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Sexual segregation, roosting, and social behaviour in a free-ranging colony of Indian false vampires (*Megaderma lyra*)

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Abstract

We investigated roosting structures and social interactions of free-living Indian false vampire bats (*Megaderma lyra*) in a colony of about 60 individuals. False vampires entered the roost between 05.00 h and 05.45 h. Emergence was between 18.00 h and 19.00 h. An analysis of roosting patterns during day time revealed that sexes partially segregated within the roost during the period of pregnancy and lactation, although individual bats differed in compartment fidelity. Our study contradicts previous views reporting that false vampires roost in contact clusters. Our findings show that false vampires roost at a median distance of 9 cm. Occasionally, however, up to five false vampires established body-body-contact, sometimes initiated by 'greetings'. Body-contact was never observed between adult males and in captivity it was restricted to mother and offspring.

Key words: *Megaderma lyra*, Chiroptera, roosting, social behaviour, sexual segregation

Introduction

Echolocation, foraging ecology, and behaviour of bats are fairly well documented (NEUWEILER 1989, 1993). BRADBURY and VEHRENCAMP (1976 b) emphasised that the distribution of food and foraging behaviour may be important for the formation and structure of groups in bats. Nevertheless; knowledge about roosting structure and social interactions among bats is still limited (e. g. BRADBURY 1977; BRADBURY and EMMONS 1974; BRADBURY and VEHRENCAMP 1976 a, b, 1977a, b;. KOZHURINA 1993; LEIPPERT 1991, 1994; PORTER 1979 a, b; O'SHEA 1980; VAUGHAN and VAUGHAN 1986; WICKLER and UHRIG 1969; WILKINSON 1985 a, b, 1986).

Indian false vampire bats (*Megaderma lyra*) are easy to keep in captivity. Hence echolocation and foraging techniques are well known (ADVANI, 1981; FIEDLER 1979; HABERSETZER 1983; MARIMUTHU and NEUWEILER 1987; MARIMUTHU et al. 1995; SCHMIDT 1992). Recently LEIPPERT (1994) discovered elaborated flight manoeuvres accompanied by social vocalisations in captive false vampires, suggesting that social interactions may be important also in this species. However, little is currently known about roosting behaviour and social organisation of free-ranging false vampires and results of previous studies are contradictory. The only study concerned with foraging behaviour of free-ranging false vampires reported merely that individuals share perches with conspecifics and do not forage in exclusive territories (AUDET et al. 1991). False vampires hang in contact clusters (BROSSET 1962) and live in year round multi-male and multi-female groups of several to hundreds of animals (GOPALAKRISHNA and BADWAIK 1989; HABERSETZER 1983) or they segre-

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gate when birth is imminent (BALASINGH et al. 1994; NOWAK 1991). Mating occurs in November and December and gestation takes almost five months (GOPALAKRISHNA and BADWAIK 1989). Data from a captive colony, however, suggest a gestation time of only three months (D. LEIPPERT, pers. obs.).

A previous study done at the same colony as the present study (BALASINGH et al. 1994) suggested that males leave the colony during the time females give birth and rear their young. However, BALASINGH et al. (1994) did not quantify these results and thus the presence of merely a few males can change this picture of a pure nursery colony. The present study aimed to collect quantitative data on sexual segregation and roosting habits of female and male Indian false vampire bats during the time when females give birth and rear their young. Furthermore, we aimed to study social interactions of this carnivorous bat species inside the day roost.

Material and methods

Field work was conducted during the end of the cool season and the beginning of the dry season between February and end of April, 1995, when females were expected to give birth and rear their young (BALASINGH et al. 1994).

