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ORIGINAL ARTICLE

Impact of reproduction on roost selection of the Indian flying fox, *Pteropus medius* (Temminck, 1825)

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ABSTRACT

A thorough knowledge of ecology and behaviour is a clear requirement for proper conservation and management of a species. The Indian flying fox, *Pteropus medius* (formerly *P. giganteus* Brünnich, 1782), lives gregariously in large trees and spends a considerable time at day roosts. The roost sites play vital roles in survival, reproduction and population persistence. This study describes changes in roost selection, colony size and behaviours of *P. medius* during reproductive and non-reproductive seasons in a large colony at Mohanlal Ganj, Lucknow (India). The colony size was significantly lower during the summer non-reproductive season (486.5 ± 121.1 SD) than during the spring (1942 ± 488.8 SD) and monsoon (2367.7 ± 277 SD) reproductive seasons. The number of roost trees utilised and roost site selection differed across the reproductive and non-reproductive seasons. The bats occupied the southern periphery of the sampled garden during the non-reproductive period (summer), whereas they shifted to the central and northern parts of the garden during the reproductive seasons and winter periods. The reproductively active individuals secluded themselves from the reproductively inactive colony members. The selection of secluded roost sites during the reproductive period demonstrates the need for social exclusion, less disturbance, and reduced mate competition. The higher population size during the reproductive period might be due to the immigration of bats, most probably male individuals, facilitating gene flow from nearby populations and thus increasing genetic diversity and species resilience.

INTRODUCTION

The Indian flying fox, *Pteropus medius* (formerly known as *Pteropus giganteus* Brünnich, 1782), is a long-living colonial species distributed throughout India and across Bangladesh, Bhutan, China, Maldives, Myanmar, Nepal, Pakistan, and Sri Lanka. Like other flying foxes, the Indian flying foxes live gregariously in large trees over the day; they leave the roost for foraging around sunset and return to the day roost before sunrise (Kumar & Elangovan 2019). *Pteropus medius* is known to live and occupy the same roost trees for many decades (Marimuthu 1988, Kumar & Kanaujia 2015). The roost sites are critical for tree roosting bats like *P. medius*, as they spend more than half of their lifetime at day roosts and use the roost sites to perform various general and social behaviours like wing fanning, grooming, sleeping, territorial defense, male-male combat and reproductive behaviours like courtship, mating, parturition and nursing of young (Nelson 1965a, Markus & Blackshaw 2002, Kumar et al. 2017a, Kumar & Elangovan 2019, Roy et al. 2020). The day roosts are vital for population persistence, offspring development, social interaction and site for reproduction (Kerth et al. 2003) and offer an opportunity for females to choose suitable and potential mates, reduces the number of rivals and conflicts and provide a safe site for mating.

Roost selection and roosting ecology have been documented in the past on various species of flying foxes (Nelson 1965b, Markus & Blackshaw 2002, Kalcounis-Rüppell et al. 2005, Connell et al. 2006, Kumar & Elangovan 2019, Mishra et al. 2019). In general, roost tree selection is based on tree characteristics, i.e., tall, large trunk and wide canopy trees (Kumar et al. 2017a) as well as it is influenced by the reproductive seasons of several bat species. The females of many bat species in temperate regions, for example, aggregate from late spring until early autumn for the gestation and nursing of their offspring (Kunz & Lumsden 2003). In addition, the social organisation is also known to vary among reproductive stages (Garroway & Broders 2007), as sometimes reproductively active males and females are segregated from the reproductively inactive males and females. The Australian coastal flying foxes (*Pteropus poliocephalus* and *Pteropus gouldi*), for instance, leave the colony during summer and form winter colonies (Nelson 1965b).

