Of these, most (95.5%; N = 111) contained ec-like vocalizations. Types *b* and *d* were absent from the recordings, while ec-like type *c* was the most frequently emitted (Fig 23).

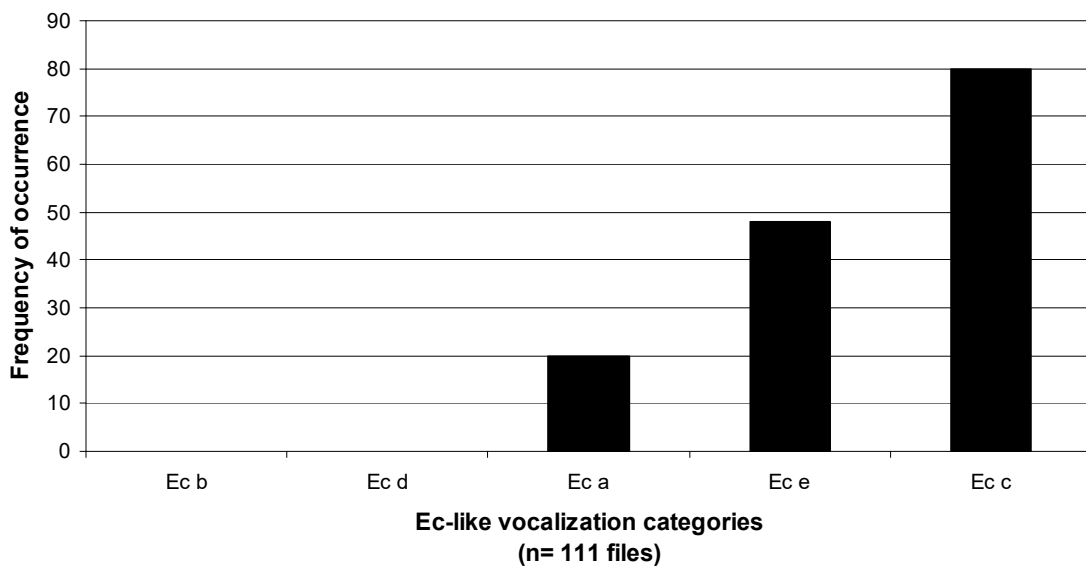


Fig. 23. Abundance of echolocation-like vocalizations of each subtype found during agonistic interactions in a colony of *R. naso*. The graph shows the number of times each vocalization subtype was encountered in the files reviewed.

Of the non ec-like vocalizations, six call types comprise 70.6% of the calls found (130): crescendo, inverted “v” *b*, down sweeps *b*, chatter, low frequency *a*, and FM trains ($p < 0.001$; $\chi^2 = 242.8$ df=

21). Other call types were found to occur only once during the interactions revised, including the rare composite calls (Fig. 24).

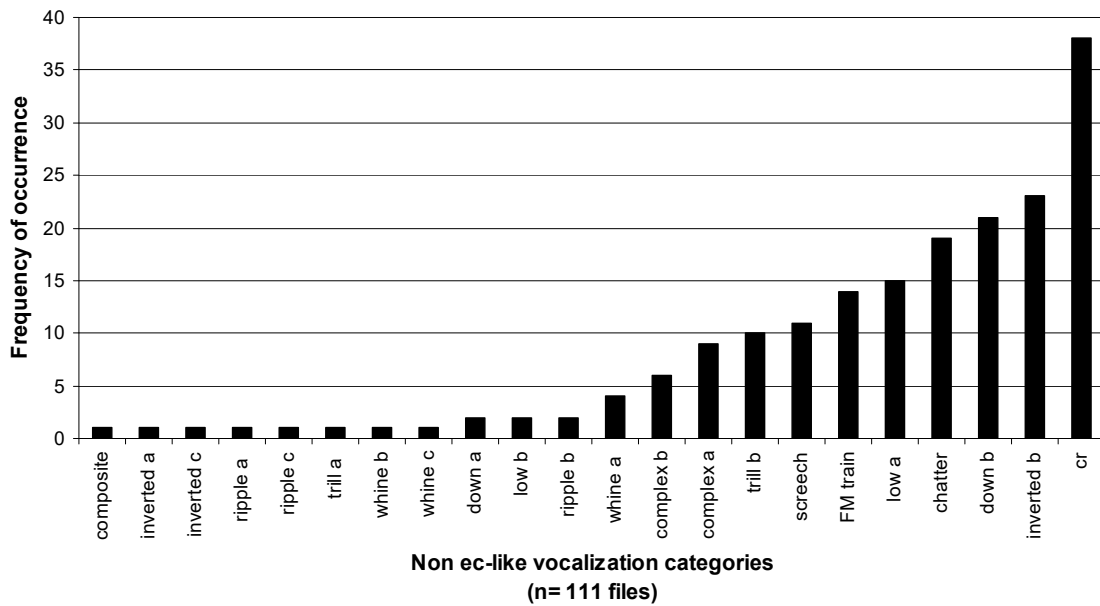


Fig. 24. Abundance of non echolocation-like vocalizations of each subtype found during agonistic interactions in a colony of *R. naso*. The graph shows the number of times each vocalization subtype was encountered during this behavioural context.

Of the aggressive interactions observed involving only two individuals, there were similar numbers of examples of female-female (8) and male-female (7) events of aggression in the sequences analysed, while male-male and pup-pup aggressions were each observed only once. However, given that there were often other members of the colony present at the roost, although not participating in the visible aggression considered, it cannot be discarded that they could have vocalized as well during the sequence. Furthermore, there were seven additional events of agonistic interactions involving several individuals in the same sequence: adults of both sexes and adults and pups. These occurred mostly associated to individuals changing positions in the roost. This further division of the interactions revealed similar trends in the vocalization types employed by the bats, to those found from the general data analysis.