Natural roosts of *Megaderma lyra* are caves but this species will also readily exploit man-made structures (AUDET et al. 1991; BALASINGH et al. 1994; MARIMUTHU et al. 1995). Cave dwelling false

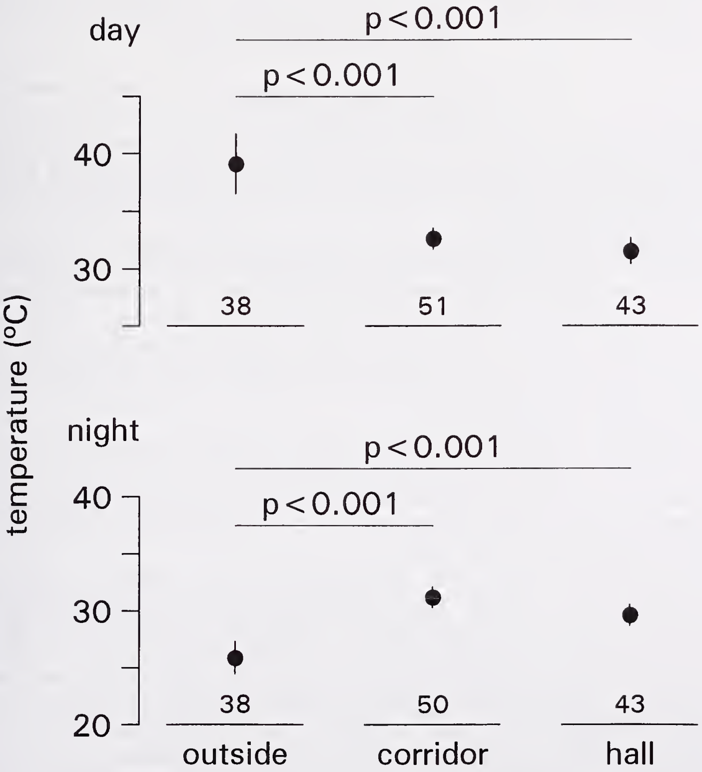

Fig. 1. Mean temperatures during the day and the night. Numbers indicate sample size. Maximum outside temperatures were significantly higher than in the hall (Wilcoxon signed-ranks test, $N = 26$, $z = 4.457$) and the corridor ($N = 28$, $z = 4.644$). Minimum outside temperatures were significantly lower than in the hall ($N = 26$, $z = -4.514$) and the corridor ($N = 28$, $z = -4.671$).

vampires are very shy and difficult to observe (HABERSETZER 1983), hence we investigated a temple dwelling colony, which readily got used to our presence. The colony of about 60 false vampires roosted in an old Hindu-temple in Krishnapuram, a small village about 15 km south east of Tirunelveli (southern India). The temple consisted of 4 main compartments: the hall, the chimney room, the corridor, and the spire. Similar to a cave the temple significantly buffered outside temperature fluctuations (Fig. 1). The area around the temple was savannah-like with *Prosopis* and *Acacia* scrubs predominating (AUDET et al. 1991) and included a lake and banana plantations.

The temple was continuously illuminated with dim red light (nine 15 W bulbs). The red light did not seem to disturb the false vampires, as bats often hung close to the bulbs.

False vampires were caught and tagged in order to allow individual identification. During 22 days one or two mist nets (4 m×2.5 m and 6 m×2.5 m) were strained between bamboo-sticks in the surroundings of the temple. During emergence between 18.45 h and 19.30 h we knelt beside the net and trapped a total of 69 bats (including recaptures of the same individuals), which were removed from the net immediately after capture. Lactating females carrying a pup were released without further handling to avoid injuries of the pup. Other individuals were sexed and weighed to the nearest gram. Forearm length was measured with a pair of vernier callipers to the nearest millimetre. The reproductive state of females (nulliparous, parous, pregnant, non-pregnant, lactating) was determined. We distinguished males with prominent and non-prominent testes.

Seventy percent of caught individuals already had been fitted with a collar and coloured plastic beads during a previous study (BALASINGH et al., 1992). The beads, however, were invisible most of the time and only a few bats could regularly be identified from these tags. To enable individual identification we tagged them with wing bands (Museum Alexander-Koenig, Bonn, Germany, size E). The bands were modified using reflecting tape of 6 different colours. The tape was glued to the bands in different colour combinations to allow individual identification of 34 individuals (>50% of the colony). We tagged males on their left and females on their right forearms.