Studies on the reproductive behaviour of *P. medius* suggest a clear seasonal dispersal of bats from their colonies to nearby areas during summer (Vyas & Upadhyay 2014). Mishra et al. (2019) also reported that the colony size of *P. medius* was, in general, larger during the spring–summer months than during winter. However, evidences suggest that they undergo reproduction at different seasons across geographical locations. The copulations of *P. medius* were observed from July to October in Tamil Nadu (Koilraj et al. 2001, Maruthupandian & Marimuthu 2013) and Bengaluru (Ramakrishna et al. 2014), from July to September at Lakhimpur-Kheri in Uttar Pradesh (Kumar & Kanaujia 2015), from July to November in Karnataka and Uttar Pradesh (Jeevan et al. 2017, Kumar et al. 2017a) and from August to October in Uttar Pradesh (Kumar et al. 2016). Further, the courtship behaviours and mating of *P. medius* were observed in St. Martin's Island of Bangladesh from February to March (Baki et al. 2015). Manandhar et al. (2018) studied the population status and behaviour of *P. medius* at two locations in the temperate environment of the Kathmandu Valley (Nepal) and found peak copulation during October. However, Mathur et al. (2011) reported two reproductive cycles in *P. medius*, from January to March and August to September in Uttar Pradesh, India. A few studies suggest that *P. medius* give birth to single young during the periods of January–March (Neuweiler 1969) and February–April (Kumar & Kanaujia 2015, Kumar et al. 2016), and April–May (Prakash 1960, Vyas & Upadhyay 2014).

Thus, considering the large variability found amongst previously collected information, it becomes important to understand the impact of reproduction on colony size and associated changes in the roosting pattern of *P. medius*. An influx of flying foxes during the reproductive season could influence roost site preference as reproductively active individuals need social exclusion, avoiding rivals and mate competition. Therefore, I hypothesised that the roost preference of *P. medius* varies with reproductive stages, as the reproductively active females may segregate from the core of the colony in order to get less disturbance and reduce intra-sexual competition to acquire potential males. In addition, the females may be relatively less social during the mating period than during the gestation and lactation periods, when they need to aggregate and defend themselves.

Further, I predicted that the colony size of *P. medius* would increase due to the immigration of reproductively active males and decrease due to their emigration soon after the mating period. The females may be forced to rejoin the maternity colony for protection after the completion of mating, as many males may disperse out of the colony. To test the above predictions, the roost site selection (i.e., selection of roost trees in a grove), social and reproductive behaviours and colony size of *P. medius* were studied with reference to their reproductive and non-reproductive seasons.

MATERIAL AND METHODS

Study area

The study was carried out in a large colony of *Pteropus medius* at Mohanlal Ganj, Lucknow, Uttar Pradesh, India between January 2018 and February 2022. The colony has existed in a garden for over two decades (personal observation), and the garden spreads over 15200 m^2 consisting of around 350 *Eucalyptus* trees along with a few trees of *Azadirachta indica*, *Dalbergia sissoo*, and *Ficus religiosa* on its periphery. The southern boundary of the garden is occupied by a few small shops and goat slaughterhouses, whereas the northern boundary is surrounded by human dwellings. The eastern boundary is covered by railway tracks and high-tension electric wires, and the western boundary is surrounded by a primary hospital and open ground.

General and reproductive behaviours of *Pteropus medius*

The general and reproductive behaviours of *P. medius,* like sleeping, grooming, wing fanning, wing stretching, yawning, fighting, vocalisation, courtship displays, genital grooming, sniffing and licking the partner and mating, were observed from a vantage point using a binocular (Celestron, 15x70) and photographed using a digital camera (Nikon, D5200). Males were recognised based on erected penis and scrotum, while females were recognised during genital grooming and urination. A group of bats that occupied a branch was randomly chosen for observation. However, the group size varied over the observation period. The behaviour of bats that occupied the adjacent trees was also checked to ensure that the behaviours of sampled bats corresponded to the bats of other groups of the colony. The behavioural observations were carried out by an observer following Markus & Blackshaw (2002) and Connell et al. (2006).