A selection of six interactions considered *mild* (0:02:06 h; 15 files) was compared to six interactions considered *extreme* (0:09:41 h; 36 files), according to the behavioural criteria described above. While the ec-like vocalizations found showed the same trend as the general data, there were some differences in the set of non ec-like vocalizations found (Fig. 25). Extreme

aggressions were associated with slightly more vocalization categories (15) than mild ones (12). The most frequent calls observed during mild aggressions were the same as in the general data for this behavioural context (crescendo, chatter, down sweep *b* and FM trains), with the exception of low frequency calls. On the other side, low frequency calls (subtype *a*) appeared as the most abundant vocal category during strong aggressions, together with the other four predominant call types.

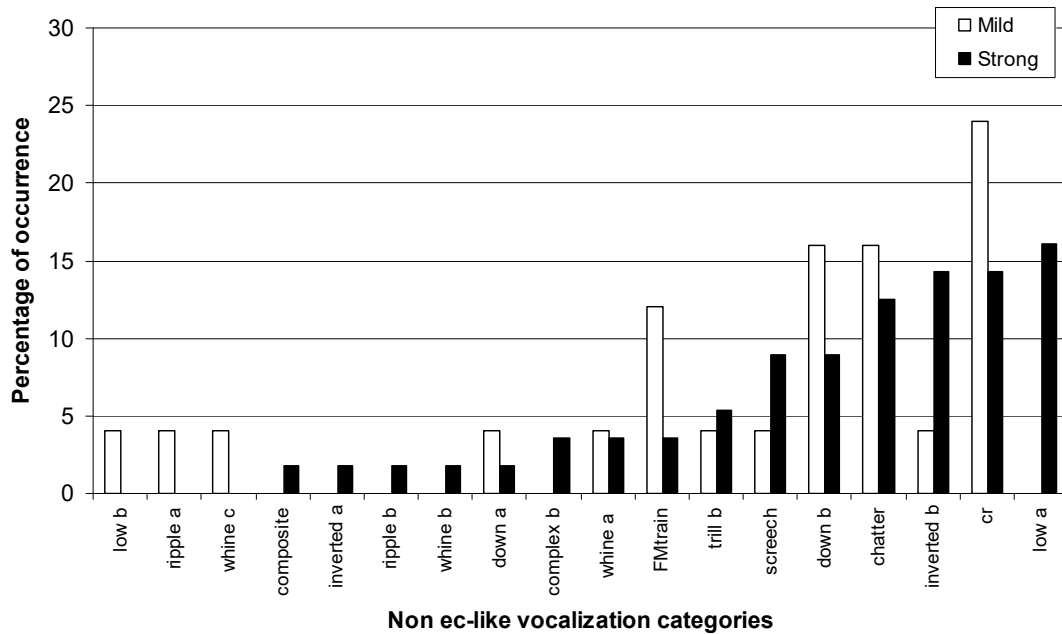


Fig. 25. Relative abundance of non echolocation-like vocalizations of each subtype found during two extremes (mild vs. strong) of agonistic interactions in a colony of *R. naso*. The graph shows the percentage of times each vocalization subtype was encountered during each behavioural context.

3) Mother-pup interactions:

Mother-pup interactions were analysed from 58 video sequences (0:55:34 h) selected according to the criteria established. Only sequences that showed clear interactions between pups and their mothers were taken into account, in one of the following situations: pup hanging from under its mother, visibly nursing or not; mother and pup reuniting after perching separately or the absence of either one from the roost; pup soliciting the mother and attempting to crawl under her, with or without success. The sequences analysed were taken from all three reproductive periods observed in the colony during the study, and each of the six pups produced was present at least eight times in the interactions observed. The total numbers of bats in the

roost during the mother-pup sequences ranged from two to nine individuals, for usually other adults besides the mothers were present. For this reason, not all vocalizations found in the corresponding sound files can be automatically attributed solely to the pups or their mothers.

Pups perching under their mothers would usually change from under one wing to the other, and could be seen stretching and even vocalizing on occasions, as well as hanging loosely for a few seconds before reassuming their previous position, tucked under the mother's wing. Mother-pup reunions were mostly initiated by the pup rather than the mother (21 vs. 6 occasions of reunion), and whether successful or not, repelling or even aggressive behaviours from the mother were seen on occasions. The mother would retreat away from the reach of the pup, or even swap it with her wing as it approached her closer. In such cases, the pup would desist its attempt in that moment and normally try again a few minutes later. Sometimes the pup had to move about the roost to reach its mother and thus would come closer to or into direct physical contact with other adult members of the colony perching in its way, which would elicit antagonistic responses from them (e.g. wing swaps).

A total of 302 sound files (1638 s) corresponding to the sequences of mother-pup reunions were revised. Ec-like calls were found in most (91.7%; $N = 277$) of the files. A sample of 65 (21.5 %) were reviewed for a finer classification, revealing that again, not all subtypes were equally abundant (Fig. 26; $p < 0.001$; $\chi^2 = 114.2$; $df = 4$), with ec-like subtypes e, c and a as the most common. Ec-like subtype d, though generally rare, had its highest abundance in this behavioural context.

For non ec-like calls, all 14 general vocalization types were found, including composite calls as the rarest type (Fig. 27). However, five call subtypes were clearly most abundant and comprised 66.4 % of the calls observed to occur ($p < 0,001$; $\chi^2 = 529.3$; $df = 21$): complex a, FM train, complex b, crescendo and up sweeps.