Observations in the day roost were conducted by one or two persons in three different compartments of the temple. We concentrated on periods in the morning and evening, when social activity peaked. Total observation time in the temple comprised 335 hours (4–6 hours per day). Most of the behavioural observations were made in the so-called chimney room. The seclusion of this room allowed us to come very close (ca. 4 m) to the bats without disturbing them. Watching individual behaviour was also possible in the corridor but sometimes obstructed by pillars. Periods of continuous observations lasted on average 2 hours.

Behavioural data were collected using the ad libitum sampling method (MARTIN and BATESON 1993). Observations were done using binoculars. Occasionally bats were briefly identified with white-light torches. After having spent at least 15 minutes at an observation point we recorded the positions of the bats either on diagrams of roosting compartments in the northern corridor, the hall, and the chimney room or registered the positions of bats in the hall and chimney room with a dictaphone. The latter method was faster and more convenient. The roosting records of the chimney room were used to calculate distances between individuals. For that purpose we covered the bar in the chimney room with yellow strokes in 15 cm intervals.

We assessed whether male and female false vampires segregated by calculating sex ratios in the hall, the northern corridor, and the chimney room using the data of the roosting records. Only individual data of banded bats were considered. To calculate distances between individuals we analysed one diagram or dictaphone record of the chimney room per day. If there were more than one plot/record per day we only considered the first one.

As there was no obvious change in the sex composition of false vampires in different compartments during the observation period we used the cumulative number of banded males and females in 3 compartments of the day roost (chimney room, N = 32 days; hall and northern corridor, N = 22 days each), to calculate the sex ratio in these compartments. We compared the results with expected values calculated from the sex ratio of banded bats. As the first records originated before we completed tagging false vampires, the number of banded males and females increased over time. To take this into consideration when calculating the expected sex ratios at each roosting compartment we counted the total number of banded males and females for every particular day. Then we summed up the number of banded females ($\Sigma\, n_{\mathrm{females}}$) and males ($\Sigma\, n_{\mathrm{males}}$) for all days on which samples were taken. Thus the expected value for females (p_{females}) was:

$$p_{\mathrm{females}} = \Sigma\, n_{\mathrm{females}} / (\Sigma\, n_{\mathrm{females}} + \Sigma\, n_{\mathrm{males}})$$

Correspondingly we determined the expected value for males (p_{males}).

To distinguish whether single bats used only one compartment or several compartments for roosting we calculated the proportion of records where an individual was sighted in the chimney room, the hall or the corridor.

Statistical analyses were done with SYSTAT 5.0 (Wilkinson 1990), following the procedures recommended by Conover (1980), Sokal and Rohlf (1996), and Lamprecht (1992). Results were considered significant if $p < 0.05$ (two-tailed). Data are presented as mean ± SD or, when skewed as median/interquartile range.

Results

Morphometrics

17 females (74%) were pregnant, one female was a nulliparous yearling (J. Balasingh, unpubl. data). The mean forearm length was 65.0 ± 1.8 mm in females (N = 23) and 65.0 ± 1.8 mm in males (N = 30). There was no significant difference between males and females (Mann-Whitney U-test, U = 382, n. s.). Body mass of non-pregnant females was 34.3 ± 2.7 g (N = 6). Males weighed 33.2 ± 1.8 g (N = 30). The difference between males and females was not significant (Mann-Whitney U-test, U = 120, n. s.). Forearm length and mass of non-pregnant females and males correlated significantly (Fig. 2; Spearman rank-correlation, $r_s = 0.404$, N = 36, $p < 0.01$). 71% percent (N = 20) of all tagged males (either collar or band) had prominent testes, whereas 29% (N = 8) had non-prominent testes. There was no significant difference in forearm length between males with prominent and males without prominent testes (Mann-Whitney U-test, U = 55.5, n. s.).

Inflight and emergence

Between 05.00 h and 05.45 h in the morning (before and during dawn) the false vampires returned from foraging and entered their day roost. Most of the animals roosted in the northern corridor (38/31–46 animals, N = 22). 12/10–15 animals (N = 32) stayed inside the chimney room and 5/2–8 animals (N = 29) mainly roosted in the hall. There was little activity during day time. In the evening activity started from 18.00 h onwards. Emergence started at dusk between 18.45 h and 19.00 h and lasted for 15–30 minutes.

