

RESEARCH ARTICLE

Social behaviour and vocalizations of the tent-roosting Honduran white bat

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Abstract

Bats are highly gregarious animals, displaying a large spectrum of social systems with different organizational structures. One important factor shaping sociality is group stability. To maintain group cohesion and stability, bats often rely on vocal communication. The Honduran white bat, *Ectophylla alba*, exhibits an unusual social structure compared to other tent-roosting species. This small white-furred bat lives in perennial stable mixed-sex groups. Tent construction requires several individuals and, as the only tent roosting species so far, involves both sexes. The bats' social system and ecology render this species an interesting candidate to study social behaviour and vocal communication. In our study, we investigated the social behaviour and vocalizations of *E. alba* in the tent by observing two stable groups, including pups, in the wild. We documented 16 different behaviours, among others play and fur chewing, a behaviour presumably used for scent-marking. Moreover, we found 10 distinct social call types in addition to echolocation calls, and for seven call types we were able to identify the corresponding broad behavioural context. Most of the social call types were affiliative, including two types of contact calls, maternal directive calls, pup isolation calls and a call type related to the fur-chewing behaviour. In sum, this study entails an ethogram and describes the social vocalizations of a tent-roosting phyllostomid bat, providing the basis for further in-depth studies about the sociality and vocal communication in *E. alba*.

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Introduction

Bats are social animals exhibiting a large spectrum of social systems with varying degree of complexity. This includes species living in perennial stable groups) [e.g. 1] and species exhibiting social structures characterized by fission-fusion dynamics [e.g. 2]. One of the factors shaping sociality in bats is social group stability. Stable group living offers various benefits, including information transfer about food and roosts, and the evolution of cooperative behaviours such as allo-maternal care, allo-grooming and food sharing [2]. In bats, vocal

communication is a major factor facilitating group formation and cohesion, thus supporting group stability [1, 3, 4]. A well-studied example, evolved to maintain group cohesion, is the contact call system in the Spix's disc-winged bat, *Thyroptera tricolor* [5]. This bat species roosts in furred leaves of *Heliconia* plants, an ephemeral and often sparsely available resource. Roosts are only inhabitable for one day; hence, *T. tricolor* is forced to find and switch to new roosts every day [6]. Interestingly, despite constant roost switching, *T. tricolor* forms very stable perennial social groups [5]. To maintain group cohesion *T. tricolor* evolved a specialized call-and-response system, including inquiry calls to locate group members and response calls to recruit group members to the roost [6]. Another foliage roosting species, which exhibits an interesting social system is the Honduran white bat, *Ectophylla alba* [7]. This is a small (i.e. 6–9 g) phyllostomid bat endemic to the Caribbean slope of Central America and known to construct and roost in tents [7, 8]. It is well known for its characteristic white fur and yellow skin colouration of the ears and nose-leaf, an adaptation primarily evolved for camouflage associated with tent-roosting [9]. However, the yellow skin colouration, particularly of the nose-leaf, appears to be a sexually dichromatic trait, suggesting a secondary function as sexually selected signal [10]. The most commonly described mating system in tent-roosting bats is polygyny (i.e. harem structure composed of one male and several females [11]). In contrast, *E. alba* forms mixed-sex groups with an average size of 5–6 individuals [12]. Interestingly, although genetic relatedness among adult social group members is very low [13], the groups are very stable over time, switch roosts together, and group members appear to have preferred individuals with whom they associate while roosting [12]. Furthermore, both sexes are involved in tent construction [8]; in contrast, it is commonly assumed that in other tent-roosting species only males construct tents [7]. In *E. alba*, several individuals engage in tent construction, a process which requires multiple nights until finalization [14]. However, it is not yet understood if these individuals all belong to the same social group.

Ectophylla alba's unusual social organization, high group stability despite the low relatedness and potential cooperative tent construction render this bat species an interesting candidate to study social behaviours and vocalizations mediating social interactions. Although the ecology of *E. alba* was intensively studied during the past decades, only very little is known about its' social behaviour [12] and information about vocal communication is restricted to a single study, describing one call type emitted on the wing close to the roost [15]. Our study aimed to describe the social behaviours and vocalizations in the roost to establish an ethogram and a vocal repertoire description of *E. alba* based on observations of wild individuals in their natural habitat.

Material and methods

Study site and subjects

We monitored two groups of *E. alba* in La Tirimbina Biological Reserve, Heredia Province, in the North-East of Costa Rica (10°26'N, 83°59'W) from May to June 2010. La Tirimbina Biological Reserve contains fragments of secondary tropical wet forest and has been the centre of detailed investigations on the natural history of *E. alba* in the last decade [8, 10, 12, 14, 16–18]. The first *E. alba* group (i.e. group 1) that we monitored consisted of four individuals (two adult males, one adult lactating female and her non-volant male pup), the second group (Fig 1A; group 2) of 6–10 adult individuals of both sexes (the core group consisted of five adult males, one adult lactating female and her non-volant male pup; the sex of the other three adult bats that joined the core group on and off could not be determined). Females are polyestrous, they give birth to a single pup in September and April [11]. Pups are born with fur and become more independent at an age of 3–4 weeks when they start to fly [14]. Bats of group 1 could be