Colony size and roost site selection of *Pteropus medius*

On the basis of the annual reproductive cycle of *P. medius*, the study period was divided into spring reproductive season (January, February and March), summer non-reproductive season (April, May and June), monsoon reproductive season (July, August, September and October) and winter season (November and December). The trees which harboured bats were identified and numbered sequentially, and the tree numbers were retained throughout the study period. GPS coordinates of each roost tree were obtained using a handheld GPS (Montana 680, Garmin), converted into decimal degrees, to plot the graphs with the corresponding average bat occupancy to the roost tree. The average tree-wise bat occupancy, number of roost trees used, and colony size were computed for every month across the study period (i.e. from January 2018 to February 2022). The monthly average bat occupancy of each roost tree, number of roost trees used, and colony size were plotted. The relation between bat occupancy and colony size was assessed by linear correlation, and the variations in colony size among seasons were analysed using a one-way ANOVA. A Tukey-Kramer post hoc test was performed for pairwise comparisons of colony size among different seasons. The number of bats occupied on individual trees was counted and summed up to get the colony size (Krystufek 2009, Vyas & Upadhyay 2014). In addition, the temperature (°C) and relative humidity (%) in the garden were recorded during the observations to understand the impact of weather conditions on roost selection. No bat was captured and no disturbance was observed during the course of the study.

The relevant institutional permit was secured vide Letter No. 214/11/DAAS/BBAU/2011 of Babasaheb Bhimrao Ambedkar University.

RESULTS

General and reproductive behaviour of *Pteropus medius*

The flying foxes occupied exclusively tall *Eucalyptus* trees, while trees of a few other species like *Azadirachta indica*, *Dalbergia sissoo* and *Ficus religiosa* were also found in the garden. A total of 63 field days yielded 109.6 hours of observation on various behaviours of *P. medius* with an average duration of 1.73 hours per day. General behaviours such as sleeping, self-grooming, wing fanning, wing stretching, yawning, fighting and vocalisation were observed at day roost. Sleep was a common behaviour observed throughout the day, and many individuals slept by wrapping their wings around the body. The colony was quite vocal when they returned from their foraging ground in the early hours of the day and in the evening just before their emergence. Self-grooming was commonly observed behaviour in *P. medius*. Grooming of the patagium, ear pinnae, genital region and body surface was observed mainly as a cleaning function, and grooming was observed after rain to wipe raindrops from the body surface. Wing fanning was frequently observed during mid-day and especially during sunny hours.

Although the sexual and courtship behaviours of *P. medius* were observed from late January to early April, and late July to early November, the peak mating was observed from late February to March during the spring reproductive season and from late August to September during the monsoon reproductive season. The bats were actively involved in courtship behaviours, including licking the partner, genital grooming, sniffing the opponent, and courting the female during peak reproductive phase. However, no courtship behaviour and mating were observed during winter (average maximum day temperature: 19.0 ± 3.6 °C), i.e., early December to mid-January. The peak mating was linked to increased colony size and suitable weather conditions during spring and monsoon seasons. The potential males consistently approached the females by sexual and courtship behaviours, like sniffing and licking the body surface and genitalia. Males approached females with partially stretched wings and wing fanning. While the females were initially generally reluctant and avoided the males by swivel behaviours, thereafter, many of them accepted mating. However, the females ignored and rejected the males that approached them without exhibiting courtship behaviours; instead, they fought and screamed at them.

Colony size and roost site selection of *Pteropus medius*

The colony size of *P. medius* fluctuated across seasons, with an average colony size of 1648 ± 791 individuals (n = 73, days of observation). The average colony size was high during monsoon reproductive season (2476 ± 478, n = 4) compared to winter (2153 ± 238, n = 15), spring (1725 ± 281, n = 39) and summer (493 ± 72, n = 15) seasons. However, courtship and mating were held during the spring reproductive season, particularly during March. The frequency of mating was lower in spring than during the monsoon reproduction period. The colony size increased before the monsoon reproductive period (July, August and September) and decreased after the completion of the mating peak (Fig. 1). A moderate colony size was observed during winter (non-reproductive season) when weaning of young individuals from their mothers occurred. The colony size during spring, summer, monsoon and winter seasons showed significant differences (One-Way ANOVA: $F_{3,69}$ = 35.79, $p < 0.001$). The Tukey-Kramer post hoc test revealed significant differences in the colony size between summer and winter (t = 9.45, $p < 0.001$), spring and summer (t = -8.14, $p < 0.001$) and monsoon and summer (t = 6.49, $p < 0.001$) seasons. However, the colony size registered during the monsoon and spring periods (t = 2.26, $p > 0.05$) and monsoon and winter periods (t = -0.36, $p > 0.05$) did not differ significantly.

