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Social grooming among Indian short-nosed fruit bats

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Abstract
Social grooming is conspicuous in group-living mammals. Bats are gregarious and may groom each other, but the motivation for such social behaviour remains unclear. Here, we describe patterns and infer function of social grooming in tent-making Indian short-nosed fruit bats. Combining field and captivity observations, we found that males and their harem of females mutually groom and apply bodily secretions to one another in tight clusters. Mutual grooming is more commonly initiated by females, before emergence flight at dusk, and during the non-mating season. The within-harem association pattern suggests males may recognize female reproductive status via social grooming. Chemical analysis of the secretions applied during grooming revealed volatile organic compounds that may be involved in chemosensory-mediated communication and/or mate choice. These fruit bat harems were previously seen as simple aggregations, with limited interactions among individuals. Our findings suggest social grooming is multi-functional, with potential implications for the bats' social lives.

Keywords
Cynopterus sphinx, mutual grooming, social network, chemical communication.

1. Introduction

Grooming is a multipurpose behaviour observed in several taxa, such as insects, fish, birds and mammals (Stein & Magnuson, 1976; Seyfarth, 1980; Schönitzer, 1986; Clayton & Cotgreave, 1994). Grooming primarily functions in protection of body surface (Spruijt et al., 1992) by enhancing individual hygiene through removal of ectoparasites and debris, and through the spread of antibacterial and antifungal agents (Spruijt et al., 1992; Mooring et al., 1996). But grooming has also implications for social life.

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Social grooming plays various roles (Dunbar, 1991) and can mediate co-operation among conspecifics (Carter & Wilkinson, 2015). Bonding (Lazaro-Perea et al., 2004), supporting coalitions (Henzi & Barrett, 1999), ensuring dominance (Singh et al., 2006), reconciling (Call et al., 1999), sharing food (de Waal, 1997), defending territory (Lazaro-Perea, 2001) and relieving tension (via β-endorphin secretion; Keverne et al., 1989) are among the various functions and benefits of grooming conspecifics. Social grooming can be unidirectional (individual A grooms individual B, but B does not groom A) or mutual (A and B groom each other) (Wilkinson, 1986; Fedurek & Dunbar, 2009). The time spent in social grooming is usually directly related to strength of association and/or kinship between the participants (Hohmann, 1999; Silk, 2006).

While social grooming is prominent among primates (Wilkinson, 1986; Dunbar, 1991), it is relatively rarely studied among the numerous gregarious bat species. The order Chiroptera contains at least 1300 species, but to date only 11 species are known to engage in social grooming (*Phyllostomus hastatus*, *Carollia perspicillata*, *Eidolon helvum*, *Rousettus aegyptiacus*, *Myotis bechsteinii*, *Artibeus jamaicensis*, *Noclitio lepronius*, *Pipistrellus kuhlii*, *Desmondus rotundus*, *D. ecaudata* and *D. youngi*; Wilkinson, 1986; Brooke, 1997; Kerth et al., 2003; Ortega & Maldonado, 2006; Ancillotto et al., 2012; Carter & Wilkinson, 2013; Carter & Leffer, 2015). Similar to other taxa, the benefits of social grooming for bats might also include identification of a food-sharing partner as in *D. rotundus* (Wilkinson, 1986), social bonding as in *Myotis bechsteinii* (Kerth et al., 2003) and recognition of roost mates through scent marking as in *N. lepronius* (Brooke, 1997). However, the role of social grooming among other bats is poorly understood, limiting our general understanding of this behaviour in Chiroptera.

A clear example is the Indian short-nosed fruit bat, *Cynopterus sphinx*. Males of this Old World species invest energy in building and defending tents to attract females for reproduction (Balasingh et al., 1995; Storz & Kunz, 1999; Chaveri & Kunz, 2010). Although their mating system remains unclear (see Storz et al., 2000a; Garg et al., 2012), we know that within tents a typical roosting group contains a single male and 'harem' females with their young (Balasingh et al., 1995). The harems have up to 38 individuals with low genetic relatedness (Storz et al., 2001), change composition almost daily (Storz et al., 2000b) and are part of a larger colony (Storz et al., 2000a). During a pilot study, we observed that both males and females within harems socially groom in a distinctive way: they hold, rub, and apply bodily secretions to one another while forming tight clusters (Video 1 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x).

Here, we hypothesize that such tight 'mutual grooming clusters' may play important roles in the social lives of Indian short-nosed fruit bats. First, we ask how these tight clusters are initiated and maintained, and whether there is any temporal variation related to reproductive activity. With field and captivity observations, we describe behavioural patterns, number and sex of participants, and whether there were daily or seasonal patterns in the mutual grooming activity. Second, we investigate the implications of mutual grooming for the association patterns among individuals. By marking individuals in the field, we measured female social associations and their use of male tents. Finally, we evaluated whether mutual grooming was involved in olfactory communication by identifying the chemical compounds in secretions applied to the body of social groomers.

2. Methods

2.1. *Study site and field behavioural recording*

The study was carried out in the botanical garden at Madurai Kamaraj University, after a pilot study to identify tents, roosting sites and tag bats (Appendix A, Figure A1). Phytophagous bats (*C. sphinx*, *Pteropus giganteus* and *Rousettus leschenaulti*) commonly forage in this area, where various fruiting trees were present including *Borassus flabellifer* and *Polyalthia longifolia* that usually provided roosting sites for *C. sphinx*. On each sampling day, we selected a tent suitable for recording behaviour and installed a video camera. Behavioural observations were carried out through continuous video recording (Olympus SP800 UZ) with diffused light between 17:30 h and 19:00 h. Videos were analysed by playing back several times to describe the behavioural repertoire (Table 1) and the time spent by focal male bats in each behavioural state (Appendix A, Figure A2).