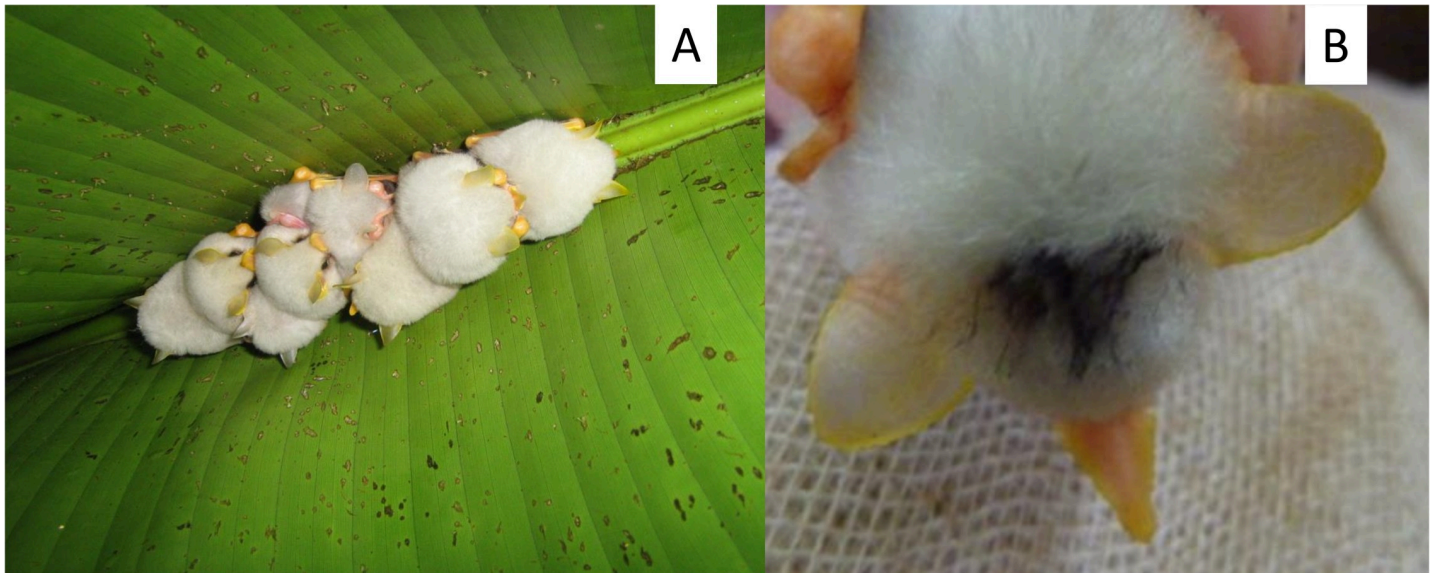


Fig 1. Observation of wild *Ectophylla alba*. **A:** Picture of group 2 roosting in the tent during the day. Clearly visible is the yellow coloration of the ears of the adult individuals, whereas the pups' ears are still almost white. **B:** Temporal colour marking of the fur to distinguish individual bats from group 1.

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individually distinguished via colour marks on their fur (Fig 1B). Therefore, this was our focal group for behavioural observations and sound recordings. We observed and monitored group 1 during 25 nights between the 07th of May and the 30th of June 2010 (during nights with heavy rainfall data collection was not possible). Group 2 was only occasionally monitored and behavioural observations obtained from this group were anecdotal and served to complement the observations obtained from the focal group 1. All statistical analyses were based on data of group 1 only. During our observation period, both groups constructed new tents in the vicinity of their old ones and subsequently switched roosts.

Behavioural observations

We conducted behavioural observations in the bats' tents using a digital video camera with night-shot function (Sony Handycam DCR-SR32) and two infra-red lights (Sony HVL-IRM). The video equipment was placed directly underneath the tent and did not seem to disturb the bats. The video camera was connected via a 5 m cable to a video walkman (Sony DV-D900E) which allowed us to store the video recordings on mini-DV tapes (Sony DVM60PR3; 1.5 h run-time) and watch the video footage in real-time without disturbing the bats. This set-up permitted synchronous behavioural observations and sound recordings (see below for details). Video footage was analysed using the VLC Media Player (v1.0.5, VideoLan, France).

Since *E. alba* roosts cryptically during the day [7], we assumed that most social interactions would take place at dawn and dusk when bats are returning to or leaving the roost, or during the night when bats return to their tent [12]. To test this, we collected behavioural data over a total of 22 hours by monitoring group 1 for 3-hour periods spread equally over six days and nights (ranging from 9:47 to 8:03 of the next day). Each 3-hour period was recorded only once, each on a different date. The 22 hours were spread over several dates to avoid a sampling bias (e.g. randomly sampling a day/night which is deviating from average). Based on this 22-hour monitoring, we calculated time budgets of the different behaviours that we observed and determined when bats were most active. Consequently, we restricted our behavioural observations and sound recordings to recordings from dusk until dawn using *ad libitum* sampling [19].

During 25 nights, we recorded the bats' behaviours in group 1 to establish an ethogram. Group 2 was observed occasionally and complemented our behavioural observations of group 1.

Each social behaviour type was considered either a state or an event [19]. States were defined as behaviours with a minimum duration of ten seconds, including behaviours during which the same motor actions were performed repeatedly (e.g., wing fluttering). Events were instantaneous and singular (e.g. wing stretching) and occurred during a state. To calculate time budgets for the different behavioural states, we used the data from our 22-hour monitoring. For each of the adult individuals in group 1 ($n = 3$) the 22 hours of observation time was split into two biological meaningful periods: the night-period, which included the time from leaving the tent at dusk to returning at dawn, and the day-period, which included the time from returning to the tent at dawn to leaving at dusk. Subsequently, we calculated the duration of each state (in seconds) and converted the durations into percentages to be able to compare these between individuals and day- and night-periods. The pup was not yet weaned and not foraging on his own; therefore, we decided not to split the 22-hour observation period for the pup.

Sound recordings

We used a high-quality ultrasonic recording setup (500 kHz sampling rate and 16-bit depth resolution) consisting of an ultrasonic microphone (Avisoft USG 116Hm with condenser microphone CM16; frequency range, 1–200 kHz) connected to a laptop computer (JVC, MP-XP741DE) running the software Avisoft-Recorder v4.2 (R. Specht, Avisoft Bioacoustics, Berlin, Germany). The broad behavioural context of each vocalization type in the vocal repertoire was assessed with simultaneous behavioural observations and video recordings ($n = 20$ nights of simultaneous video and sound recordings). Sound and video recordings were synchronized with a bat detector (Pettersson D980, Pettersson Elektronik, Uppsala, Sweden) that was set on frequency division mode and connected to the audio channel of the video camera.