The roost site selection of *P. medius* differed across the seasons and was significantly influenced by the reproductive status, colony size, bat occupancy per roost tree and number of roost trees used. Akin to colony size, the average bat occupancy per roost tree was high during the monsoon reproductive season (52.8 ± 36.0 bats/tree) (Fig. 2). The least bat occupancy was observed during summer and was associated with small colony sizes (Fig. 2). The average bat occupancy per roost tree increased with increasing colony size and showed a positive correlation (r^2 = 0.510, n = 73; Fig. 3). The colony size increased due to the immigration of bats during the reproductive season and decreased due to emigration during non-reproductive season. The bats occupied mainly the trees of the southern part of the garden during summer (non-reproductive season, Fig. 4B). However, the reproductively active bats moved to the central and northern part of the garden during spring (Fig. 4A) and monsoon (Fig. 4C) reproductive seasons. The females secluded themselves from subadults (small in size) and other non-reproductive individuals, and occupied the trees at the central and northern part of the garden.

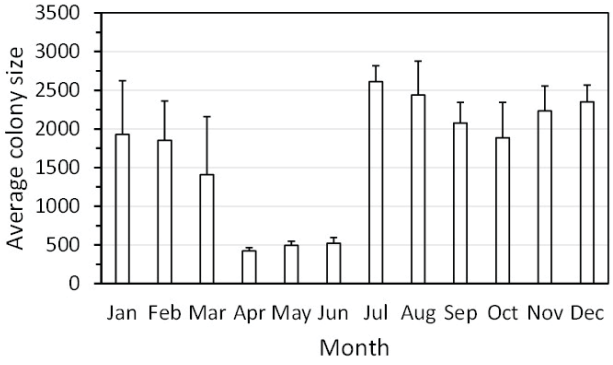

Fig. 1 - The average *Pteropus medius* colony size during spring (reproductive season, January – March), Summer (non-reproductive season, April – June), Monsoon (reproductive season, July-September) and Winter (non-reproductive season, October – December). The error bars show standard deviations. The average colony size was obtained by pooling the data from January 2018 to February 2022.

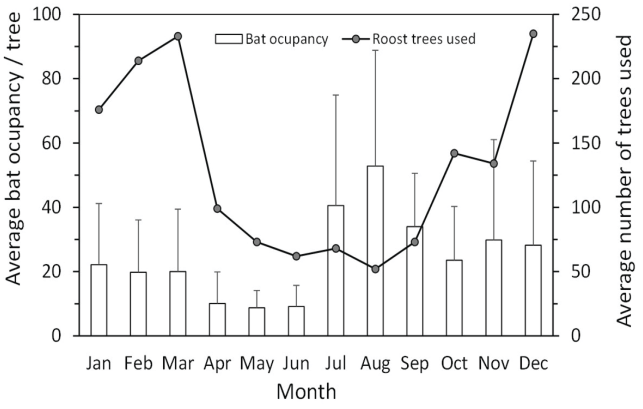

Fig. 2 - Average bat occupancy per roost tree and average number of roost trees used during Spring (reproductive season, January – March), Summer (non-reproductive season, April – June), Monsoon (reproductive season, July-September) and Winter (non-reproductive season, October – December). The error bars show standard deviations. The average bat occupancy and roost trees were obtained by pooling the data from January 2018 to February 2022.