2.2. *Association patterns*

To explore the association patterns among tagged individuals, we surveyed the area for 85 days (between January and December 2012), identifying individuals in tents using binoculars (Olympus 10 × 50 DPS I) and digital

Table 1.
Behavioural states of males of the Indian short-nosed fruit bat (*C. sphinx*).

Behaviour	Description
Resting relaxed (RR)	Eyes closed and no movement of ear pinnae
Resting alert (RA)	Eyes open with frequent movement of ear pinnae
Self-grooming (SG)	Self-scratching with hind limb, self-licking and smearing saliva
Mutual grooming cluster*	Mutual grooming in tight cluster formation
Tent marking*	Male depositing saliva on tent by licking
Wing fanning*	Male fanning wing towards incoming females
Arresting*	Male prevents females from emerging out of the tent by stretching and covering the female with both the wing
Hugging*	Arresting behaviour sometime culminates into hugging of females with fore hand

An asterisk (*) indicates a rarer behaviour.

video camera (Olympus SP800 UZ). We then performed two independent analyses.

First, we calculated the strength of social relationships among identified females sharing a given male's tent, using the half-weight association index (HWI; Whitehead, 2008). Here, this index quantified the proportion of times a pair of females were observed together in the same tent relative to the number of times seen in different tents:

$$\mathrm{HWI} = \left(\frac{x}{x + y_{\mathrm{AB}} + (\frac{1}{2(y_{\mathrm{A}}+y_{\mathrm{B}})})}\right),$$

where x is the number of sampling periods (days) with females A and B observed together, y_{A} is the number of sampling periods with just A identified, y_{B} is the number of sampling periods with only B identified and y_{AB} is the number of sampling periods with both A and B identified (Whitehead, 2008). This approach considers the 'gambit-of-group hypothesis', i.e., individuals identified together are considered to be in association (Whitehead & Dufault, 1999). The logistical limitation of capturing and marking all individual bats violates the assumption that if one individual is identified in a sampling period, then all of its associates are also identified; in this case, the HWI is the least biased index (Whitehead, 2008; Johnson et al., 2013). We illustrated the resultant association matrix as an one-mode network, in which nodes representing individuals are connected by links whose thicknesses are proportional to the HWI values.

Second, we inferred individual variation in female tent use. We plotted a two-mode network, in which females were linked to males according to the number of days they were seen using their tents, and calculated nestedness degree based on overlap and decreasing fill (NODF, Almeida-Neto et al., 2008). A nested network would indicate that some females are less selective (use tents of many males), and that the more selective females tend to be in the most used tents. We checked the significance of nestedness with a null model approach. We generated 1000 theoretical two-mode networks by filling binary adjacency matrix based on the empirical rows and columns totals (Bascompte et al., 2003), then calculated their NODF to build a benchmark distribution. The empirical NODF value was considered significant when falling outside of the 95% Confidence Interval (CI) of this distribution.

2.3. *Temporal grooming patterns: observations in captivity*

To study the temporal pattern of occurrence of mutual grooming clusters, we carried out observations in captivity. Bats from the same colony were captured using mist net from a village, Melakkal (9°56′21″N, 77°58′01″E) located about 10 km away from the sampling area at the M.K. University campus. The captured bats were collected in a cotton bag and transported to a flight room facility (3.1 m length × 2.4 m width × 4.0 m height) available in the Department of Animal Behaviour and Physiology, Madurai Kamaraj University, Madurai, India. We attempted to provide the best conditions in captivity to minimize disruptions to their natural behaviour. A bamboo basket hanging at the roof of the flight room served as the tent, and a single basket per male because females rarely roost alone in the wild (Chattopadhyay et al., 2011). An automated timer was used to maintain a 12:12 h light-dark cycle. Before the behavioural sampling sessions, bats were allowed to acclimatize in a free flight room for 10 days. After this period, they were repeatedly seen exhibiting behaviours observed under natural conditions (e.g., males marking the basket, fanning their wings, and attempting to mate).

We performed two sets of observations, each one containing one male and six females: set I occurred during the non-mating season (June–July 2015) while set II occurred during mating season (September–October 2015). In each set, we recorded the bats' behaviour continuously for 20 days, using commercially available CCTV cameras. From these footage, we were able to use 15 days' worth of video, which we played back and scanned for the occurrence of mutual grooming clusters every minute. These data were plotted as actograms (Appendix A, Figure A3), and we used chi-square analysis to test seasonal variations in the formation of grooming clusters. By the end of each set of observation, the bats were released at the site of capture after sunset.

2.4. Scent marking sampling and chemical analysis

We investigated whether the formation of mutual grooming clusters was related to chemical communication by searching for Volatile Organic Compounds (VOCs) on the wet surface of the individuals after grooming. We collected samples from seven bats from three different tents present in palm trees (see Table A1 in Appendix A). After the formation of these clusters, we captured the bats from the tent with a hoop net, and used sterile cotton moistened with ethyl acetate (Merck) to collect a sample of the bodily secretions applied during grooming by rubbing about 30 times on the wet body areas. The cotton ball was then soaked in 1 ml of ethyl acetate. Using a 10 ml glass syringe, the content in the cotton ball was squeezed into a 2 ml amber vial (Sigma-Aldrich). As an internal standard, 270 μM cholastane (Sigma-Aldrich) was added to four samples. We tested whether there were any impurities in the materials by performing all the steps above on a control cotton sample (except rubbing on the bat). All the samples were stored in -20°C until the VOCs analysis.

The collected and control samples were subjected to Gas Chromatography-Mass Spectrometry (GC-MS) for the identification of VOCs following the method described by Caspers et al., 2009 with few modifications (Appendix B). We then searched the identified VOCs in pherobase database (EI-Sayed, 2013) to infer their role in chemical communication of other animal systems (Table B1 in Appendix B), but discarding the compounds present in the control samples.

2.5. Ethical statement

The marking of bats, captive studies and sample collection for chemical analysis were approved by Internal Research and Review Board (IRB), Ethical Clearance (EC), Biosafety and Animal Welfare Committee, Madurai Kamaraj University, Madurai, India.