On one occasion, the video recordings contained two previously unknown vocalization types which were only recorded with the camcorder's built-in microphone and not with the high-quality ultrasonic recording setup. Therefore, these two vocalization types were excluded from our acoustic analyses but we discuss the behavioural context in the results and corresponding spectrograms can be found in the supplements.

Acoustical analyses

Prior to acoustic analyses, vocalizations were visually classified into distinct social call types (i.e., social refers to calls other than echolocation calls) based on spectro-temporal features in the spectrograms; the different behavioural contexts in which vocalizations occurred were annotated based on behavioural observations of bats in the roost. Subsequent acoustic analyses were conducted to characterize the different social call types and assess their acoustic distinctiveness. We used Avisoft-SASLab Pro (v5.0, R. Specht, Berlin, Germany) for acoustic analyses. Only calls with good signal-to-noise ratio that were not overlapped by other calls or background noise were selected for acoustic measurements (116 in total; 5–41 per call type). All calls were multiharmonic and some had an undulating structure (more than one frequency modulation). Since different harmonics were emphasized (i.e., had the largest amplitude) in different social call types, we used the strongest harmonic for measurements; we thus selected harmonics that contributed most to the acoustic impression of different social call types. We determined the start and end of calls manually based on the oscillogram. Subsequent measurements were taken from spectrograms created with a Hamming window with 512-point fast

Fourier transform and 93.75 per cent overlap (frequency resolution: 977 Hz; temporal resolution: 0.064 ms). For all calls, we measured one temporal parameter (duration) and three spectral parameters (peak frequency at the start, middle and end of each call). Thus, we used four parameters per call to assess the acoustic distinctiveness of different vocalization types.

Statistical analysis

We simultaneously included all four acoustic parameters in a discriminant function analysis (DFA), all of which were checked for multicollinearity. We used an 'n-1' cross-validation procedure which classified each call based on discriminant functions established with all social call types other than the one being classified. Prior probabilities were adjusted to unequal group sizes. All statistical tests were performed with SPSS (v.22, SPSS Inc., Chicago, IL, U.S.A.)

Results

Social behaviours

We observed six behavioural states and ten different behavioural events occurring in the tent-roost ([Table 1](#)). Most behaviours were observed during both the day- and night-period. The states "fur chewing" and "playing" were only observed during the night, whereas the event "change position" was only noted during the day. However, outside of the 22-hour observation period, "change position" was also observed during the night.

Adult bats exhibited two main activity peaks, one before sunset and one around sunrise. This coincides with the time at which adult bats leave and return from foraging at night. The activity peaks were characterized by increased self-grooming, wing stretching and frequent position changing in the roost. The analysis of the 22-hour observing period ([S1 Dataset](#)) revealed that during the day-period, the adult bats spent the majority of time resting (male 1: 91.9%, male 2: 96.7%, female: 77.4% of the time). A short amount of the time they spent auto-grooming (male 1: 8.1%, male 2: 1.5%, female: 1.5% of the time) and, in the case of the female, nursing (21.2%). Male 2 was attacked by a mosquito during the 22-hour observation period and spend considerable time with distress behaviour (i.e. vigorously shaking the body and lashing out with half-opened wings, 1.74% of the time). The female nursed the pup three times before leaving for foraging at sunset and twice in the early morning after returning to the tent at sunrise. The longest nursing duration was observed at 06:00 when the female nursed her pup for one hour and 21 minutes.

During the night-period, adult bats spent most of the time foraging (i.e., were absent; male 1: 96.5%, male 2: 95.2%, female: 95.9% of the time). The female visited the tent twice during the night to nurse her pup (3.6%) and spent some time resting (0.5%). One of the males visited the tent only once, whereas the second male visited the tent five times and stayed for a short period. During their visits, males were resting (male 1: 0.3%; male 2: 0.8%) and self-grooming (male 1: 1.08%, male 2: 2.5%). Furthermore, they engaged in fur chewing (male 1: 2.14%, male 2: 1.4%).

The pups' main activities (22h-period was not split in day- and night-period) constituted of resting (63.7%), nursing (12.8%), auto-grooming (8.5%) and changing position in the tent (0.9%). Although changing position was usually considered an event, in this case, it was defined as a state because the pup was continuously changing his position in response to being gently bitten by an adult male (i.e., male fur chewing behaviour). At night, the pup was absent for short periods of time (14.1%). At this stage in ontogeny, the pup engaged in first flight attempts. However, compared to the other group members, the pup was the least time away from the tent. Furthermore, the pup occasionally engaged in a behaviour which was defined as play ([Table 1](#)). Note that some states were not observed during this continuous 22-hour

Table 1. Ethogram describing behaviours of *E. alba* observed in the day-roost.

State or Event	Behaviour	Description	Estimated frequency of occurrence	Performing sex	Age	Occurrence during states
S	Resting	Roosting motionless, often with concealed faces (not to be equated with sleeping)	Very common	Both sexes	all	-
S	Scanning	Echolocating with twitching ears and nose-leaf, often directed at the ground below the roost	Very common	Both sexes	All	-
S	Self-Grooming	Tending to coat and wings with tongue and hind feet	Very common	Both sexes	All	-
S	Fur chewing	Conspicuous, prolonged licking and/or gentle biting the fur of conspecifics (of both males and females and pups) between the shoulder blades and coating it with saliva	Rare	Only males	Adults	-
S	Allo-Grooming	Mother tending to coat and wings of her non-volant pup with her tongue	Common	Only females	Adults	-
S	Nursing	Pup attaches to teat of mother and extracts milk	Common	Only females	Adults	-
S	Licking	Soliciting maternal care by licking the corners of her mouth or her belly; often followed by nursing	Common	Both sexes	Pups	-
S	Twitching	Maternal signal for the pup to release the teat	Common	Only females	Adults	-
S	Shaking	Rapid whole-body muscle contractions, presumably for thermoregulation	Rare	Both sexes	Pups	-
S	Playing	Conspicuous, prolonged and seemingly playful engagement with a torn piece of leaf in the roost	Rare	Both sexes	pups	-
S	Startle posture	Raising of half-opened wings high above head and back, followed by covering face with raised half-open wings	Rare	Both sexes	Pups	-
S	Flight practice	Rapid wing fluttering while clinging to the roost surface with hind feet	Common	Both sexes	Pups	-
E	Yawning	Exposing gum and teeth	Common	Both sexes	All	Resting Cleaning Nursing
E	Changing position	Climbing to a different roosting position within the day-roost	Very common	Both sexes	All	Resting
E	Wing stretching	Stretching of one wing	Very common	Both sexes	All	Resting Cleaning Nursing
E	Hitting	Aggressively hitting conspecifics with partly outstretched wing	Rare	Both sexes	Adults	Resting
E	Urinating/Defecating	Urinating/Defecating by arching back; never when in body contact with conspecifics	Rare	Both sexes	All	Cleaning