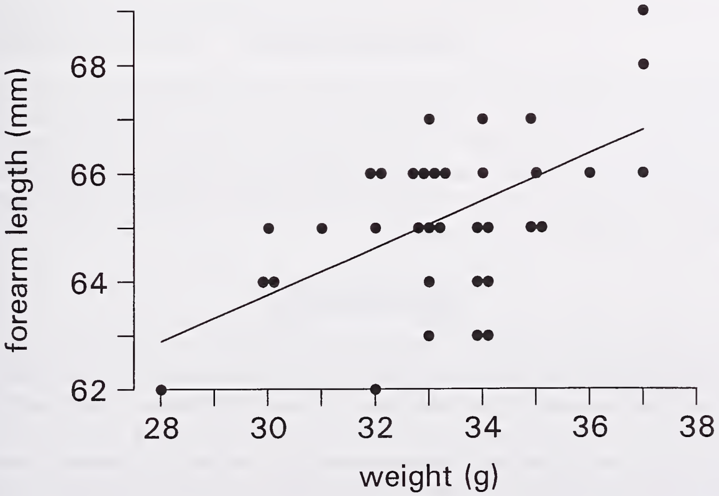

Fig. 2. Forearm length and weight of captured Indian false vampires (N = 36) excluding pregnant females and unbanded bats (y = 0.436x + 50.692).

Table 1. Median numbers of banded female and male false vampire bats at three roosting places inside the day roost.

part of temple	N	sex	min. no.	1st quartile	median no.	3rd quartile	max. no.
chimney room	32	♀♀	1	2.5	4.5	5.5	7
	32	♂♂	0	0.0	1.0	1.0	2
hall	22	♀♀	0	0.0	0.0	0.0	1
	22	♂♂	0	1.0	1.0	2.0	5
northern corridor	22	♀♀	0	1.0	1.5	2.0	4
	22	♂♂	1	3.0	4.5	5.0	8

Table 2. Total numbers of banded Indian false vampires in several parts of the day roost ($p_{\text{♀♀exp}}$ = expected proportion of females, $p_{\text{♂♂exp}}$ = expected proportion of males).

part of temple	N	no. of ♀♀	no. of ♂♂	$p_{\text{♀♀exp}}$	$p_{\text{♂♂exp}}$	binomial test
chimney room	32	130	22	0.463	0.537	$p < 0.001$
hall	22	1	37	0.466	0.534	$p < 0.001$
northern corridor	22	36	102	0.467	0.533	$p < 0.001$

Sex ratios at different roosting compartments of the day roost

In total 53 individuals were tagged either with collars (BALASINGH et al. 1994) or wing-bands. We recorded 23 females (43.4%) and 30 males (56.6%). The overall sex ratio was not significantly biased (Binomial test, $N = 53$, $x = 23$, n. s.).

Males and females tended to segregate in different compartments of the day roost (Tab. 1 and 2). In the chimney room 86% of all banded bats were females. This sex ratio was significantly female-biased (Tab. 2) and all males present were yearlings. In the hall and the northern corridor the sex ratio was significantly male-biased (97% and 74%, Tab. 2).

Compartment fidelity

From 31 identified banded bats 12 were seen in only one compartment 16 in two different compartments, and 3 in all three compartments. A total of 13 individuals was recorded in the chimney room (Fig. 3 a), another 13 in the hall (Fig. 3 b), and 25 individuals in the corridor (Fig. 3 c). Four banded bats were never seen in any roosting compartment. Two false vampires temporarily left the day roost after they had been banded. They spent one day or two weeks in a ruin close to the temple.

Individual spacing

Individuals usually kept a minimum distance to conspecifics. The median value for the distance of individuals was 9/5–14 cm ($N = 321$, Fig. 4). However, individuals did also establish close physical associations which we termed body-contact. Typically individuals joined each other by touching each other's bellies ($N = 84$). Belly-to-back ($N = 10$) or belly-to-wing ($N = 2$) contacts were also observed. Sometimes one animal embraced the other with its wing-membranes and up to 5 individuals could be involved in body-contact.