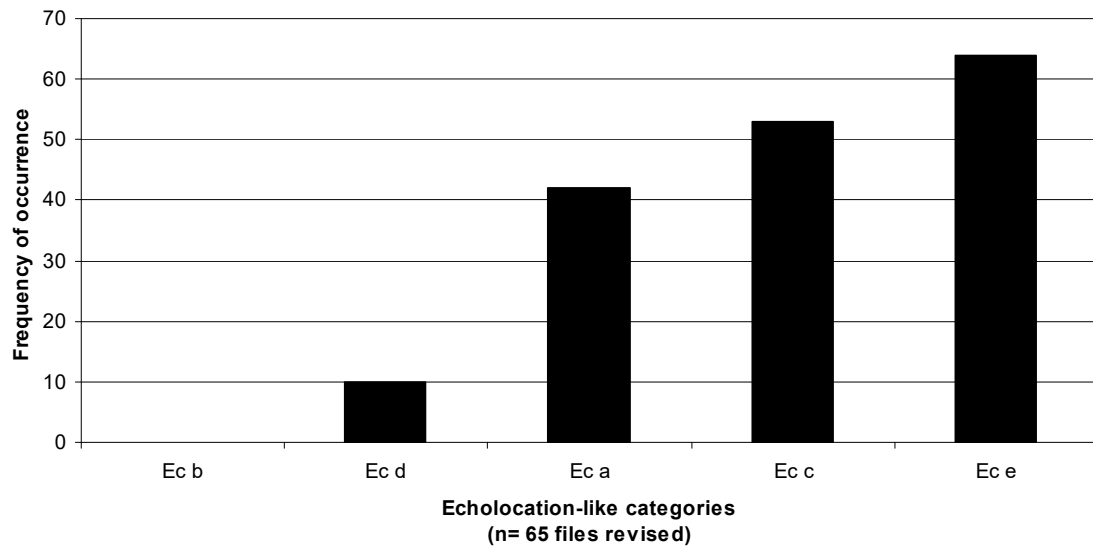


Fig. 26. Abundance of echolocation-like vocalizations of each subtype found during mother-pup interactions in a colony of *R. naso*. The graph shows the number of times each vocalization subtype was encountered in the files reviewed.

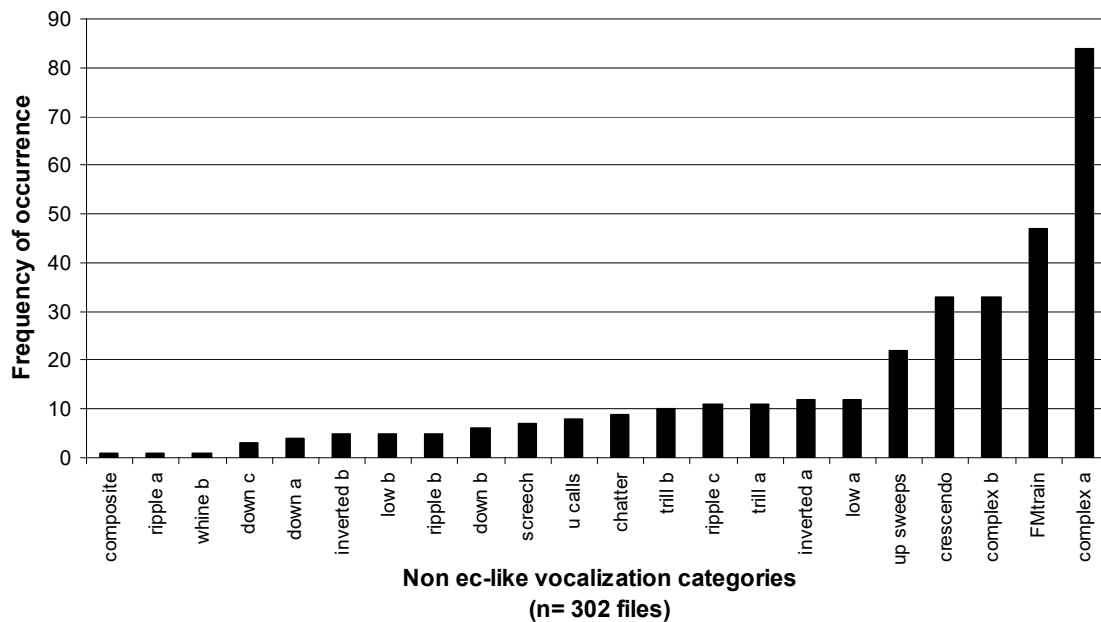


Fig. 27. Abundance of non echolocation-like vocalizations of each subtype found during perching interactions in a colony of *R. naso*. The graph shows the number of times each vocalization subtype was encountered during this behavioural context.

4) Courtship:

Sequences classified as courtship interactions showed a male approaching one specific female from the back, seeking physical contact and clearly trying to mount her from the back, observations which strongly suggested a sexual context for the interaction. They were generally labelled as “courtship” rather than “attempted and successful mating” because of the observer’s difficulty to precisely determine the difference between these two cases.

These interactions were not common throughout the study period, and were usually difficult to detect because they lasted only a few seconds. A selection of 10 such sequences of high quality were analysed, all obtained from six different nights (0:15:04 h). All involved the male who was most constantly together with the group, interacting with each of the four adult females of the colony at least once. All the interactions observed occurred between the male and a certain female while other members of the colony were present at the roost. Additionally, on seven occasions the male performed this behaviour with a female which had her days-old pup attached to her.

The typical interaction sequence would develop as follows: the male approached the female from the back while constantly vocalizing. He then crawled forward climbing on top of her back, until his body was directly on top of hers and their heads were almost at the same level. In this position, he moved his head up and down so that he tapped with his chin on her back, after which the female would sometimes arch her back and bend her head backwards towards him. The male then pressed his hip downwards towards the female’s body and quickly thrust forward several times, after which he tapped her back with the chin again and moved away.

On three of the sequences analysed, the male merely approached the female from the back without physical contact, while still vocalizing constantly. On one occasion, the female was clearly aggressive to the approaching male at first, turning to him and beating him with her wing; the male retreated and tried to mount her again successfully after several seconds. However, usually (six cases) she remained immobile while the male performed.

The vocalizations emitted by the bats during these 10 courtship interactions were recorded on 106 sound files (636 s). As in all behavioural contexts, echolocation-like calls were the most frequent. Ec-like type b calls were far more abundant than the other subtypes (Fig. 28; $p < 0.001$; $\chi^2 = 95.8$; $df = 4$) Furthermore, it was clearly observed that this call subtype was the vocalization predominantly emitted by the male while approaching the target female.