3. Results

3.1. Field behavioural observations: the ‘mutual grooming clusters’

Our field observations totalling 61 days (between January and October 2012) revealed that before sunset male and female members of a harem arise from daytime rest and initiate self-grooming. This activity included scratching the body with hind limbs, licking anogenital area, depositing saliva on the ventral side of the wing membrane and smearing it on the body surface. When individuals licked their anogenital region, they attained a bent posture, which stimulated other harem members to partake in mutual grooming. They typically inserted their heads underneath the initiator’s wing membrane, resulting in an event we defined as a ‘mutual grooming cluster’ (Video 1 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x).

We have observed 128 mutual grooming clusters on 55 (out of 61) different observation days. Mutual grooming clusters lasted from 10 to 280 s (mean duration ± SE = 41.4 ± 3.66 s). The number of bats present in a single grooming cluster varied between 2 and 8. Individuals in these clusters typically held each other, applied saliva (and possibly anogenital secretions) on their bodies and mutually rubbed one another for few seconds. After detaching from the mutual grooming clusters, individuals usually self-groomed (further spreading secretions from mutual grooming) and subsequently rested for a short period before emerging out of the tent. After grooming, the bats’ neck, head and facial areas became visibly wet, and they appeared relaxed, which was evident from reduced ear pinnae and eye movement. Additionally, male bats often deposited saliva onto their tents (Video 2 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x) and fanned their wings (Video 3 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x; see also pre-emergence activity budget in Figure A2 in the Appendix), while females usually aggregated in a large cohesive group after grooming.

On average, males spent 1.5% of their time in mutual grooming clusters. The proportion of time allotted in mutual grooming was lower than in self-grooming (Figure 1). The duration of participation in mutual grooming clusters also varied significantly among males ($\chi^2 = 71.12$, df = 6, $p < 0.0001$).

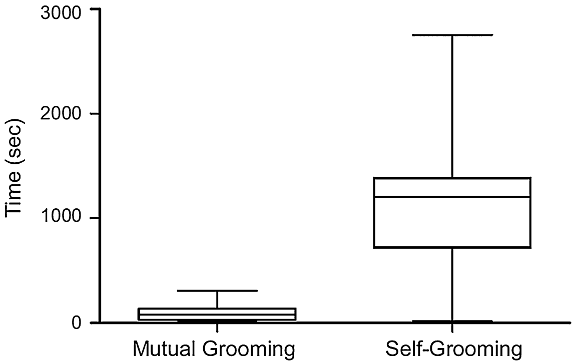

Figure 1. Time spent (in s) by all male bats ($N = 7$) in self-grooming and mutual grooming (Table 1). The whiskers represent maximum and minimum values.

The average number of adult females in the colony varied during the observation period (Figure 2): the number of female bats in the colony was greater during the mating season (mean ± SE $= 15.64 \pm 0.75$) than the non-mating season (mean ± SE $= 8.60 \pm 0.39$; $t = 9.036$, df $= 79$, $p < 0.0001$). Females initiated mutual grooming clusters more often (82.5%) than males ($\chi^2 = 37.96$, df $= 1$, $p < 0.0001$). Although male bats were infrequent initiators of grooming clusters, they were frequent participants (observed participating in 78.9% of the clusters). Whenever two different grooming clusters were formed simultaneously by females ($N = 15$), the male would join both, one after another. When two females in the same tent did not participate in the same grooming clusters, the male would form a groom-

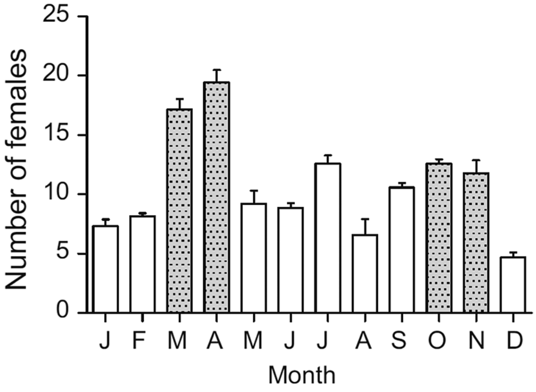

Figure 2. Mean number of females in the colony during mating (filled bars) and non-mating seasons (open bars). Whiskers represent Standard errors.

ing cluster with one female first, then another cluster with the other female ($N = 4$). Similarly, when a male maintained two different tents that were occupied by females, the male participated in the grooming clusters of both tents. We have observed a similar trend in male behaviour in captivity: males would join females that did not participate in grooming clusters ($N = 3$). Harems typically contained females that often and rarely participate in mutual grooming and females that do not. In most cases, not all females in a tent participated in the grooming clusters ($N = 109$), we observed the participation of the entire harem in only 14.9% of events.

3.2. Association patterns and female variation in tent use

Females varied in the number and strength of associations with other females with which they shared a tent (Figure 3). For example, females f2 and f4 were observed roosting together in July 2011; since then we have observed them together in the same colony (Botanical Garden, M.K. University) in the years 2012, 2013 and 2014; moreover, tagging these individuals by previous researchers (2008) showed that their interactions have lasted at least 5 years. As contrasting examples, f2 and f4 associated weakly with f8 and f3, respectively (Figure 3).

There was also individual variation in tent use by females ($\text{NODF}_{\text{rows}} = 68.52$; 95% CI = 29.63-65.86, $p = 0.017$), with some visiting more males (e.g., f4, f2) than others (e.g., f8, f83). However, we did not detect a difference between the overall nestedness degree of this two-mode network and the null expectation (NODF = 61.98; 95% CI = 32.09-63.63; Figure 4), which suggested there was not a strong rank from less to more selective females.