Body-contact was initiated in three different ways. Neighbouring false vampires shuffled towards each other, a bat could pass over other individuals to reach the partner,

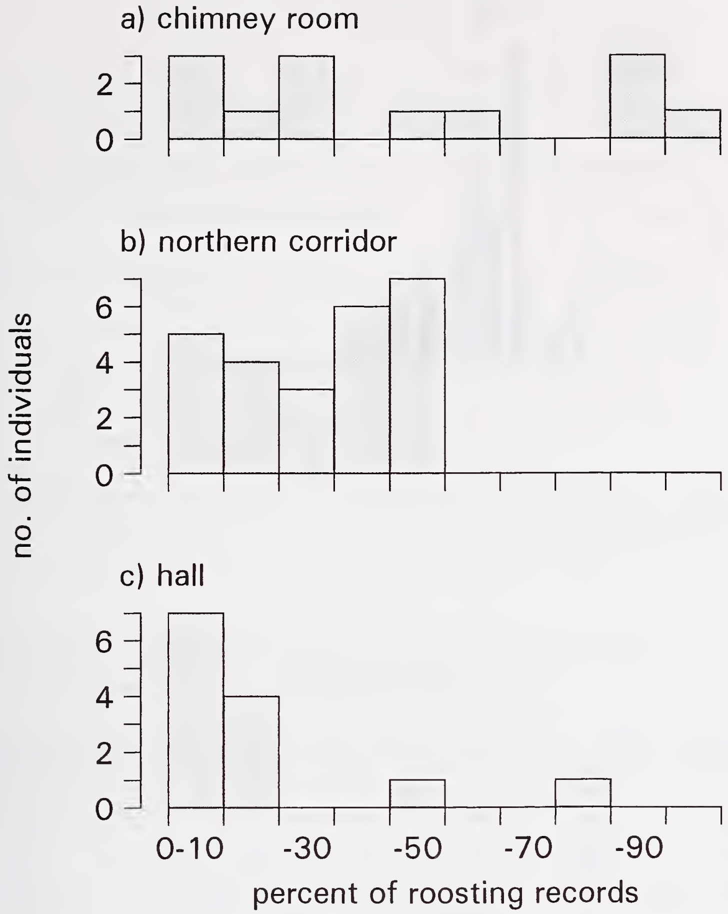

Fig. 3. Numbers of individuals present in proportion of roosting records in a) the chimney room, b) the northern corridor, and c) the hall.

or a false vampire flew to another individual. In 14 out of 49 observations of body-contact initiations a 'greeting ceremony' preceded body-contact. The false vampires sniffed each other and then they mutually rubbed their muzzles before making body-contact. Body-contact with 'greeting' lasted 6/1–8 min (N = 14), whereas body-contact without greeting lasted 2/1–8 min (N = 35). There was no significant difference in body-contact duration with or without 'greeting' (Kolmogorov-Smirnov two-sample test, D = 0.229, p = 0.59).

During body-contact every bat clung to its hanging place with one leg, but often the legs of two bats crossed over. Twice we heard soft purring sounds emitted by body-contact partners. Because these sounds were of low intensity we could not determine whether false vampires always vocalise during this behaviour. False vampires also hung in body-contact and groomed each other (N = 3).

We saw 47 body-contacts where at least one tagged individual was involved, both partners could be identified in 19 cases (Tab. 3). Body-contact occurred between females, between females and males, and between males with non-prominent testes. Body-contacts between males with prominent testes were never observed. Females did not have body-