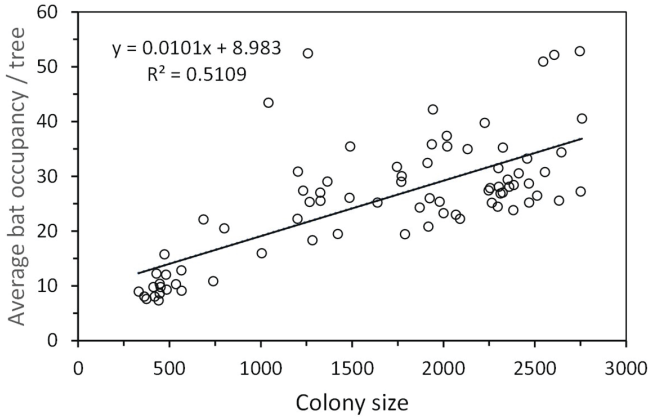

Fig. 3 - Shows the average bat occupancy per roost tree and corresponding colony size from January 2018 to February 2022.

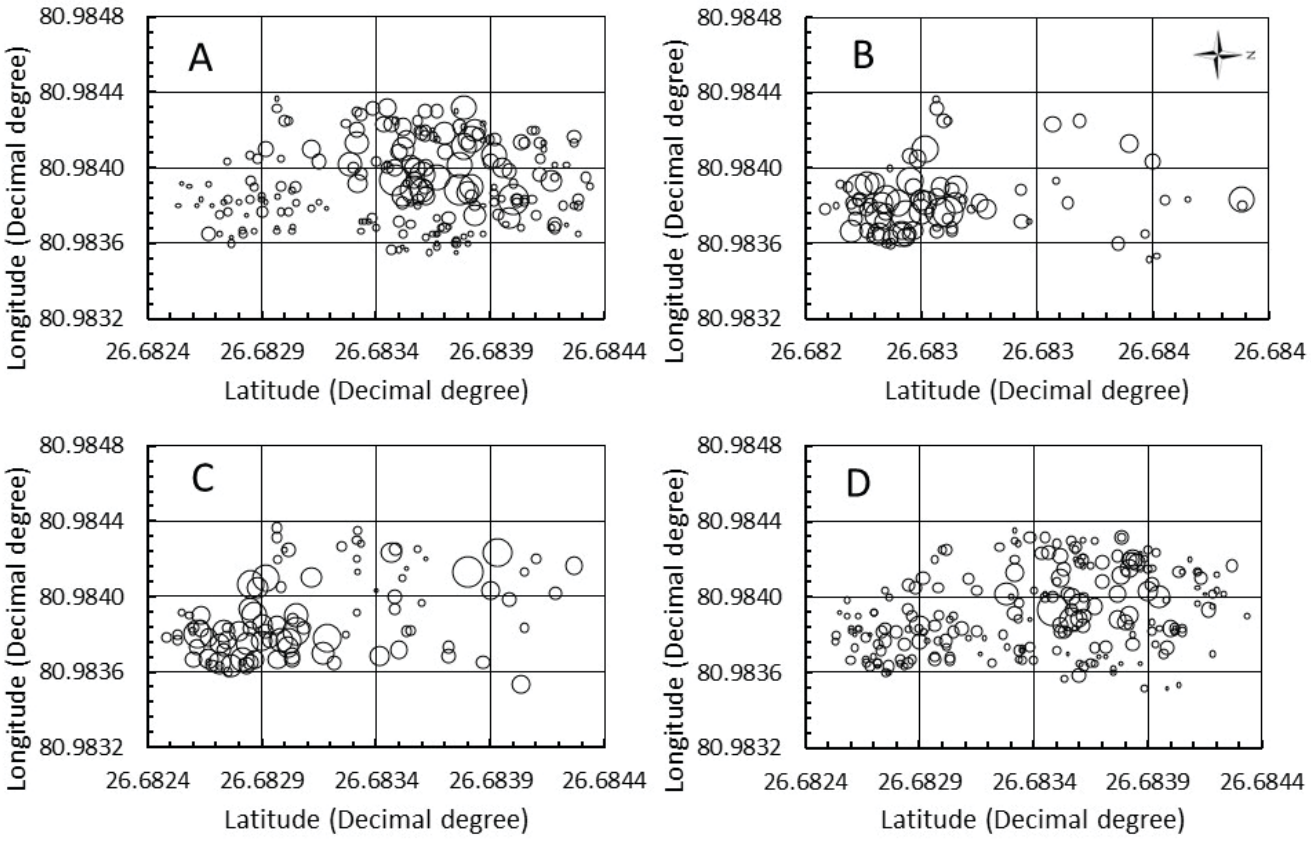

Fig. 4 - Roosting pattern of *Pteropus medius* during Spring (**A**), Summer (**B**), Monsoon (**C**) and Winter (**D**) seasons plotted in XY scattered bubble plots. The locations of roost trees were plotted using GPS coordinates (i.e. decimal degrees of N & E) and the entire plot area is the garden. The size of markers (hollow circle) shows the relative group size of bats roosting on a particular tree, i.e., the smaller the circle, the lesser the group size, and the larger the circle, the bigger the group size. The number of markers shows the number of roost trees used by *Pteropus medius* during a particular season. **A**) Spring (reproductive season, January – March), **B**) Summer (non-reproductive season, April – June), **C**) Monsoon (reproductive season, July-September) and **D**) Winter (non-reproductive season, October – December).

Thereafter, the males reached the females and exhibited courtship displays. Although a few mating pairs were observed during early winter period, they preferred to roost amid of the garden, probably to avoid harsh winter (Fig. 4D). Thus, I suggest that *P. medius* might select the roost sites according to their reproductive status and colony size. The temperature and relative humidity at the roost site ranged from 7 – 40 °C and 44 – 91%, respectively. The highest mean temperature was observed during May (34 ± 5.3 °C), while the lowest temperature was observed during January (19.4 ± 6.4 °C).

DISCUSSION

General and reproductive behaviour of *Pteropus medius*

The general and social behaviours (e.g. sleeping, grooming, wing fanning, wing stretching, yawning, fighting, and vocalising) observed in *P. medius* were widely found in other flying foxes. Sleep was the most common behaviour that occurred throughout the day. A similar behaviour was observed in *Pteropus dasyallus* (Funakoshi 1991). About 83% of individuals of *Pteropus poliocephalus* were asleep during daytime, and the percentage of sleep varied over the day and seasons (Connell et al. 2006). Grooming