3.3. Daily and seasonal patterns of mutual grooming

The temporal pattern of occurrence of mutual grooming clusters in captivity was similar in both observation sets: in set I, they were observed between 15:57 h and 18:13 h while in set II they were observed between 16:05 h and 18:27 h (Figure 5). During the rest of the time (18:30 h to next day 15:30 h) no mutual grooming clusters were observed. Bats emerged out of the basket for foraging about 20 min after the lights were turned off. Similar to field observations, the male moved among different females and joined the females that were not part of the grooming clusters. Other behaviours (wing fanning, marking the basket with saliva, arresting the females, and mating; Table 1) were observed during the reproductive season only. The occurrence

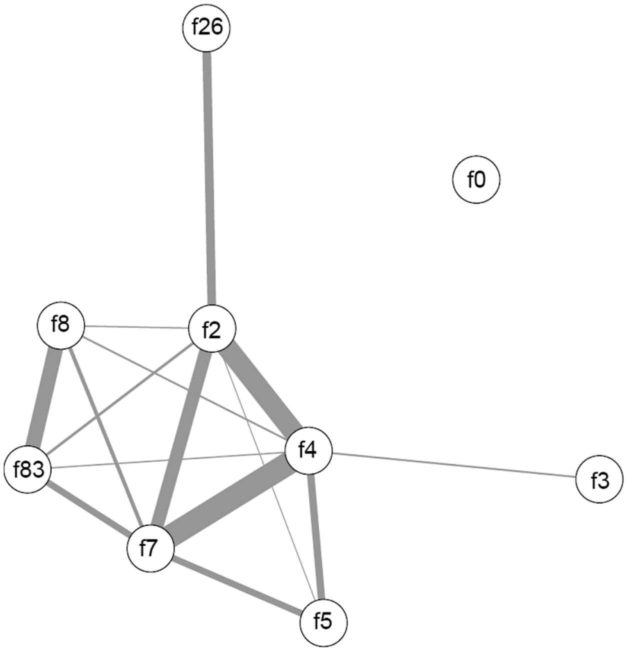

Figure 3. Social network of female Indian short-nosed fruit bats in the colony. Nodes represent individually marked females, which are connected (except f0) by links whose thicknesses are proportional to strength of association quantified by the half-weight association index.

of grooming clusters was more frequent during non-mating (mean ± SE = 6.07 ± 0.52) than mating season (mean ± SE = 3.67 ± 1.24) ($\chi^2 = 9.534$, df = 1, $p = 0.0002$).

3.4. *Chemical analysis*

We have tentatively identified 108 VOCs from the wet areas of the body of individuals engaged in formation of mutual grooming clusters. Nearly half (42.6%) of these compounds are known to be involved in chemical communication of other animal social systems. The chemical nature of these compounds are given in Table B1 in Appendix B. We acknowledge, however, that these are preliminary findings and further analysis comparing the secretions applied during grooming with those of non-groomed bats is warranted.

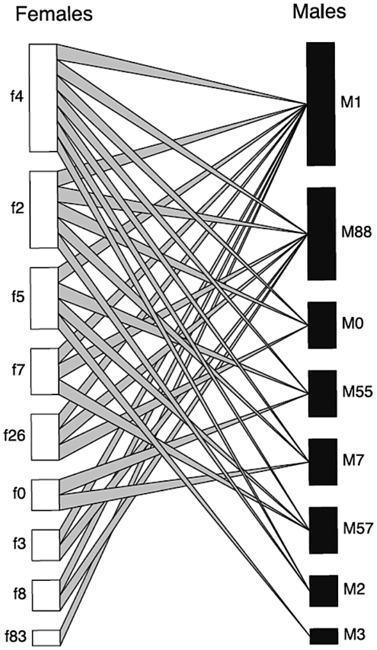

Figure 4. Two-mode network of females connected to males by the number of times they were found in their tents. Node size is proportional to number of observed interactions.

4. Discussion

Our observations reveal potential affiliative and cooperative behaviour within harems of Indian short-nosed fruit bats, previously thought to be simple aggregations with limited interactions among individuals (Kerth, 2008). We found that this species frequently engages in a distinctive form of social grooming: within the tents built by males (Balasingh et al., 1995), individuals groom each other forming tight clusters, almost daily before the emergence flight at dusk. After mutual grooming, individuals are visibly wet with saliva and secretions from sebaceous glands and the anogenital area. These secretions contain several volatile organic compounds — nearly half of which are known to participate in animal chemical communication. Females varied in social association strength and tent use across the colony. Combined, these findings suggest that social grooming may have chemosensory-mediated functions — such as mate choice, individual and/or group recognition — and may also serve for males to gain information on female reproductive status. In what follows, we discuss these possible functions of mutual groom-

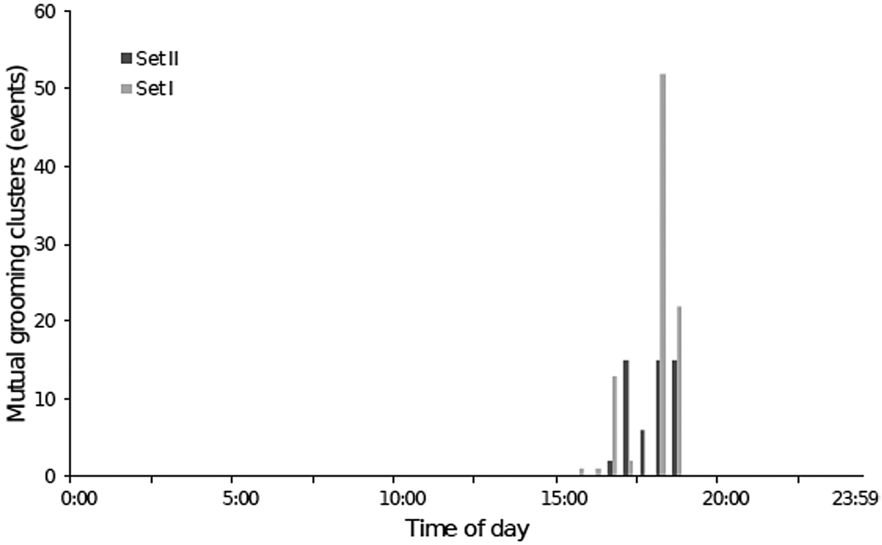

Figure 5. Temporal pattern of occurrence of mutual grooming clusters. Grooming was only observed before the start of emergence flight. *Y*-axis indicates the number of events observed in each of the two independent sets of observation in captivity.

ing and their implications for the social lives of the Indian short-nosed fruit bat.