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recording; therefore, they are not included in the calculation of time-budgets but are nevertheless described in the ethogram. Two unusual and rare behaviours are subsequently described in greater detail; namely “fur chewing” and “play”.

“Fur chewing” in males. After manoeuvring behind the back of a roosting group member, males were observed licking and gently biting the fur between the shoulder blades for a prolonged time (up to 13 minutes, Fig 2). While chewing the fur, males were sometimes simultaneously trembling their folded wings. After chewing, the bitten individual showed a visible patch of wet fur from the saliva biting individual. In most cases, males were chewing fur on the back of a female, but it was also observed that males chewed on the back of each other. In one occasion, a male that returned to the roost performed this behaviour on the pup who was roosting alone in the tent (for about 6 minutes, see S1 Video). The individual being bitten remained mostly still, sometimes started self-grooming, wing stretching and changing the position, with the fur chewing individual firmly clinging on. Eventually, the individual being bitten (if it was not the pup) also engaged in biting/licking another group member.

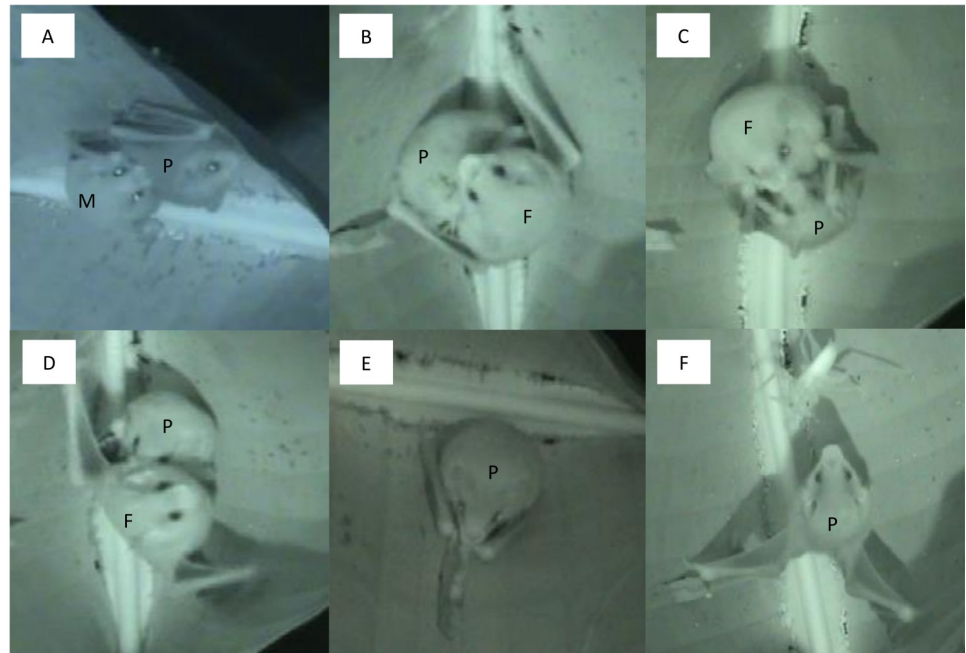


Fig 2. Social behaviours of *E. alba*. **A:** Fur chewing behaviour. The male (M) is chewing/licking the back of the pup (P). **B:** Nursing. The pup (P) is attached to the nipple of the female (F). **C:** Licking. The pup (P) is licking the mouth of the female (F) to solicit nursing. **D:** Twitching. The female (F) is shaking the pup (P) off after nursing. **E:** Play. The pup (P) is playing with a torn leaf piece inside the tent. **F:** Startle response. The pup (P) shows the typical wing posture when frightened, in this case by a grasshopper that has wandered into the tent. For detailed descriptions of the behaviours see [Table 1](#).

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“Play” in pups. While being alone in the tent, the pup started to investigate a torn, dangling piece of the roost leaf (see [S2 video](#), [Fig 2](#)). First, the pup started sniffing the leaf piece, and soon after used both thumbs/claws and wrists to grasp the leaf piece. Once grasped, the pup started chewing on the piece. The pup chewed on the leaf piece for a few seconds, stopped and started scanning. This behavioural sequence was repeated several times. Sometimes, the pup also started cleaning, wing stretching or moving around after chewing on the leaf piece. At one time, the pup was observed to inspect the modified midrib of the tent (i.e. the part of the leaf which is modified during tent construction to collapse the leaf next to the cut to achieve the typical shape of *E. alba* tents, see [\[8\]](#)). Afterwards, the pup turned back to the leaf piece and started chewing again, while simultaneously using the wrists and claws grasping and holding on to it. Chewing could get quite vigorous, and eventually, the pup started to bend the leaf piece to some extent.