was a common behaviour of *P. medius* and was observed throughout the day and seasons. Males licked the body surface and genital regions of the females in order to enhance the mating and strengthen the bonding. However, genital licking by males with erected penis and stretched wings were used as part of courtship displays. The males of *P. medius* licked the face and vaginal region of the female prior to copulation (Baki et al. 2015). Individuals of *P. medius* were actively involved in licking the body surface, scruff, and genital region of females and exhibited courtship displays and copulations over the day (Jeevan et al. 2017).

Colony size and roost site selection of *Pteropus medius*

The results of this study revealed that the roost selection of *P. medius* differed across seasons and was related to reproduction and colony size. The colony size and number of used roost trees during summer were significantly low (Fig. 1 and 2), probably due to the emigration of several individuals, mostly males after the reproductive season. Thus, the aggregation of bats on a few roost trees during the summer (Fig. 4B) explains the gathering of postpartum females with suckling pups, females which accomplished mating during spring reproductive season and a few reproductively inactive females and males. Further, the colonies were female-dominated during the non-reproductive period, and thus, they needed to defend themselves and their offspring in the absence of their male partners, as the males did not contribute to paternal care. Therefore, the female-associated functions such as pregnancy, parturition, lactation and maternal care and defense forced the females to aggregate. However, during the reproductive phase, the females dispersed from the maternal colony and occupy secluded places as they required social exclusion, less disturbance and reduced mate competition (Fig. 4A and C). Courtship and sexual selection were observed in the maternal colony, although after these behaviours, they secluded themselves from the colony. The widespread distribution of bats in the garden during winter and early spring suggests segregation of sexes and other social groups, such as subadults and non-reproductive males or females.