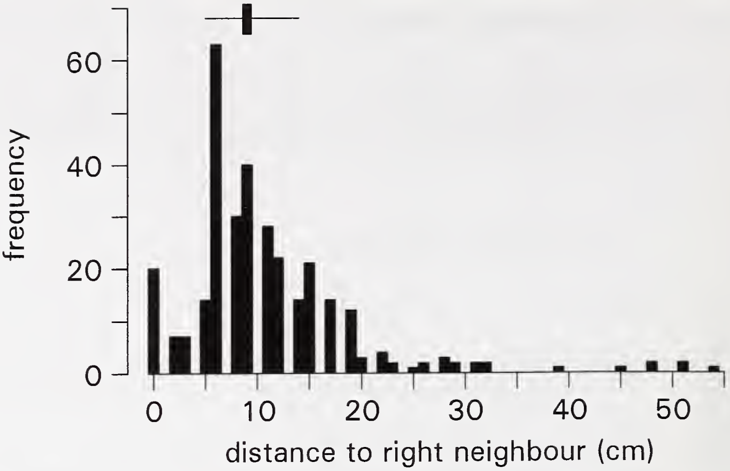

Fig. 4. Distances to the nearest right neighbour (N = 321). The box-plot in the upper left corner indicates median value and interquartile range.

Table 3. Frequency and duration of body-contacts between identified partners. The last two columns show the total number of body-contact in which the respective false vampire was involved including those where only one partner was identified. All males involved had non-prominent testes (bc = body-contact).

1st bat	2nd bat	3rd bat	no. of bc	duration of bc (min)	number of total bc	
					1st bat	2nd bat
♀008	♂016		4	7, 25, 1, –	9	12
♀008	♂025		1	0.3	9	1
♀008	♂741		2	2, 12	9	14
♀015	♀739	♂741	1	4	2	3
♂016	♂741		3	10, –, –	12	14
♂016	♀778		1	–	12	1
♀020	♀017		2	7, 18	8	3
♀020	♀686		1	12	8	2
♀020	♀701		1	10	8	3
♀028	♂741		2	1, 10	2	14
♀739	♂741		1	15	3	14

contacts more frequently with females than with males (Wilcoxon signed-ranks test, N = 9, z = 0.071, p = 0.94), but in all except three body-contacts (which took place always between the same two males) at least one female was involved.

'Greeting' occurred also without body-contact (N = 13). False vampires responded to individuals which initiated 'greeting' in three different ways: They returned the 'greeting' (N = 9), they ignored the 'greeting' (N = 2) or they made an aggression call (N = 2). When the receiver ignored the 'greeting' or made an aggression call the 'greeting' animal immediately retreated. Individual 'greeting'-data showed that animals of all sex combinations greeted (female-female: N = 3, female-male: N = 3, male-male: N = 3). All males involved in greeting had non-prominent testes.

Discussion

A previous study (Gopalakrishna and Badwaik 1990) suggested that false vampires avoid light, emerge only when it is completely dark and return to the roost before dusk. We could not confirm these results in our study colony. Most of the false vampires hung in the brightest compartments of the temple: corridor and chimney room. Furthermore the false vampires emerged at dusk and inflight lasted until dawn. In three other temple dwelling colonies we also found the false vampires roosting in rather bright areas of these day roosts.

Individual false vampires did not hang in contact clusters as suggested by Brosset (1962), but hung at a median distance of 9 cm which allowed them to stretch their forearms or groom themselves without interference. However, they 'clustered' when they got disturbed and had no opportunity to retreat. Hence, it is likely that the animals in this previous study (Brosset 1962) were not habituated to the presence of observers. Hanging in contact clusters might be disadvantageous: individuals may disturb each other, aggressions may be triggered more easily, and the transfer of ectoparasites may be facilitated. It is unlikely that false vampires face thermo-energetical limitations in a day roost which significantly buffered fluctuation of outside temperatures and provided constant ambient temperatures of more than 30 °C. In a captive colony spacing is common with ambient temperatures of only 25 °C (D. Leippert, unpubl. data). Given these temperatures we consider false vampires unlikely to gain energetic advantages through clustering.

Social behaviour

False vampires regularly engaged in individual body-contacts. This behaviour possibly derives from mother-pup relationships. Pups older than 4 weeks clung to their mothers in such a position (pers. obs.). The same position is known from mother and pup in the yellow-winged bat, *Lavia frons*, that roost on tree branches and where this behaviour seems to be related to thermoregulation (Vaughan and Vaughan 1987; Wickler and Uhrig 1969). Grown-up yellow-winged pups hung in close contact with their mothers when the ambient temperature was 22 °C, but they hung separately when the ambient temperature was 28 °C (Vaughan and Vaughan 1987).