Only 10 non ec-like vocalization types were found in the sound files recorded (Fig. 29). It is noteworthy that these non-ec calls were very infrequent; each recorded less than 10 times each in 106 files. As in the other behavioural contexts, most of the call types were found in very low abundances (just once or twice in this case), while two call types are the most common: crescendos and FM trains. ($p < 0.05$; $\chi^2 = 22.5$; $df = 11$).

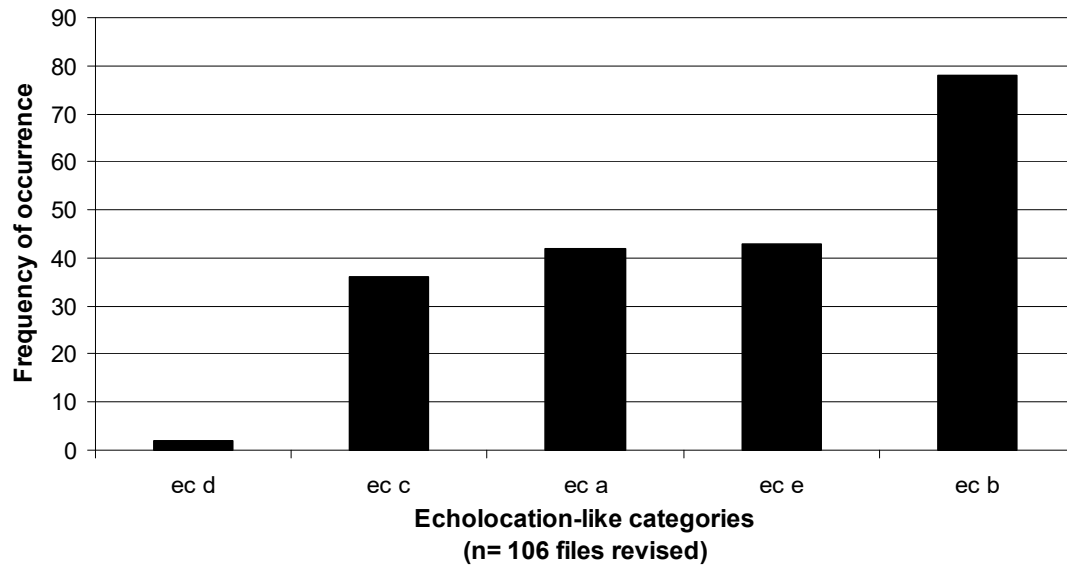


Fig. 28. Abundance of echolocation-like vocalizations of each subtype found during courtship interactions in a colony of *R. naso*. The graph shows the number of times each vocalization subtype was encountered in the files reviewed.

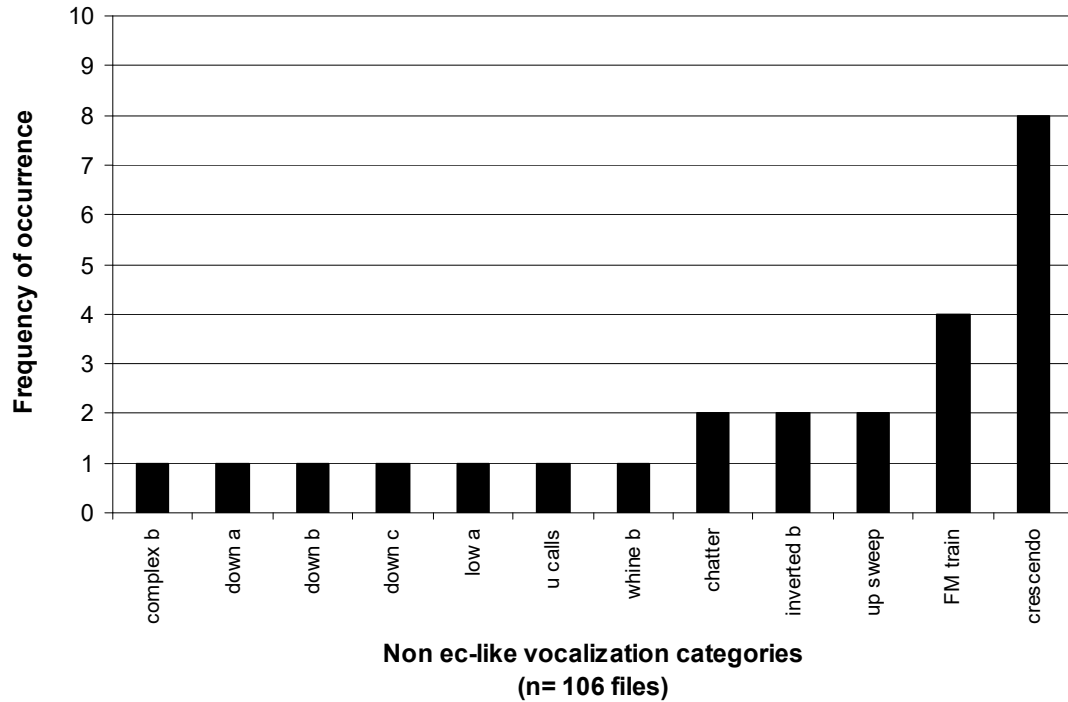


Fig. 29. Abundance of non echolocation-like vocalizations of each subtype found during courtship interactions in a colony of *R. naso*. The graph shows the number of times each vocalization subtype was encountered during this behavioural context.

A general evaluation of the top most abundant vocalization categories in each behavioural context shows that, although variations in the specific set and abundance of each call type appeared, four vocalizations were among the most common in three or all four of the behaviours analysed. On the other hand, four other vocalizations found as most abundant in one specific context were not found to be important based on numbers of occurrence on either of the other interactions (Table 19).

Table 19. Main vocalization categories found during 4 behavioural contexts analysed from a colony of *R. naso*.

