VIGILANCE ARCHITECTURE AND TEMPORAL VARIATION IN EMERGENCE-RETURN OF A KEYSTONE BAT: THE INDIAN FLYING FOX (*Pteropus giganteus*)

DISSERTATION SUBMITTED TO SAURASHTRA UNIVERSITY, RAJKOT, IN PARTIAL FULFILLMENT OF THE MASTER'S DEGREE IN WILDLIFE SCIENCE

Submitted by

Pratik Das

Under the supervision of

Shri Salvador Lyngdoh

Dr. S. P. Goyal

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

June 2019

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that Mr. Pratik Das of the Wildlife Institute of India has carried out a piece of original research work entitled **"Vigilance Architecture and Temporal Variation in Emergence–Return of a Keystone Bat: The Indian Flying Fox (*Pteropus giganteus*)"**, in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot. These investigations were carried out under our supervision at the Wildlife Institute of India from November 2018 to June 2019. We also certify that this work has not been submitted for any other degree of any university.

Date: 30th June 2019

(Shri Salvador Lyngdoh)	**(Dr. S. P. Goyal)**
Scientist D	**Subject Matter Specialist**
Supervisor	**Co-Supervisor**

पत्रपेटी सं० 18, चन्द्रबनी, देहरादून – 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640114, 2640115, 2646100 फैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100 Fax : 0135-2640117
ई–मेल/E-mail : wii@wii.gov.in वेब/Website : www.wii.gov.in

DECLARATION

I, **Pratik Das**, hereby declare that the research work entitled **"Vigilance Architecture and Temporal Variation in Emergence–Return of a Keystone Bat: The Indian Flying Fox (*Pteropus giganteus*)",** carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of research work. This research work was carried out under the supervision of **Shri Salvador Lyngdoh**, and **Dr. S. P. Goyal** at the Wildlife Institute of India from November 2018 to June 2019. I hereby declare that this work has not been submitted for any other degree of any university.

Date: 30th June 2019

Place: Dehra Dun

(Mr. Pratik Das)
Student
XVI M.Sc. Course

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ACKNOWLEDGEMENT

"If you want to go fast, go alone. If you want to go far, go together." —African Proverb. This piece of work signifies more of the second part of the proverb.

My deepest thanks and gratitude to my supervisors, interns, and field assistants without whom this dissertation would never have materialized.

I gratefully acknowledge our Director Dr. V. B. Mathur, our Dean Dr. G. S. Rawat and Research co-ordinator WII for providing all the support and facilities to carry out this research. I thank PCCF Forest department, Assam State for granting permission.

A very special thanks to our Course Director and Assistant Course Director of XVI M.Sc., WII who held our hand and guided us through this beautiful journey of two years. Their contribution made this last main event i.e. The Dissertation extremely smooth. Thank you, Sir, for having my back at critical times. Next, I would like to sincerely thank Dr. Parthankar Choudhury, HOD, Department of Ecology and Environmental Science, Assam University Silchar who provided logistic support at my field site in Cachar, Assam. Be it a need of equipment, or an issue with locals, or any technical information about my study site Sir was always there.

It is difficult to describe in words how much thankful I am towards my supervisors Shri Salvador Lyngdoh and Dr. S. P. Goyal. Their relentless support and guidance are way much more than one can ask for. It takes an extra effort to bring the maximum out of a student like me, which they always took. The only bit I can do to thank my supervisors will be by revisiting this work and furnishing it to a greater level.

On field nothing can motivate more than an energetic team. No matter what the hurdles are, be it rain, scorching heat, freezing dawn, annoying locals, etc. when friends cum interns are around everything is possible. Syed Amjad Ahmed, Prasanta Das, Devasish Goala, Debolina Nath and Pranjal Bhattacharjee, I sincerely thank you people for making my field days most memorable and successful. Exceptional thanks to Debolina and Pranjal for being there at those crucial desperate times. Team Flying Fox can never be forgotten.

I am grateful to my part time field assistants, Tinku kaku, Bappa mama, Sudangshu da, Sadhan mama, and Shonkor kaku with whom I accomplished many objectives and helped me connect to locals. My deepest gratitude to those families and people who took great care of me and made my stay in field very comfortable.

I am also indebted to Stotra da, Keshab da, Ashish and Himangshu who rescued me from dire conditions. I would love to thank my family for their unconditional love and support at all times, especially when life shows its harsh face. In the end, this journey of two years and the crucial phase of dissertation would not have been this fruitful without my M.Sc. friends. Friends made this journey fun but a few among them made fun more pleasurable and difficulties more tolerable. Thank you.