Social vocalizations

E. alba produced ten distinct social call types in addition to echolocation calls, and for most call types the broad behavioural context in which they were uttered could be defined. The social call types SC9 and SC10 were not included in the statistical analysis because they were only recorded once with the microphone of the camcorder (S1 Fig in [S1 File](#)). Our visual classification of the remaining eight social call types was confirmed by the classification success of the cross-validated DFA (88.8% of all call types were classified correctly; [Table 2](#), [Fig 3B](#), further information about statistical fit: S1 Table in [S1 File](#)). The acoustic parameter that contributed most to the distinction of social call types was peak frequency in the centre of the call;

Table 2. Classification success [%] of the cross-validated discriminant function analysis for eight social call types.

Social calls	SC1	SC2	SC3	SC4	SC5	SC6	SC7	SC8	No. of calls
SC1	95.0 (19)	0.0	0.0	0.0	5.0 (1)	0.0	0.0	0.0	20
SC2	0.0	62.5 (5)	0.0	0.0	12.5 (1)	0.0	25.0 (2)	0.0	8
SC3	0.0	0.0	100 (12)	0.0	0.0	0.0	0.0	0.0	12
SC4	0.0	0.0	0.0	100 (15)	0.0	0.0	0.0	0.0	15
SC5	20.0 (1)	20.0 (1)	0.0	0.0	60.0 (3)	0.0	0.0	0.0	5
SC6	0.0	4.9 (2)	0.0	0.0	0.0	92.7 (38)	0.0	2.4 (1)	41
SC7	0.0	33.3 (3)	0.0	0.0	0.0	0.0	66.7 (6)	0.0	9
SC8	0.0	0.0	0.0	0.0	0.0	16.7 (1)	0.0	83.3 (5)	6

Classification table showing how many call types were correctly classified to social call types. The number in each box indicates the correct classification of each correct call type (row) assigned to each predicted call type (column), i.e. each row sums up to 100%. Numbers in brackets depict the number of calls (total call number: N = 116). The total number of measured calls per type is indicated to the right of the matrix.

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followed by peak frequency at the start and the end of the call, whereas duration only played a minor role (S2 Table in S1 File). A conspicuous feature of the social vocalizations in *E. alba* is the suppression of the fundamental frequency and the lower harmonics in some of the call types (SC1, SC2; SC5-SC7, Table 3, Fig 3A).

The DFA included acoustic measurements obtained from the harmonics that contributed most to the acoustic impression of different social call types. As a control, we calculated a second DFA including acoustic measurements of the fundamental frequency which corroborated the results of the first DFA (S3–S5 Tables in S1 File).

Furthermore, for seven out of ten social call types the broad behavioural context in which they were uttered was elucidated (Table 4). Three social call types were uttered in an affiliative context, namely SC2, SC3, SC5 (Fig 3). Two social call types were uttered in the context of mother-pup interactions, namely SC4 and SC6 (Fig 3). In agonistic context, two social call types were uttered (see supplements), namely SC9 and SC10. Echolocation calls were uttered during flight and during alert behaviour in the roost (i.e., scanning, see Table 1). Most social call types were uttered singly and monosyllabic; SC7 once consisted of multiple syllables (Table 4).

Discussion

This study provides the first description of the behavioural ethogram and social vocalizations of *E. alba* in the roost. We identified 16 different behaviours, including two particularly interesting ones; the “fur chewing” behaviour performed by adult males, and the description of a pup behaviour which very likely meets the criteria defining play in animals [20]. Moreover, we described ten distinct social call types, and for seven call types, determined the behavioural context.

The temporal occurrence of social behaviours showed clear differences between day and night periods. During the day, aside from the two main activity peaks at dusk and dawn, the bats were almost exclusively resting. Roosting quietly during the day could be owned to avoid alerting day predators, such as primates [21, 22] but could also be a method to save energy. At night, as expected, adult individuals spent most of their time foraging but paid short visits to their tent. During her visits at night, the female was regularly nursing her pup. Former research also showed that, during their visits at night, females spent a considerable amount of time nursing and/or grooming the pup, especially during early ontogeny before pups became more independent [12]. Because pups are born almost furless, maternal care is especially