Vocalization category	Perching	Agonistic	Mother-Pup	Courtship
Crescendo	x	x	x	x
FM train	x	x	x	x
Chatter	x	x		x
Up sweep	x		x	x
Complex a	x		x	
Inverted b		x		x
Trill b	x			
Down sweep b		x		
Low freq a		x		
Complex b			x	

DISCUSSION

Vocalization repertoire of R. naso

I described part of the vocal repertoire of *R. naso*, consisting of 15 categories and 30 sub-categories of distinct vocalizations employed during social interactions. As expected, the great majority of the calls differed structurally from echolocation calls, which is consistent with my first hypothesis and can be derived from the bats' need to have different signals that convey various messages in different social situations. The repertoire showed a surprisingly high structural diversity, ranging from simple pulses similar to echolocation search phase signals to calls composed of several syllables, with pronounced frequency modulations and several harmonics.

The social vocalizations of *R. naso* (Table 18) can be fitted in the four structural groups described by Pfalzer and Kusch (2003) addressing social calls of the phylogenetically distant vespertilionid bats. These authors grouped calls of 12 species according to their sonographic structure into *squawk-like* or loud, harsh, long duration signals, *repeated* or numerous short, downward sweeping FM pulses, *cheep-like* or curved structured signals produced singly or as double pulses, and *complex* or calls composed of several individual FM and narrow bandwidth signals emitted in a certain arrangement. The structural similarities of *R. naso*'s social calls with these general groups are notable, especially between *squawk-like* calls and a screech, *repeated* calls and an FM train or chatter, *cheep-like* calls and u-shaped calls, down sweeps or inverted-*v*'s, and *complex* vocalizations and *R. naso*'s own complex calls.

The most abundant vocalization type emitted by *R. naso* during interactions consisted of signals resembling the species' echolocation calls in search phase. I identified five subtypes of these calls. My observations suggest they are used for more than scanning the immediate surroundings by ultrasound. I propose that echolocation-like calls emitted by roosting *R. naso* serve a communication function and convey, probably in addition to information about the physical environment, also social information.

First, their sheer abundance (over 90% of the calls recorded) suggests that they may serve a function additional to the continuous evaluation of the physical environment throughout the night. Given the costs associated with vocalizations, especially high intensity sounds like echolocation (Speakman *et al.* 1989; Lancaster & Speakman 2001), the benefits of producing

such sounds must outweigh the costs for the caller. Since I recorded the bats at the roost, when they returned from their foraging bouts, it is likely that the calls were not directed at searching for food from their perch. Second, I found that single bats of either sex would not emit these calls as often and abundantly as they did when accompanied by others (pers. obs.). Third, some of the echolocation-like call subtypes were clearly associated with specific behavioral interactions such as male courtship behavior. All these observations support my suggestion that the benefits to the bats from their constant ec-like vocalizations at the roost might come from a communication function of the calls, which would justify energy expenditure.

One potential function I suggest for this constant calling behavior is that of advertising the presence of a certain bat(s) in the roost. Bats perching in the roost by themselves might have used these calls to let other absent members of the group know where to reconvene after their respective foraging bouts. There were five different places of the building used as night roosts by the colony, and most group members would return within 10 minutes of the first bat to the specific location chosen for the night, after each period of absence (pers. obs.). Additionally, if the echolocation-like calls are able to carry individual information, then the roosting bats would be able to advertise their identity and presence to the other group members during their periods of low activity, which might serve as a means of maintaining group cohesion. The ability of bats to individually recognize conspecifics by their echolocation calls has been shown by Yovel and collaborators (2009) for *Myotis myotis* and by Kazial and collaborators (2008a) for *Myotis lucifugus*, thus, the encoding of individual signatures in these echolocation-like calls of *R. naso* might be a possibility.

By examining the non echolocation-like social calls, it is evident that some syllables are used in multiple contexts. Some call types in the repertoire are composed of one syllable type (monosyllabic calls) emitted singly or in irregular groups, such as inverted “v”s or down sweeps (subtype *a*). As basic units, some syllables may be also emitted in groups (e.g. down sweeps *a* vs. FM trains) or combined with others into multisyllabic calls (e.g. inverted “v”s and u-shaped calls vs. complex calls). As in *Tadarida brasiliensis*, a possible advantage of combining the same syllables into different calls is that the vocal repertoire can be expanded without having to invent new syllables (Bohn *et al.* 2008). Such vocal flexibility seems to be contributing to a larger vocal repertoire than I previously expected for the species.

Trills, ripple and whines are three call types with sinusoidal modulations in their structure. In general, there was a large variability in their spectral structure which was also evident in the

results of the DFAs performed (Fig. 20). These showed much dispersion among the individual calls, evidence of the high variability in the values of the parameters measured in order to describe them and test their distinctiveness. In *S. bilineata*, these types of modulated calls potentially reflect individual identity and qualities of the caller (Davidson & Wilkinson 2004; Behr *et al.* 2006). However, since my experimental set-up did not allow me to assign specific calls to their emitter and since this was not always possible from my visual observations, more observations are needed to unravel specific details about this variability observed.

Link between vocalizations and behavior

One of the main challenges faced in this study was that of linking groups of vocalizations from the repertoire to the specific behavioral situations in which they occurred. I hypothesized a high level of specificity between social calls and distinct behaviors. However, although I did find some cases of prominent call-behavior association, I also found a generalized and dominant use of just four of the vocalization categories in all the behavioral contexts under study: crescendos, FM trains, chatters and up sweeps (Table 19). Crescendos and FM trains occurred predominantly in all four behavioral contexts, while chatters and up sweeps occurred in three of them. Other studies have also found that similar calls are emitted in different contexts and thus seem to serve different functions, possibly because social call function might depend more on context than on structure alone (Barlow & Jones 1997). In this sense, a certain call type which conveys identity or dominance can have different meanings in varying social situations and with different individuals involved (Carter 2007).

Moreover, I classified the behavioral situations according to the most prominent types of interactions observed in each case, though other types of interactions could have also occurred more subtly during them. For example, an interaction that I classified as mother-young might have also contained some agonistic conflict between the mother and young involved, or during periods in which the bats were perching without any visible interaction, the male could have continued his attempts of sexually addressing a female in the group. As an unequivocal assignment of each individual vocalization type to the specific motivation of the caller as well as overall context was not possible, I see my results as an important step to lay the ground for future, more detailed studies, ideally with an experimental background testing the function of the calls for example with playback experiments and modifications to the calls.