4.1. Chemical communication: scent marking and mate choice

We found differences in the patterns of self- and social grooming among males of Indian short-nosed fruit bats, suggesting the two activities have different functions in addition to hygiene. The secretions applied on their bodies during social grooming might play a role in chemical communication and scent marking. During mutual grooming clusters, smearing saliva on body was frequent, and the penis glandes were commonly seen out of the fore skin. The wing membrane of this species contains sebaceous glands (Baskaran et al., 2015), whose secretions such as squalene and cholesterol (Picardo et al., 2009) we identified in the bat's body after grooming. Saliva and secretions of anogenital region and sebaceous gland are involved in chemical communication in several mammalian species (Booth, 1987; Kiyokawa et al., 2000; Hayes et al., 2004). Indeed, nearly half (46 out of 108) of the volatile organic compounds we identified from grooming cluster participants are known to function in chemical communication. Moreover, the formation of grooming clusters resembles the scent marking behaviour of fishing bat *N.*

leporinus (Brooke, 1997) and some of the volatile organic compounds may serve this function. Squalene, for example, is known as a fixative (Alberts, 1992), which could increase the fade-out time of other compounds, and so the time for conspecifics to recognize the scent.

Recognizing chemical cues may have implications for mate choice, and for minimizing inbreeding. Although the complete dispersal of juveniles from the natal colony reduces inbreeding (Storz et al., 2000b, 2001), genetically-related individuals from both sexes are found within the harems (Chattopadhyay et al., 2011). Given the well-known negative effects of inbreeding on the survival and reproduction (Charlesworth & Charlesworth, 1987), behavioural mechanisms that aid the discrimination between kin and non-kin, preventing mating between close relatives, are usually favoured (Pusey & Wolf, 1996). Learned signature mixtures of chemosensory cues associated with major histo-compatibility complex (MHC) are one such mechanism (Yamazaki et al., 1986, 1992; Wyatt, 2014). MHC molecules are secreted in body fluids, such as saliva (Wobst et al., 1999), and provide olfactory identity to an individual (Yamazaki et al., 1986).

Behavioural observations during mutual grooming lend some support for the hypothesis on olfactory-mediated mate selection. First, males mark their tents with saliva (Video 2 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x; Balasingh et al., 1995) and subsequently fan their wings (Video 3 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). These behaviours are much more frequent during mating seasons (Doss et al., 2016), suggesting that males may disperse scent to attract females to their tents. Second, when receptive females scan the available tents in the colony, they land in, inspect, and sniff the tent. At this time, males examine the incoming females by sniffing their abdomen or anogenital region. We have observed males restricting the entry of certain females and chased them away with bites and wing flapping ($N = 12$; Video 3 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). Finally, the high frequency of male participation in social grooming (78.9%), plus the close physical interactions with females during grooming clusters, may allow males to gain information on the female reproductive status via chemical cues and/or examination of the physical attributes of their abdomen.

4.2. *Social associations: bonding and mate searching*

Given this potential role for chemical communication, we further suggest that social grooming may also be involved in individual and group recognition, bonding and establishment of associations within the harem. While females of other bat species do form long-term associations (Wilkinson, 1986; Wilkinson & Boughman, 1998; Patriquin et al., 2010; Kerth et al., 2011), the strength of association among females in the short-nosed fruit bat is generally low (Storz et al., 2001). Our findings generally reinforce this pattern, with females from different tents within the colony associating with various frequencies. In the short-term, it is possible that mutual grooming may help individuals familiarize each other with the scents of harem members before the departure flight to assist recognition when they return to the roost. In the long-term, some females remain in the colony from one parturition period to next (Storz et al., 2001), having therefore opportunities to engage in longer relationships. We showed an example, although anecdotal, of two females (f2, f4) forming associations that lasted at least 5 years.

The heterogeneity in associations observed here may be related to the individual variation in tent attendance, in which some females are less selective and roost with more males in the colony than others. Being less selective and roosting with several males likely reflects active search for mate and/or shelter and protection (on three occasions females used the tent as a parking site for young ones while foraging). Males vary in their ability to build tents; for instance, three of our identified males (M7, M55, and M88) were not successful in building tents (A.R. pers. obs.). Moreover, tents have limited duration (between 5 and 8 months; A.R. pers. obs.) when built in palm leaves because rain and wind that often terminally damage tents. Therefore, it is possible that uncertainty in the male ability to build a tent coupled with short duration of the tents in palm trees may cause females to periodically switch their tents with in the colony.

There are frequent conflicts among harem females for spacing within the tent during parturition and lactation period ($N = 7$; Video 4 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). But because they engage in close bodily interactions during grooming clusters and usually form a single group after, we hypothesize that mutual grooming may promote conflict reduction and maybe bonding among some females (see Pellis & Pellis, 2010). Females could also try to bond with males after social grooming (e.g., Fedurek & Dunbar, 2009). Other than social grooming, we have observed female sniffing male anogenital area ($N = 2$; Video 5 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x) and certain affiliate interactions from females towards males, such as nibbling (soft bites; $N = 8$; Video 6 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x) and prodding ($N = 5$; Video 7 in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x), possibly for initiation of mating or grooming clusters.