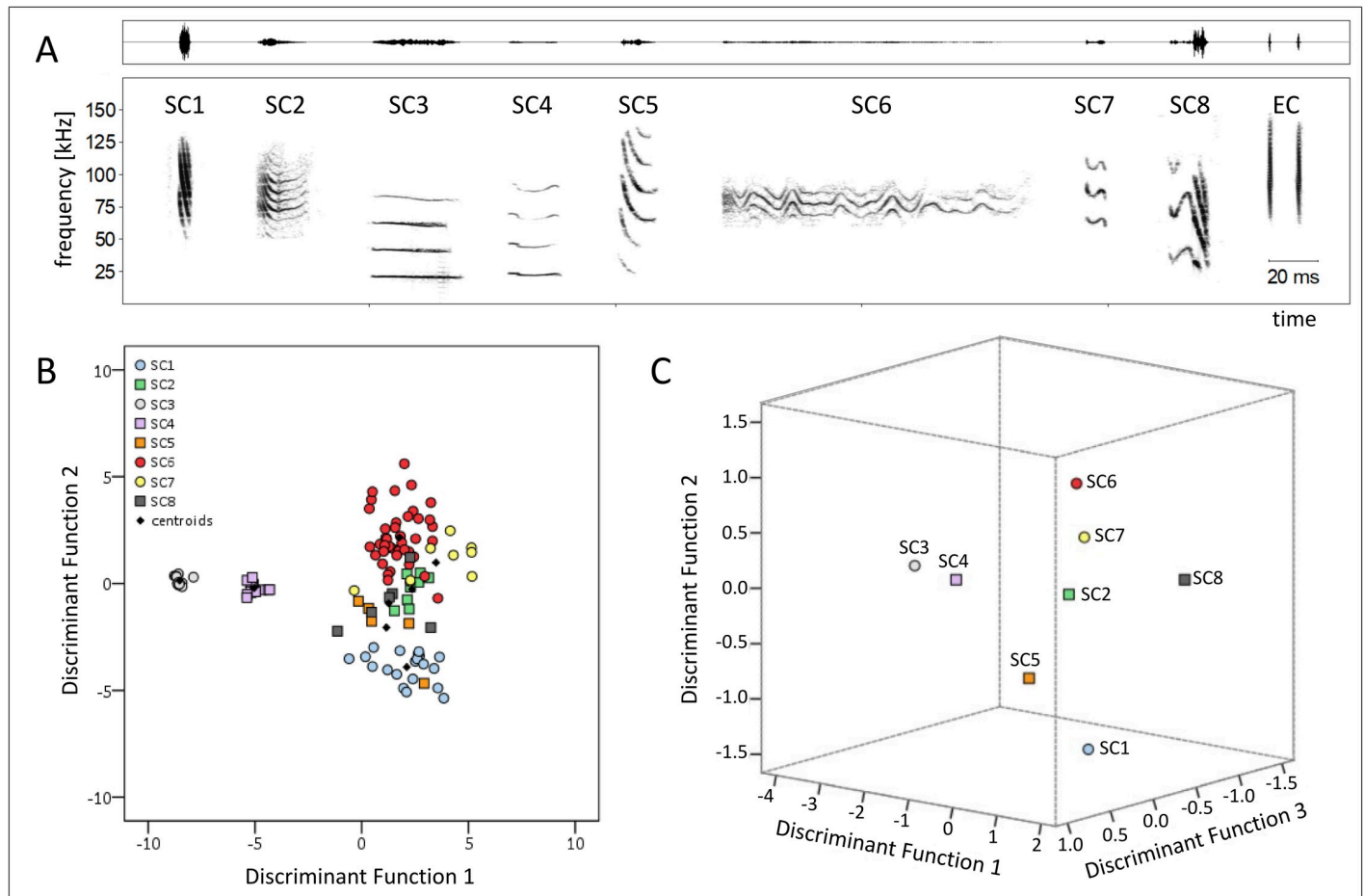


Fig 3. Eight social call types of *E. alba*. A: Spectrograms depicting eight social call types (SC1-SC8) and two echolocation calls (EC) of *E. alba* for comparative reasons. The spectrograms correspond to the natural appearance of those call types; i.e., suppression of the lower harmonics in types SC2, SC5, SC6, SC7. Social call types SC9 and SC10 are only depicted in the supporting information (S1 Fig in S1 File) as they are not included in acoustic and statistical analyses. Information about acoustic parameter measurements is given in Table 3. The context in which the social call types were emitted is described in Table 4. Spectrograms were created using a 1024-point FFT and a Hamming window with 87.5% overlap. B: The spacing of eight social call types of *E. alba* in a two-dimensional signal space defined by the two most important discriminant functions. Each social call type is represented by a distinct symbol, small black symbols represent centroids (i.e., the geometric centre of all calls per type in the DFA signal space). Note that EC are not included in the DFA.

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crucial during the first days after birth, probably for reasons of thermoregulation. Adult males mostly engaged in self-grooming during their roost visits at night. Furthermore, the most interesting behaviours, “fur chewing” performed by adult males and “play” in pups, were both only observed at night. However, additional data collection will be necessary to finally clarify that these two behaviours only occur at night. As described in the results, “fur chewing” was performed by males only. Our observations conform to the description of the behaviour in a former study [12]. A new observation in our study was that adult males perform “fur chewing” not only on adult males and females but also on pups. From the behavioural response of the bitten individuals, both adult and pup, it seemed that “fur chewing” did not cause any pain (see also [12]). At most it was possibly perceived as irritating (e.g., for a while, the pup who was being bitten tried to shake off/get away from the male; see S1 Video) as the bitten individual hardly showed any serious attempts of escape or strong resistance.

It remains speculative if “fur chewing” is a behaviour for scent-marking group members or if it is a form of allo-grooming. Allo-grooming is mainly observed in stable social groups (e.g.

Table 3. Acoustic parameters of eight social call types.

Social calls	N	Duration [ms]	Peak freq. start [kHz]	Peak freq. centre [kHz]	Peak freq. end [kHz]	Measured harmonic
SC1	20	5.01 ± 1.2	116.6 ± 13.0	79.8 ± 78	57.6 ± 6.2	3rd
		r [3.2–7.7]	r [90.8–143.6]	r [65.2–90.8]	r [44.5–67.4]	
SC2	8	9.6 ± 4.8	94.3 ± 4.7	83.5 ± 4.2	80.2 ± 5.8	10th
		r [3.5–17.0]	r [88.8–105.5]	r [78.1–89.8]	r [70.1–86.9]	
SC3	12	50.5 ± 6.5	21.0 ± 0.6	20.4 ± 1.3	20.5 ± 1.6	1st
		r [41.7–60.7]	r [20.5–22.4]	r [19.5–24.4]	r [19.5–25.3]	
SC4	15	24.4 ± 6.5	41.3 ± 2.7	39.7 ± 1.5	40.0 ± 2.3	2nd
		r [15.1–35.4]	r [38.0–46.8]	r [37.1–42.9]	r [36.4–44.8]	
SC5	5	7.1 ± 2.4	99.6 ± 19.2	72.4 ± 5.9	65.9 ± 3.9	3th
		r [5.1–11.9]	r [77.1–133.2]	r [67.3–80.0]	r [60.8–72.5]	
SC6	41	49.1 ± 20.4	86.3 ± 8.8	84.3 ± 6.3	86.3 ± 8.3	8th
		r [16.0–103.7]	r [72.2–113.8]	r [74.6–101.7]	r [71.2–105.9]	
SC7	9	9.4 ± 2.8	93.5 ± 11.7	91.5 ± 10.2	93.2 ± 13.8	4th
		r [6.2–15.5]	r [69.5–113.2]	r [69.5–102.5]	r [64.0–108.0]	
SC8	6	19.0 ± 4.5	83.0 ± 9.2	87.7 ± 11.2	60.6 ± 11.9	3th
		r [12.1–24.0]	r [73.2–100.5]	r [71.04–107.0]	r [41.7–81.0]	

The table depicts mean, standard deviation and range (r) for each social call type averaged over all calls measured per type (column 2). The frequency parameters were measured in the harmonic which contained the most energy (column 7).