The population fluctuation observed in *P. medius* was similar to those reported by Sinha (1980) and Purohit & Vyas (2009), who found a peak population during January and a reduced colony size during May. The reduction in population size was explained by seasonal and local migrations. However, the present study revealed that the fluctuation in the colony size was associated with reproduction. Although the colony aggregation and segregation of *P. medius* varied temporally and geographically, the cause was more strongly related to their reproductive cycle. A large congregation of *P. medius* at Targol dam site in Gujrat, India, underwent population fluctuation, where a few colonies shifted to nearby areas and returned back to the maternal colony during summer. Manandhar et al. (2018) observed the behaviour and population dynamics of *P. medius* in Nepal and found relatively reduced population sizes during January and July and a population growth during October, which coincided with the peak frequency of copulation. Similarly, the colony size of *P. medius* increased during August–September (monsoon reproductive season) and decreased during the summer and winter seasons (non-reproductive periods) (Jeevan et al. 2017).

The seasonal shift of roost sites in relation to the reproductive cycle was observed in *Pteropus pselaphon*. Colonial roosts were observed during winter, while they were widely dispersed during summer. The summer roosts were used by solitary bats as well as nursing females (Sugita et al. 2009). *Pteropus pselaphon* roosts colonially during the mating season (December–April/May), while the colonial aggregation breaks into solitary colonies during the non-mating season (Sugita et al. 2009). Population fluctuations were also observed across seasons in *P. poliocephalus*, with which the minimum population was observed during autumn and winter, and the peak population was associated with courtship and mating behaviours during March–May. The ratio of females to males was also very low (Eby 1991, Connell et al. 2006). The colony movement of *Pteropus vampyrus natunae* in peat swamp forest (Sarawak) was linked with pregnancy and maternal care (Gumal 2004). Mass copulation was observed in *P. medius* from July to September, and parturition was observed from February to March. The offspring was cared exclusively by females (Kumar & Kanaujia 2015).

In other studies, the population of *P. poliocephalus* increased to the maximum during December–January, as in late January, they began to leave the colony. The larger population observed during December–January was due to the arrival of bats from a number of small camps (Nelson 1965b) because adults of *P. poliocephalus* dispersed during non-breeding seasons (winter). There is considerable variation in the reported *P. poliocephalus* colony size variation across months and years. However, a large number of bats were also observed during the mating season (Parry-Jones & Augee 1992) and seasonal roosts shifting from one site to another, and population fluctuations were observed (Gulraiz et al. 2015). For example, Rao (2017) observed two mating seasons in a year, with individuals copulating during

October, giving birth during April–June and others mating during December. Akin to Mathur et al. (2011) and Rao (2017), the current study revealed the occurrence of two mating seasons, i.e., spring reproductive season and post-monsoon reproductive season.

CONCLUSIONS

The outcome of this study shows that the flying foxes use the day-roosts for various behavioural processes to fulfil their life history needs like social interaction, population persistence, reproduction, and offspring development. The fluctuation in colony size across seasons is associated with the reproduction of *P. medius*. The bats occupied the southern periphery of the garden during the non-reproductive season and shifted to the central and northern part of the garden during spring and monsoon reproductive seasons. This shows the requirement of different roost sites for survival, as well as sites for courtship and mating, offspring development and population sustenance. Further, the selection of secluded roost sites during reproductive seasons demonstrates the need for social exclusion, less disturbance and reduced mate competition. It is well-known that roost sites are declining due to urbanisation and industrialisation, and as a result, the population of flying foxes are also declining throughout its range. Therefore, more studies are required on this aspect at different geographic zones to understand the habitat requirement for effective conservation of *P. medius*.

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