Body-contact in free-living false vampires sometimes was preceded by 'greeting' behaviour and accompanied by purring sounds. In small captive groups body-contact was only observed between mothers and their offspring (D. Leippert, unpubl. data). Our field data were insufficient to test whether body-contact in free-living false vampires is restricted to close relatives or whether individuals choose their partners opportunistically. If body-contact is selective we suggest that it helps to establish and maintain bonds between individuals of a distinct group of close relatives.

Roosting structure

Balasingh et al. (1994) suggested that males and females inhabit separate roosts during the period of parturition but did not quantify their results. Males and females did not inhabit a separate roost in our study, but there was a partial segregation of sexes within the roost. There was no indication that single males monopolised hanging sites for the establishment of harems. As we only observed the colony during the time when females were either pregnant or lactating, we do not know whether this partial segregation lasts throughout the year.

The majority of identified bats used more than one compartment for roosting. Within the compartments they frequently changed sites. Only 31% of identified individuals roosted in the chimney room in almost every record. In the corridor we only found individuals roosting there in less than 50% of all records. Since the facilities in the corridor did not allow a reliable detection of individuals we may have missed some individuals roosting there more often. This could also be the reason why some banded false vampires were sighted only rarely or not at all. Unlike the chimney room and the corridor the hall was not occupied by bats throughout the day and hence we did not expect to find bats roosting there permanently.

In contrast to our findings cage dwelling false vampires seemed to choose particular sites for roosting (Habersetzer 1983). However, as Habersetzer (1983) did not observe banded individuals he might have observed different individuals using the same sites.

The social organisation of false vampires inside this day roost does not follow simple patterns. There is a partial sexual segregation at least during the breeding period. Individuals keep a minimum distance to conspecifics, but sometimes engage in body-contacts. Currently there is no quantitative evidence that individuals associate with certain other individuals. As some false vampires seemed to form small groups during evening emergence (pers. obs.) tracking such groups into their foraging grounds and investigating their composition and dynamics may help to answer these questions. If groups of false vampires should share foraging territories, links between food abundance and distribution, foraging behaviour, group size, and group composition might be expected, similar to those found in social carnivores (MacDonald 1983).

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Zusammenfassung

Geschlechtertrennung, Schlafplatz- und Sozialverhalten in einer freilebenden Kolonie von Indischen Falschen Vampiren (Megaderma lyra)

Wir untersuchten das Verhalten an Hangplätzen und die sozialen Interaktionen von Indischen Falschen Vampiren (*Megaderma lyra*) im Tagesquartier einer Kolonie von ca. 60 Tieren. Die Falschen Vampire flogen zwischen 5.00 h und 5.45 h in das Tagesquartier ein und verließen es wieder zwischen 18.00 h und 19.00 h. Eine räumliche Analyse der Verteilung von markierten Individuen im Tagesquartier ergab, daß es eine partielle Geschlechtertrennung während des Zeitraums der Trächtigkeit und Jungenaufzucht gab. Dennoch wählten die Individuen nicht immer den gleichen Hangplatz und wechselten auch innerhalb des Tagesquartiers in verschiedene Räume. Unsere Studie widerspricht früheren Ansichten, nach denen Indische Falsche Vampire in engen Kontakttrauben hängen. Wir fanden vielmehr, daß sie auf Lücke hängen und einen mittleren Abstand von 9 cm einhalten. Jedoch kam es hin und wieder vor, daß sich 2 bis 5 Tiere aufsuchten und in engem Körperkontakt zusammenhingen. Diese engen Kontakte wurden manchmal durch eine ‚Begrüßung', die aus gegenseitigem Schnauzenreiben bestand, eingeleitet. Körperkontakte wurden nie zwischen adulten Männchen beobachtet, in Gefangenschaft kamen sie ausschließlich zwischen Mutter und Kind vor.

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