My analyses of vocalizations permit first characterizations of signals from free-living animals in search of patterns that might give insights about their function. I am somewhat limited in my interpretations since, as Pfalzer & Kusch (2003) noted, I can only analyse calls punctually (by measuring specific parameters such as maximum frequency, for example), while bats can interpret the calls as a whole (hear their “melody”) and thus distinguish finer relevant details in them. Additionally, other features such as the tone of the calls, and physical or chemical expressions accompanying the vocalizations, were beyond the reach of this study and are certainly involved in the communication process (Wilson 1980; Owings and Morton 1998). Nevertheless, the observed relationship between form and function in vocal communication allows me to make educated interpretations of my observations.

I predicted that the spectral characteristics of the social calls of *R. naso* should comply with Morton’s (1977) MSR for bird and mammalian vocal communication: basically that vocalizations emitted in hostile contexts would be low-frequency (low-pitch), wide-bandwidth (noisy) sounds, while vocalizations emitted in fearful or appeasement contexts would be high-frequency (high-pitch), narrow-bandwidth (tonal) sounds. Crescendos, the most abundant call type found in all behaviors studied, had their highest relative abundance during agonistic interaction periods. According to MSR, they should be low-frequency and noisy if coding for hostile motivations. However, they are typically composed of only tonal, relatively high-frequency syllables, since only their starting syllables are in the lower frequency range. As atmospheric attenuation is stronger for higher frequencies than for lower frequencies (Griffin 1971), the initial low-frequency parts of crescendo calls would suffer less attenuation and thus might be potentially perceived as louder by the other bats in a short distance range. In contrast, the high frequency end of the crescendo would attenuate faster, which might be useful to avoid the call reaching far to potential predators. However, so far the overall structure of crescendos and my contextual information about their use does not entirely fit my prediction based only on MSR. As August and Anderson (1987) noted, there are more levels of selection on the design of animal vocalizations that are affected by other factors, such as the ability to be localized and factors associated to distortion of the sound, which are for now beyond the reach of my study.

FM trains are composed of calls with short duration, broad bandwidth and high repetition rate, all three are characteristic of signals known as “distress” or “irritation” calls in several other species of bats from different families: Brown (1976) reports “irritation buzzes” from *Antrozous pallidus*, that are used by this species to threaten other bats or alert them of possible danger.

She recorded them from bats during handling as well as from mothers weaning their young. They might be a warning signal to prevent physical aggression between individuals. Pfalzer & Kusch (2003) noted that similar calls in vespertilionids (*repeated*) are associated with increased irritation of individuals, which may occur when a bat is handled or during interactions between females and their pups. Carter (2007) found similar calls in *Diaemus youngi*, which he termed “buzzes”. They occurred when the bats were fleeing an aggressive encounter. Bohn *et al.* (2008) also reported such “irritation calls” that were emitted by *T. brasiliensis* when jostled by another bat in the roost or when disturbed by a handler. This interpretation of the social function of FM trains would comply with my observations as this vocalization type was always emitted of individuals that were in a group of roosting bats and thus may have been somewhat irritated from one or another individual nearby.

The social function of the other two prominent call types, chatters and up sweeps, is more difficult to infer from their structure alone. Chatters were frequently recorded from bats right before they left or upon return to the roost, suggesting they might be some kind of contact (Gould 1977) or directive call (*sensu* Brown 1976). Brown (1976) noted that directive calls from *A. pallidus* were used by individuals right before leaving the roost to forage or upon return at dawn. They were sometimes answered by others in the roost or in flight. An analogous “contact note” is used in birds to coordinate group movements (Collias 1960). The short duration as well as their broad frequency range would render chatter calls easy to localize (Schnitzler & Kalko 2001), supporting the assumption that they might serve the function of advertising the exit or return of the caller (Brown 1976; Fenton 1985). However, chatters were also emitted in trains that sometimes led up to trills. Thus, their function might be modified according to the behavioral context in which they are produced (Barlow & Jones 1997) and the use of other associated vocalization types.

Perching interactions- I observed that roosting bats carried out some behaviors in synchrony, such as grooming, swaying (*sensu* Bradbury & Emmons 1974) and urinating. This has also been noted in previous studies of the species (Dalquest 1957, Bradbury & Emmons 1974, Knörnschild *et al.* 2009a). I suggest that some of the echolocation-like calls might serve the function of coordinating such synchrony; very frequently, after periods of absolute silence, the echolocation-like vocalizations began when one or two of the bats engaged in grooming, stretching, or gently rocking sideways, a frequent behavior in this species. It has been

hypothesized that this synchrony motion might play a role in the bats' cryptic roosting habits (Knörnschild *et al.* 2009a).

Almost all call types described in this vocal repertoire occurred while the bats were perching, without visible interactions among the individuals (Fig. 22). However, as noted before, very subtle interactions might have also occurred among the immobile individuals, which could have remained invisible to the observer because they could have been resolved only vocally by the bats. For example, slight conflicts between individuals might have elicited irritation or even mildly aggressive signals, pups may have briefly solicited care from their mothers, and the male might have continued his courting behavior towards a female only vocally, without physically approaching her. Therefore, it was not possible to make further interpretations of the vocal repertoire recorded during this behavioral context.

Agonistic interactions- Crescendos occurred most frequently in this context. Although dominated by the same four call types present in other behaviors, the highly modulated calls that have more potential for individual identity and information content (whines, ripples, trills) than other types emitted mostly in this context, such as down sweeps or FM trains (Table 18). Screeches and composite calls, though quite rare, were also found to be relatively more abundant during these interactions than in other contexts (Table 18). These harsh, low frequency vocalizations would be expected to associate with agonistic interactions according to Morton's (1977) MSR, and thus their presence in this context complies with my prediction. Low frequency pulses, the tonal signals with the lowest frequency range of the repertoire, were also prominent here. Closer examination of examples from two sides of the behavioral gradient (mild vs. extreme aggressions) showed that this call type tended to increase in abundance as conflicts escalated (Fig. 25).