4.3. Temporal patterns: predator avoidance and flight performance

The captive observations suggested that social grooming in this species is characteristic of a particular time of the day: at dusk, before the emergence flight. This timing suggests predator avoidance. We observed on three occasions predators such as crow and shikar (*Accipiter badius*) attacking and feeding on individuals of short-nosed fruit bats during daytime (e.g., Appendix A, Figure A4). The movement and behaviours involved in the grooming activity makes the tent noisy and visible during daytime, which could attract predators. So, restricting social grooming before emergence flight can conceal them from daytime predators. Mutual grooming also appears to be an energetically demanding activity because it involves smearing of secretions on the body. Hence, to conserve energy and water content, bats may restrict this activity to a particular time interval. Body wetting reduces anxiety and enhances flight manoeuvrability (Brilot et al., 2009), making it possible for the wetness due to pre-emergence grooming activity to influence the mood and flight performance.

4.4. Conclusions and the way forward

Our findings suggest that social grooming in Indian short-nosed fruit bats have multiple possible functions other than hygiene. Social grooming may assist recognition and mate choice through chemical cues, with males potentially identifying the reproductive status of female in their harem or enhancing their receptivity for mating. Through physical contact, social grooming may promote bonding among members of a harem. At the physiological level, social grooming might influence the mood and flight manoeuvrability.

While our study advances the idea of grooming playing several roles in the lives of Indian short-nosed fruit bats, we acknowledge that these roles remain speculative, waiting for empirical tests. Further studies departing from the hypotheses we lay out here will improve our understanding of interspecific variations in social grooming investment and the implications of grooming behaviour for sociality of bats. Moreover, accounting for genetic relatedness and kinship in social grooming of short-nosed fruit bats might illuminate the underlying mechanisms of this potentially cooperative behaviour.

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Appendix

The videos described below are part of the online version of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

Video 1. Mutual grooming cluster formation. In the tent of male M2, there are four females, three of which are aggregated which, including female F7 (white). The female which is separated from the aggregation initiates the grooming cluster. The bat with dark brown coat is male M2. The first one to join the female initiator at 0:36 is the male, which is then followed by the other individuals. The male detaches itself from the ball at 2:45 and all the females remain together, continuing self-grooming. The wetness on the bats body surface is visible from 2:35 onwards.

Video 2. Males marking tent with saliva. Male M7 (white) licks to deposit saliva in its tent before the emergence flight.

Video 3. Male wing fanning. Male M7 fanning wing, possibly to disperse scent to attract females. Seven females land while the male fans its wings with intermittent licking. Females f0, f3 (green), f4 (yellow) and f2 (blue) land at 0:4, 1:55, 2:07 and 2:13, respectively. The male rejects a landed female at 2:38 with bites. At 1:42 there is a “chip chip” vocalization by intruder male in the colony; wetness on the coat of most of the landed females suggests that they have participated in grooming behaviour before emerging out. The sniffing behaviour among females observed at 0:28, 1:51, 1:56 and 2:12 suggest sampling of olfactory cues.

Video 4. Conflicts among females. A female without pup tries to move, but due to spacing limitation it hooks on to another female which is carrying pup at 0:24. In response, the female with pup applies strong bites on female without pup. All the biting attempts were made by female with pup towards female without pup.

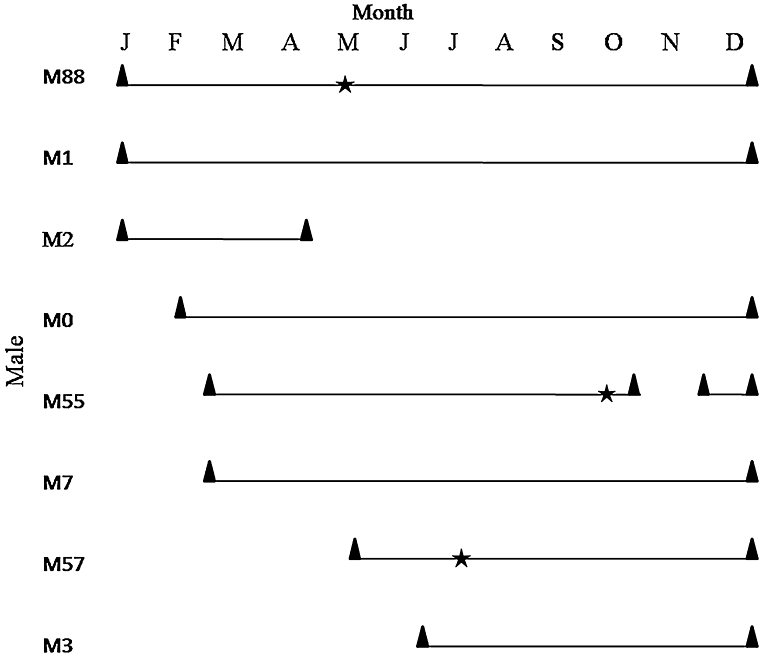

Figure A1. Temporal occurrence of the sampled male Indian short-nose fruit bats in the colony. Black triangles indicate the month an individual (rows) joined the colony. Black stars indicate the month they were tagged. When we started our observation in January 2012, there were three harem males, including (M2) and a solitary male (M0). During the subsequent sampling period, M7 and two more males joined the colony at different times and were also tagged. Male M2 abandoned the colony in April 2011, and when M3 joined the colony it started using the abandoned tent of M2 until the construction of new tent. In total we carried out observations on eight different harems. All the males were tagged except M1, which remained untagged throughout the study.

Video 5. Female examining male anogenital region. A female examines the anogenital region of male M57 (orange, white, green) by sniffing it between 0:5 and 0:12.

Video 6. Female nibbling male. Female f2 (blue) applies soft bit on male's M0 (yellow) ear pinnae at 0:8 during grooming activity.

Video 7. Female prodding male. There are 10 females in the tent, and eight of them are with their pup. The bat with dark coat is male M1 roosting near the female f4 (yellow). At 0:15 a female without pup hook on to male and bites it near the chest area, and male assumes a submissive posture.