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Table 4. Behavioural context of the social call types.

Social call	Production mode	Syllable type	Behavioural context	Frequency of occurrence	Sex	Age	Total number of recordings
SC1	In series	Monosyllabic	Unknown	common (9)	Both sexes	All	21
SC2: Grooming/biting call	Singly	Monosyllabic	Emitted while male gently bites or grooms the neck of a female	common to rare (5)	Males Females?	Adults	9
SC3: Contact call 1	Singly	Monosyllabic	Emitted on the wing by individuals flying in the vicinity of the tent (both empty and occupied tent), and emitted while leaving the tent	common to rare (4)	Unknown	Adults	12
SC4: Maternal directive call	Singly	Monosyllabic	Emission immediately followed by nursing	common to rare (5)	Females	Adults	15
SC5: Contact call 2	Singly	Monosyllabic	Emitted on the wing by individual flying in the vicinity of the tent; and emitted while leaving the tent	common (8)	Unknown	Adults	11
SC6: Isolation call	Singly	Monosyllabic	Solicitation of nursing	common to rare (5)	Both sexes	Pup	42
SC7	Singly	Monosyllabic	Unknown	rare (2)	Unknown	Unknown	9
		Multisyllabic					
SC8	Singly	Monosyllabic	Unknown	common to rare (5)	Unknown	Unknown	11
SC9	In series	Monosyllabic	Aggressive/Distress	rare (1)	Both sexes	Unknown	N/A
SC10: Screech	In series	Monosyllabic	Aggressive/Distress	rare (1)	Both sexes	Adults	N/A

The frequency of occurrence corresponds to the number of recording sessions during which the social call type was recorded. The number of nights during which the calls were recorded with the accompanying behavioural context are given in parentheses. Sex denotes the sex of the emitter of a given social call type. Age denotes which age group (pup/adult) uttered the social call type. The number of recordings depicts the sum of all recordings analysed (summed up for all nights). Note that for some nights several recordings were analysed.

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harems, maternity colonies) with varying degree of relatedness [2]. Besides strengthening of social relationships, allo-grooming is also exchanged for other social benefits [1, 2, 23, 24]. So far, allo-grooming among adult individuals (not including mother-pup grooming) was described for a few bat species only [2]. However, in contrast to other species where allo-grooming was observed [e.g. 1, 23, 24], *E. alba* seems to restrict grooming to a very specific spot on the back, not including other body parts (this study and [12]). Furthermore, after “fur chewing” a visible wet spot remained on the back of the receiver (S1 Video). This is reminiscent of the scent-marking behaviour of group members in *Noctilio leporinus* and *Cynopterus sphinx* [25, 26]. *Noctilio leporinus* females, who form stable perennial groups, rub their heads on other females’ heads and backs to scent-mark them [25]. In *C. sphinx*, individuals form so-called grooming clusters, where individuals hold on to each other while distributing saliva on body parts of group members [26]. In both species, scent-marking was associated with group member recognition. In *E. alba*, “fur chewing” could have a similar function—group recognition through scent. *Ectophylla alba* forms very stable social groups [12], although the genetic relationship between adult individuals is very low [13]. It is known that groups switch together to new roosts, which are usually close to the currently occupied tent within a small area [17]. Tent construction is costly; time spent manipulating a leaf cannot be invested in foraging, and construction requires several nights [14]. Furthermore, *E. alba* has specific requirements to its roosting microhabitat [21], probably limiting the availability of potential roosting areas and, therefore, increasing the value of suitable places. A scent signature could assist the identification and recognition of social group members joining a roost. This would also explain why males perform this behaviour not only on females but also on pups. Nevertheless, besides scent-marking “fur chewing” could also strengthen social bonds between individuals, as observed in other species [2]. It remains to be investigated which function(s) the observed “fur chewing” plays in *E. alba*.

A behaviour characterized as play in animals is defined as (i) a non-fully functional behaviour, (ii) being spontaneous and voluntary, (iii) different from a formal performance of functional behaviour, e.g. exaggerated or incomplete, (iv) repeatedly performed during a period of an individual’s life, and, (v) performed only when the animal is free from stress [20]. There are several hypotheses about the function of play in young animals [27], and despite opposing views regarding certain aspects, most agree that one of the main functions of play is to refine one’s motor skills [28]. Play behaviour is grouped into three categories; social play, locomotor play and object play [28]. Studies about play in animals are very scarce, and in bats, it has only been observed in a few occasions. Social play was described in *Pteropus giganteus*, where young individuals engage in play-fight and wrestling, first with their mothers, later among sub-adult individuals [29]. Similar play fighting was also described for other Pteropodidae species [30]. Young vampire bats engage both in object- and social play, the latter involving mounting, wrestling and chasing [31]. The pups’ handling of the torn leaf piece, which we observed for the first time in this study, meets the criteria of object play behaviour. The pups’ object play might be a precursor to later actual tent construction behaviour. Adult tent construction involves biting and puncturing the leaf using the teeth, and further extension of these holes by claws until the leaf collapses next to the cut [8]. By grasping a part of the leaf with the thumbs and repeatedly pulling it up, down, and inward the leaf bends downward forming the final shape of the tent [8]. Several motor patterns of adult tent construction are found in the pup’s object play; the chewing of the leaf, the grasping of a leaf piece with the thumbs and wrists and finally the bending and moving of the leaf piece (but instead of using the thumbs the pup used both thumb and mouth; see S2 Video). The pups’ behaviour is reminiscent of motor patterns used by adults in tent construction, but not yet fully functional (criteria i & iii). The pup was free from stress, voluntarily engaging with the leaf piece (criteria ii & iv). Moreover, this

behaviour was observed several times during different nights (criterion v). However, our sample size is restricted to observations of a single pup. The observed behaviour could also be explained by curiosity towards an unexpected object (torn leaf piece) present in the roost.