All these results comply with Morton's (1977) theoretical predictions for vocalizations during aggressive interactions. Highly variable signals such as whines, ripples and trills, could be individually distinguishable to communicate the identity of the caller (Bradbury & Vehrencamp 1998). Recognition of individuals is important in maintaining cohesion in social groups, and it could also play a role in deescalating a conflict within group members (Wilkinson 2003). On the other hand, low frequency sounds are coupled with larger body sizes (Morton 1977). Thus, a lower frequency vocalization could persuade a weaker opponent to cease further hostile behaviors, which would be advantageous from the caller's perspective for resolving the conflict without physical risk (Wilson 1980, Morton 1977). Additionally, as the frequency of a sound

decreases, so does the tension of the membrane that produces the sound, automatically producing harsh sounds (Morton 1977). Both low frequency and harshness render sounds apparently louder with respect to the listening individual, another characteristic that is important for agonistic calls (Bradbury & Vehrencamp 1998).

Mother-young interactions- The situations in which a female was interacting with her pup, whether before or after it became volant, were dominated by complex calls, which were identified by this study for the first time as the infant isolation calls of the species (Fig. 8). Isolation calls are signals emitted by pups to solicit attention or care from their mothers (Gould 1977, Wilkinson 2003, Bohn *et al.* 2006, Knörnschild & Helversen 2008). *R. naso*'s isolation calls also have the characteristic "double-syllable" ("double-note" *sensu* Gould 1973) structure noted in several other species of bats (Brown 1976, Barclay *et al.* 1979, Porter 1979, Brown *et al.* 1983, Fenton 1985, Sterbing 2002, Bohn *et al.* 2007). Their tonal, high frequency shape, related to the small size (and age) of the caller, also complies with the predictions of Morton's (1977) MSR for infant sounds, which should elicit positive ("friendly" *sensu* Morton 1977) responses in the surrounding adults. Additionally, double-syllable calls are normally harmonic rich and have downward-modulated syllables, which is a common design for recognition signals that can encode valuable individual information (Bradbury & Vehrencamp 1998; Pfalzer & Kusch 2003; Wilkinson 2003).

Given their social function, it was not surprising either to have found complex calls rather frequently also during perching (Fig. 22) and agonistic interactions (Fig. 24). Pups were present in these situations and were therefore involved in the activities of the whole group, certainly requiring their mothers' attention at times.

The least frequent of the echolocation-like calls found in the repertoire of *R. naso* (subtype *d*) had its highest abundance during mother-pup interactions (Fig. 26). My behavioral observations revealed that this call type was produced by the pups. Although the parameters measured were not entirely sufficient to statistically separate this call subtype from the rest (Fig. 19), the visual examination, lower maximum frequency and the irregularly curved QCF part of the call in the spectrogram, provided first evidence for structural distinctiveness. Such characteristics comply with the reports from pups' vocalizations in other mammal species, which are known to typically increase in frequency and progress from a stage of structurally irregular calls to the adult rendition as they age (Janik & Slater 1997; Knörnschild *et al.* 2006; Knörnschild *et al.* 2009).

Courtship interactions- During the courtship or sexual interactions analysed, my most prominent finding was that the male continuously emitted an ec-like call (subtype *b*) while approaching the female and during the brief moments in which he mounted her. This was therefore the most frequent call type recorded in this context. Thus, I believe that it serves the function of a mating call in this species. Mating calls or vocal signals associated with sexual interactions are known from other bats, and range from quite simple, repetitive signals (*Hypsignathus monstrosus*, Bradbury 1977; *Myotis lucifugus*, Barclay 1979; other flying fox species, Wilkinson 2003) to the elaborate songs created by *S. bilineata* as part of their complex courtship behavior (Behr & Helversen 2004; Voigt *et al.* 2008). Though I did not find a sophisticated song display during the courtship behaviors of *R. naso*, the existence of a mating call in the species certainly challenges my initial prediction of a rather simple vocal repertoire for these bats.

In contrast to the other behavioral contexts, I found that very few non ec-like vocalization types occurred during courtship interactions, each at very low abundances (Fig. 29). This may be explained by the short duration of this type of interaction, and the predominant intentions of the male that mostly produced the mating call. In addition to ec-like calls, crescendos and FM trains were the most common calls emitted by the bats, suggesting that at least one of the individuals involved was briefly irritated or distressed.

R. naso and S. bilineata: comparing elements of the vocal repertoire

I predicted that the vocal repertoire of *R. naso* would be simpler and less elaborate than that from *S. bilineata*, on the basis of the latter's more complex social organization, and its typically enclosed roosting habits. My first exploratory evaluation of the spectral characteristics of *R. naso*'s vocalizations resulted in 15 vocalization categories composed of 30 different vocal subtypes. The latest vocal repertoire accounts of *S. bilineata* by Behr & Helversen (2004) and Knörnschild (2009) identified nine vocalization types, which were defined more from a behavioral context and call usage perspective. Since my analysis does not fully share a common base with these studies, a comparison of both repertoires in terms of number of vocal types can not be made. Beyond this level, Wilkinson (2003) mentioned three other levels by which vocal repertoire complexity in bats can be assessed. These deal with 2. the number and order in which syllables are combined, 3. the individual variations in the acoustic features of the calls, and 4. the ability to modify vocalizations by vocal learning (Wilkinson 2003).

I have already reported that I found *R. naso* to combine certain syllables to form composite syllables in varying orders. Some syllables emitted singly may also appear together with others in call trains (e.g. FM trains, chatters) or multisyllabic calls (crescendos, complex calls). No songs or elaborate arrangements of individual syllables were identified from either males or females, while only a few multisyllabic calls were found as compound elements in the species' repertoire. At this level, the vocal complexity of the males of *S. bilineata* is therefore higher; the combination of its basic call types into extensive songs is known to involve many more individual syllables, which are specifically arranged for their use in a courtship or territorial context (Davidson & Wilkinson 2004, Behr & Helversen 2004). The third and fourth levels of complexity proposed by Wilkinson (2003) have been only explored for *S. bilineata*. Their vocal repertoire is known to include both individual signatures in syllables of the male songs (Behr & Helversen 2004; Behr *et al.* 2006) and strong evidence for vocal learning during pup development (Knörnschild *et al.* 2009b). In the case of *R. naso*, I suggest the potential of some calls of the repertoire to encode individual identity, but certainly further studies with experimental components are needed to elucidate these topics clearly.