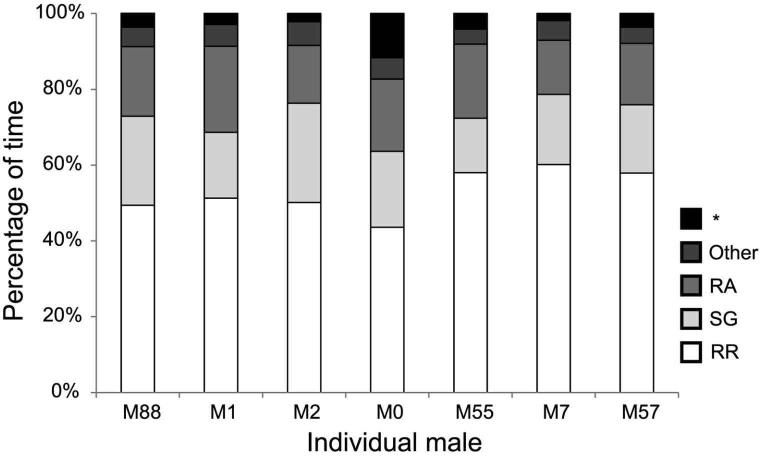

Figure A2. Pre-emergence activity budgets of male bats. The shades in each bar represent time allocated for each activity: RR, resting relaxed; SG, self-grooming; RA, resting alert; Other, other unclassified behaviours; Asterisk, combination of all other classified behavioural states, including mutual grooming clusters. The description of each behavioural state is given in Table 1. Data on M3 were not available.

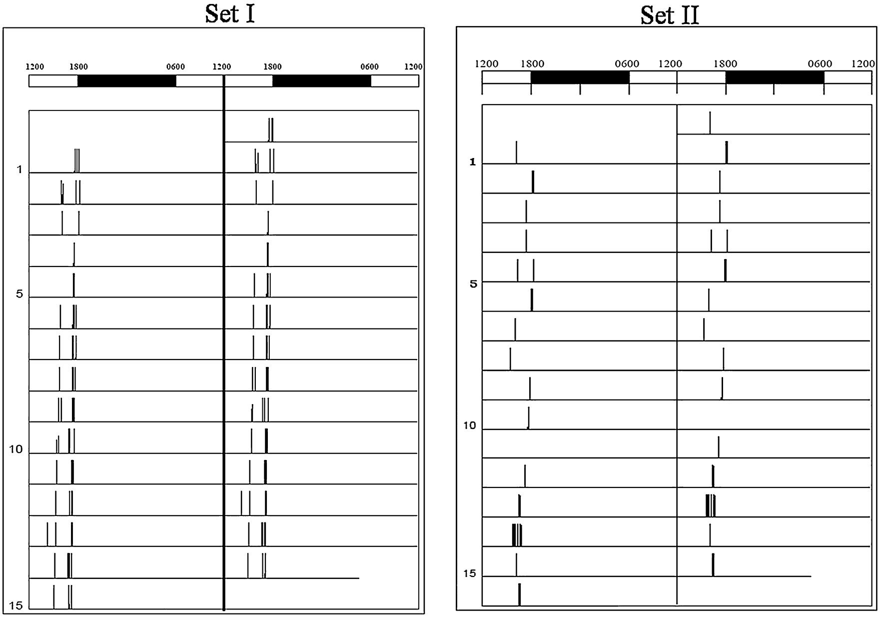

Figure A3. Actogram for the mutual grooming clusters observed in captivity. Top axes indicate day (white) and night time (black), and black bars indicate occurrence of mutual grooming clusters.

Figure A4. The bird of prey Shikar, *Accipiter badius*, feeding on Indian short-nose fruit bat, *C. sphinx*. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

Appendix A

Pilot study, bat capture and tagging

We carried out a pilot study for 15 days between July and September 2011 to identify tents and roosting sites in the trees, to tag individual bats and test collection of behavioural data with video recording. The study area was located in the botanical garden at Madurai Kamaraj University, where the climate is tropical dry-wet (rainy season from October to December) and various fruiting trees are present (e.g., *Polyalthia longifolia*, *Syzygium cumini*, *Parkia timoriana*, *Ficus religiosa*, *Cassia fistula*, *Mimusops elengi*, *Madhuca indica*, *Azadirachta indica*, *Terminalia catapa* and *Crescentia cujete*). The daytime census revealed 30 individual adult bats in five tents distributed in two palm trees. Out of these 30 bats, one male (M2) and three females (f2, f4, f5) were already tagged with a necklace by previous researchers. The untagged bats were trapped using nylon mist nets of 2.6 m × 6 m with a

Table A1.
Sampling sites (GPS coordinates) for scent marking sampling.

	Sampling site	Harem size	Sample size	Date
1	Adaikampatti (9°56′14″N, 78°00′14″E)	2M/1F	2M/1F	12 June 2014
2	Nagamalipudukottai (9°56′12″N, 78°03′8″E)	1M/2F	1M/1F	5 July 2014
3	Puloothu (9°56′53″N, 78°02′58″E)	1M/6F	1M/1F	6 July 2014

M, male; F, female.

mesh size of 38 cm (Avinet, Dryden, NY, USA), when they emerged out for foraging, and tagged with custom made nylon necklace (0.63 g) containing distinctive coloured plastic beads and reflective coating. We have tagged three males (M0, M3 and M7; see Figure A1) and nineteen female bats between October 2011 and January 2012. During the North East monsoon of November 2011, three out of the five tents fell down, causing most of female bats to leave the colony. Daytime census in the first week of December 2011 revealed 11 bats in two tents and a solitary bat roosting adjacent to the harem group. To test the video recording, we searched for bats in palm trees during evening hours, selected a tent suitable for recording, and carried out focal sampling (Altmann, 1974) between 18:00 and 20:00 h (total 450 min of video).