The repertoire size of *E. alba* described here is within the size range of the vocal repertoire sizes of other phyllostomid bats (*Glossophaga soricina*: n = 15 social call types [32]; *Glossophaga commissarisi*: n = 8 social call types [32]; *Carollia perspicillata*: n = 10 social call types [33]; *Phyllostomus discolor*: n = 12 social call types [34]). Our description of the vocal repertoire (and also the ethogram) is incomplete because we did not observe courtship behaviour, territorial defence or tent making. Nevertheless, the repertoire described here most likely includes the majority of the social call types. Most of the social call types were affiliative (SC2-SC6), and although the exact context of call types SC1, SC7-SC8 was not elucidated, they were uttered in neutral, non-aggressive situations (Table 4). This corresponds to the observed behaviours; aggressive/agonistic behaviour like “wing hitting” was only rarely observed (Table 1). The only aggressive/distress vocalizations (S1 Fig in S1 File) were recorded during an incident when a mosquito stung a bat in a sensitive spot on his back that was temporarily hairless because of a telemetry tag that had recently fallen off. Similarly, an earlier study never noticed agonistic behaviour in the group they observed [12]. So far, it is still unknown whether males exhibit aggressive behaviour in the mating context, and, for example jointly defend a tent or their roosting area.

The pup isolation call of *E. alba* is different from the isolation calls of other phyllostomid bats because its fundamental frequency and the lower harmonics are suppressed (Fig 3, Table 3). In other phyllostomids studied so far, most of the sound energy of pup isolation calls is located in the fundamental frequency (*P. hastatus*, *P. discolor*, *G. soricina*, *C. perspicillata* [35, 36–38]). This particular spectral characteristic of *E. alba* isolation calls might be an adaptation to its roosting ecology. The tents offer less protection from predation compared to the roosting sites of the other species due to their resistance and stability (i.e. leaf versus cave or tree hole) and probably also due to their location (in the understory, less than 2m above ground) [14]. Restricting the isolation calls' sound energy to a narrow high-frequency band could create a communication channel for *E. alba* that is circumventing the hearing range of some predators; for instance, it is known that small primates successfully predate tent roosting bats [22]. The isolation call of *E. alba* also differs in its duration from the isolation calls of the other species. Why these isolation calls have such a long duration and whether this is possibly related to the intensity of solicitations for nursing could be investigated in further studies.

The social call types SC3 and SC5 were uttered on the wing, in the vicinity to the roost, and while leaving the tent. The call type SC3 is similar to the social call described in an earlier study where this specific social call was recorded in the vicinity of tent roosts and once before entering the roost [15], thus corroborating our observations. Correspondingly, we hypothesise that the social call types SC3 and SC5 serve as contact calls. They are probably not used to attract and recruit group members for roosting, a function that contact calls recorded in other foliage-roosting bats have [6, 15], but might facilitate the coordination of group formation. However, the purpose of group formation in the vicinity to the tent is completely speculative at this point. Besides the potential function of group formation, these calls might additionally signal roosting area occupancy to other social groups roosting in the vicinity. In both scenarios, group member recognition is crucial; therefore, in future studies, it would be interesting to investigate if the social call types SC3 and SC5 encode a vocal group signature and if they elicit phonotaxis in receivers.

The affiliative social call type SC2 was uttered before “fur chewing”, always by the active (i.e., fur chewing) bat. We never recorded a vocal response of the passive individual. To our knowledge, there is no other study describing a social call associated with scent-marking and/or allo-grooming. This social call might be an appeasement vocalization to signal non-

aggressive intention towards the passive individual. Further, it might simultaneously strengthen dyadic relationships between individuals. *E. alba* seem to prefer to associate with particular group members within the roost [12], and this call might encode an individual signature facilitating social interactions. However, it is not known if “fur chewing” occurs more frequently between particular group members. For some of the call types the behavioural context is rather broadly defined (e.g. SC3, SC5); in this case, more recordings paired with behavioural observations and playback experiments will be necessary to obtain detailed knowledge about the function of the calls and for describing the specific behavioural context.

Overall, our research contributes to the growing number of studies on social behaviour and vocal repertoire descriptions in phyllostomid bats. Our results allowed us to raise new questions and formulate hypotheses about particular social behaviours and social call types which can be tested in future observational and experimental studies. With our study, we hope to initiate further research about social behaviour not only in *E. alba* but other bat species, and especially encourage further vocal repertoire descriptions of bats to assess the communicative capacity of this speciose taxon.

Supporting information

S1 Video. Male fur chewing. This video captures the pup and an adult male together in the roost at night (the other four individuals of this social group are absent). Directly after landing in the tent, the male briefly smells the pup and directs himself behind the pup. Immediately, he starts biting/chewing the pup’s fur. The biting is accompanied by wing trembling. The pup seems irritated, trying to move around. At some point, it attempts to stretch its wing. After a few seconds, the male starts cleaning himself. At the end of the video the pup turns around and a wet part can be spotted on its back.
(WMV)

S2 Video. Pup play behaviour. This video captures the pup alone in the roost at night. The detailed description of the pup’s behaviour can be found in the results section of the study.
(WMV)

S1 Dataset. 22-hour observation period of group 1. This Excel sheet includes information on behavioural states and events observed during the 22-hour observation period of the four individuals of group 1.
(XLSX)

S1 File.
(PDF)

S2 File.
(JPEG)

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Permit

The research was conducted in accordance with the Costa Rican government, i.e. the National System of Conservation Areas (Sistema Nacional de Areas de Conservación; resolution 152-

2009-SINAC and 128-2011-SINAC; permit issued by Javier Guevara). According to Costa Rican law, an additional approval by an Institutional Animal Care and Use Committee (IACUC) was not required, because all sampling procedures were specifically approved as part of obtaining the research permit. Sampling procedures included capturing the bats to mark them temporarily with fur coloration before release and conducting behavioural observations and sound recordings at the bats' day-roost. The study did not involve endangered or protected species.

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