I found that several of *R. naso*'s calls share similarities with those known to be used by *S. bilineata* (Behr & Helversen 2004; Behr *et al.* 2006). Although the main frequencies of the calls of *R. naso* were higher than the calls of *S. bilineata*, there are striking structural resemblances between the call types termed chatters, screeches, and trills of the two species. Composite calls of *R. naso* showed a structure similar to calls termed long buzzes in *S. bilineata*, while whines resembled quasi-CF calls of the latter because of their predominant QCF component. Furthermore, the call type termed "bark" in the repertoire of *S. bilineata* (Behr & Helversen 2004), reminded of an ec-like call (subtype *a*) of *R. naso* with the main energy in the first harmonic, because both call types are composed of a pure QCF component.

Some of these calls seemed to serve similar functions in both species. Screeches were recorded from both males and females in both species and are related to agonistic encounters in both cases (Behr & Helversen 2004). Trills of *R. naso* were predominantly associated with mother-young and agonistic interactions. Their potential to encode individual signatures would be useful during both mother-pup contact and aggressive contexts, a question which remains to be explored quantitatively for this species. In the case of *S. bilineata*, trills are the main component of the courtship song of the males (Behr & Helversen 2004). Furthermore this signal encodes

the individual identity of the caller and is often used in female mate choice (Behr & Helversen 2004).

Composite calls were the rarest vocalization type in my sound recordings, appearing only during agonistic and mother-pup interactions. According to Morton's (1977) MSR, their structural characteristics should be a mix between the low frequency, harsh sounds expected for aggressive contexts, and the upwardly modulated tonal sounds expected for appeasing or "friendly" situations. Unfortunately, as those calls were very rare, their potential social function could not be unequivocally established for *R. naso* during this study. In *S. bilineata*'s repertoire, the similarly structured long buzzes occur in an agonistic context, as part of the territorial song of the males. In this species, the calls' acoustic characteristics were correlated to the reproductive success of the males (Behr *et al.* 2006). Certainly more detailed studies on the use of composite calls by *R. naso* will render valuable information for the understanding of the social behavior of the species. Finally, chatter calls form a rather common element of the vocalization repertoire of *R. naso* and were also found rather frequently in *S. bilineata* not associated to any particular behavior. Thus, a comparative examination of this similarly structured call type is also not possible yet from our data.

According to the most recent molecular phylogeny of the emballonurid family (Lim & Dunlop 2008), the genera *Rhynchonycteris*, *Saccopteryx* and *Centronycteris* form a clade within the Diclidurini tribe. My observations that *R. naso* and *S. bilineata* share striking similarities in certain elements of their vocal repertoire suggest that these shared traits might have been already present in their common ancestor, and have been shaped distinctly by their differing social behaviors and roosting habits.

The highly diverse vocal and social behavior repertoire of *S. bilineata* is the result of a strong sexual selection force acting upon the males and shaping the overall social interactions in the species (Voigt *et al.* 2008). From a sexual selection point of view, the somewhat simpler vocal repertoire and the lack of obvious visual displays found in *R. naso* suggest that this evolutionary force has acted upon different behavioral (or physical and/or physiological) traits in this species, and has not yet pushed the diversification of their vocal repertoire as far as in *S. bilineata*.

Furthermore, the different roosting ecology of both species might also play a role in the complexity of their vocal social communication and behavior. In nature, *S. bilineata* colonies use rather cryptic roost sites which are typically enclosed from direct access of potential predators

(tree cavities and buttress spaces), while *R. naso* typically roosts in the open, exposed surfaces of tree boles, boulders and river walls. Its morphology, roosting position and cryptic behavior are likely to be adaptive to keep overt displays at a minimum, which might draw attention of potential predators to their location (Bradbury & Emmons 1974; Knörnschild *et al.* 2009). I am aware that my observations were conducted at night when visibility is obviously much reduced, but two anecdotal observations of the bats' behavior in the presence of two potential predators suggest that their primary strategy is to remain still and blend in, as has been reported by other researchers as well (Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976; Knörnschild *et al.* 2009). Once when a boa snake approached the roosting spot of the bats under the lodge's roof; they remained immobile until the animal came very close, at which point they all flew simultaneously away from the roost and out of the building. Another time, an omnivorous bat, *Phyllostomus hastatus* (Phyllostomidae) came into the building and flew around several times, coming very close to their roost and echolocating continuously. In this case, the reaction of *R. naso* was to keep absolutely quiet and motionless, until the spear-nosed bat had left the building. If blending in against an exposed roosting background is the predominant strategy to avoid predation in this species, then any social behaviors that make them become obvious will not be favored by selection, including overt visual displays and loud, far-reaching vocal signals. In this sense, despite of their frequent vocal interaction throughout the night, the particularly high frequency of their social calls should be strongly attenuated in the air and might be above the hearing range of many potential predators as well, which represents a further advantage for their crypsis in their open roosts.

This first description of the vocal communication repertoire of *R. naso* reveals a richer array of social calls than was previously expected for the species. I was able to determine certain clear trends of call-behavior association based on my observations of the bats at the roost. Certainly, some common call types seem to serve different social functions depending on the context in which they are used. However, this first assessment could not assign a specific behavioral context to every vocalization category encountered. *R. naso's* vocal repertoire shares several structural similarities with that of the well-studied *S. bilineata*, which suggests these communication traits were already present in their common ancestor. The different social organization and roosting habits of both species might have played a role in the evolution of their communication and social systems. Further experimental studies that follow up from my findings on *R. naso's* social dynamics and vocal communication will shed more light over the factors influencing these aspects of social behavior in nature.

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