Appendix B

Gas chromatography-mass spectrometry (GC-MS) analysis

The samples were analysed in a GC-MS (GC-MS-QP2010 Plus) coupled with an internal desorption system TD 20) having a DB5 column (30 m, film 0.25 m, internal diameter 0.25 mm). Sample volume of 2 μl was injected in splitless mode, helium as carrier gas at a flow rate of 1.21 ml/min, the oven temperature was 50°C/min with 3 min initial hold at 280°C at a rate of 4°C/min and final hold was for 20 min at 280°C. The ionizing voltage for the carrier gas was 70 eV. The compounds were tentatively identified by similarity index between the recorded mass spectra and WILEY8.LIB and NIST08.LIB library spectra provided by the software of the GC-MS system (GC-MS-QP2010 Plus, Shimadzu, Tokyo, Japan). In Table B1 we have included only the compounds which had similarity index 85% or above for further analysis.

Table B1.
Volatile organic compounds identified from the wet body surface and their role in chemical communication in various animal system, as retrieved from the Pherobase database, available online at http://www.pherobase.com.

Compound	Chemical communication system
4-Hydroxy-4-methyl-2-pentanone	Insect
2-Methylbutanoic acid	Insect, mammal
Triethyl phosphate	
L-(–)-Menthol	
(3Z)-3-Tetradecene	Insect
Dodecane	Insect, reptile
2,3-Dihydro-1-benzofuran	
2,4,4-Trimethylhexane	
1-Pentacosanol	
Tetradecane	Insect, arachnid
1-Pentadecene	Insect, arachnid
17-Pentatriacontene	
1-Octadecene	Insect
Diisobutyl phthalate	
1-Nonadecene	Insect, arachnid
Ethyl (9Z)-9-octadecenoate	Insect
1-Isopropyl-1-methyl-2-nonylcyclopropane	
1-Tetracosanol	Insect, reptile, mammal
1-Icosanol	Insect, reptile, mammal
1-Heptacosanol	Reptile
9-Hexacosene	Insect
Pentatriacontan	Insect
trans-Squalene	Insect
Cholesterilene	
3-Phenyl-2-butanol	
1-Dodecene	Insect
1-Tridecene	Insect
Phthalic acid	
Oxacycloheptadec-8-en-2-one	
(9Z,12Z)-9,12-Octadecadienoic acid	Insect, reptile, mammal
2-{[(2-Ethylhexyl)oxy]carbonyl}benzoic acid	
Nonadecane	Insect and reptile
Squalene	Insect, reptile and mammal
Triacontane	Reptile and mammal
Cholesta-3,5-diene	
1,3,5,7-Cyclooctatetraene	
1-Heptadecene	Insect, arachnid

Table B1.
(Continued.)

Compound	Chemical communication system
Eicosane⟨n−⟩	
Methyl 17-octadecynoate	
Hexadecanoic acid	Insect, arachnid, reptile, mammal
1-Isopropyl-1-methyl-2-nonylcyclopropane	
2-Tetradecyloxirane	
1,54-Dibromotetrapentacontane	
Henicosyltrifluoroacetate	
1-Triacontanol	Arachnid, reptile
Undecane	Arachnid, insect, reptile
1-Isopropyl-4-methylbicyclo[3.1.0]hexan-3-one	
1-Pentadecanol	Reptile, mammal
2-Propyl-1-decanol	
(9E)-9-Octadecene	
Pentadecane	Insect, arachnid, reptile
(9E)-9-Icosene	
Heptadecane	Arachnid, insect, reptile
Dibutyl-phthalate	Insect
1-Heneicosanol	Insect
1-(Hexylsulfanyl)hexane	
5,24-Trimethyltetracontane	
(13Z)-13-Octadecenal	Insect
Octadecylchloroacetate	
(3β)-Cholest-5-en-3-ol	Annelid, insect, amphibian, reptile, mammal
Isopropylbenzene	
1,1,3-Triethoxypropane	
Nonylcyclopropane	
2,4,7,9-Tetramethyl-5-decin-4,7-diol	
3,7-Dimethylnonane	
4-Octylphenol	
Dodecyl-acrylate	Reptile
2-Bromdodecane	
2-Icosanylbenzene	
2-Tetradecyloxirane	
Palmitic acid	Arachnid, insect, reptile, mammal

Table B1.
(Continued.)

Compound	Chemical communication system
3-Methyleneundecane	
2-Ethylhexyl-4-methylpentylsulfite	
Cycloicosane	
Methyl 8-(2-hexylcyclopropyl)octanoate	
(11Z)-11-Octadecenoic acid	Insect
Vinylcyclooctane	
(5E)-3-Methyl-5-undecene	
Hexadecyl acetate	Arachnid, reptile, insect and mammal
Bis(2-ethylhexyl) adipate	
Icosyl acetate	Insect
2,2′-Methylenbis[4-methyl-6-(2-methyl-2-propanyl)phenol]	
Pentadecanal	Insect
Dioctadecylphosphonate	
2,6,10,15-Tetramethylheptadecane	
Acidephtalique	
1-Octacosanol	Insect, reptile
1,15-Pentadecandiol	
Isobutyl pentyl oxalate	
4-Methoxybenzaldehyd	Insect
3,7-Dimethylnonane	
5-Methyl-1-heptanol	
Cyclodecene	
Hexadecylpentafluoropropanoate	
Phenol	Arachnid, insect, mammal, reptile
N,N-Diethyl acetamide	
E-11,13-Tetradecadien-1-ol	Insect
Hexadecane	Insect, mammal, reptile
3-Methylcyclooctene	
4-Methyl-2-propyl-1-pentanol	
(2Z)-3-Methyl-2-undecene	
2-Ethylhexyl hexyl sulfite	
3-Heptadecanol	
1,1-Dichlor-2-dodecanol	
1,2,4-Trimethylcyclopentane	
(13Z)-13-Octadecenal	Insect
Dotriacontane	Insect, reptile
1-Octadecanol	Mammal, insect, reptile