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SUMMARY

Pteropodids like Indian Flying fox roost gregariously and externally in tree canopies. Such species may be strongly exposed to environmental stresses such as heat, light and predation. In such conditions, social structuring of animal aggregation may be an outcome of competition for roosting preferences and hierarchy. Vigilance is one such manifestation of competition in canopy roosting bats, which can vary temporally, and according to the spatial position. The current study investigated the function of vigilance in terms of environmental vigilance (anti-predatory), social vigilance and environmental cues bats used to synchronize their emergence and return. I found that the *Pteropus giganteus* fruit bats showed varying levels of vigilance according to roosting architecture. Bats showed significant increase in environmental vigilance towards the periphery of the roosts (n=3), thus confirming the edge effect hypothesis. Bats however, displayed no significant variation with respect to guard effect or social vigilance as roosting positions were observed from periphery to core. Bats also displayed increasing social vigilance from core to peripheral areas of the roosting colony. Overall bats displayed an increase in vigilance towards peripheral positions. The overall mean emergence and return onset time was 17:30:46 ± 00:02:38 Hrs. and 04:44:10 ± 00:05:39 Hrs respectively. The mean emergence initiation time for bats was 17:17:32 ± 00:02:32 Hrs. during late winter and 17:45:59 ± 00:01:12 Hrs. during early summer respectively. Similarly, return initiation was observed to be 05:01:00 ± 00:03:18 Hrs and 04:16:35 ± 00:06:40 Hrs. respectively during the late winter and early summer. Both emergence and return significantly varied between two seasons ($t = -9.65$, $p < 0.0001$ and t =

6.51, $p < 0.00001$ respectively). However, it was found that emergence and return times were significantly correlated with sunset ($r= 0.96$) and sunrise ($r=0.98$).

1. INTRODUCTION

Bats are nocturnal flying mammals which form the 2nd largest order Chiroptera (1411 species) in its class Mammalia. Among bats, Flying foxes are the most common and familiar among bats and extensively studied (Molur et al., 2008). Flying foxes have been shown to contribute immensely towards ecological functions as a viable key stone species (Kumar et al 2017). Its key ecosystem function as an efficient seed disperser and pollinator is highly acknowledged. In India, however, there is limited information on fruit bats including flying foxes in spite of them being gregarious roosters. Most studies have been limited to status surveys and sporadic information on behavioural aspects (Marimuthu, 1988; Rahman and Choudhury 2017). Flying foxes are large frugivorous bats that roost externally in tree canopy. Most of them are gregarious roosters that form huge aggregations called camps or colonies. Being an external rooster they are exposed to all kinds of environmental variation (temperature, light and heat), predators and disturbances. The Indian Flying fox (*Pteropus giganteus*) is one such typical species, which is very abundant and widely distributed throughout the Indian subcontinent (Kumar et al., 2018).

Almost all bats forage at night and major part of the day they rest at their day roosts. Thus, roosting contributes to more than half of an average bat's life. However, unlike a common notion, bats do not sleep throughout the day at roosts. As bats spend over half their lives roosting, it is assumed that selective pressures of its roosting environment may have played a very crucial role in its evolution, behaviour and ecology. In a general sense, resting is their primary objective at roosts followed by social behaviour and other maintenance activities.

One such socio-behavioural outcome of gregarious aggregating fruit bats such as the *Pteropus giganteus* is social structuring in terms of spatial and temporal segregation in roosting architecture (position). These positions may be analogous to leks in mammals where centrality may indicate higher fitness of individuals (Klose et al., 2009). Social structuring thus may arise due to increased competition for reproduction and safety needs. Such needs may manifest as trade-offs between fitness-safety in terms of social and environmental costs. Safety can be examined, as an animal's perceived risk to predation or threats in terms of 'Vigilance' (Lima et al., 1999). In flying foxes resting is an extremely important 'non-activity', while vigilance is a costly behaviour. Thus, vigilance will vary in terms of spatial exposure to perceived risks (social or environmental) in a roosting colony of bats. Hence, spatial architecture of roosting will be mediated by nature of perceived risks which can be measured by vigilance behaviour. Furthermore, vigilance behaviour in flying foxes will be determined by its spatial position with individuals at the centre showing higher intra-specific vigilance for territoriality while peripheral animals may show increased inter-specific vigilance against potential predators.

Evening emergence and return of bats is a major manifestation of the circadian rhythm (Welbergen 2017). Many studies have shown that bats are a model species to study such rhythms due to their collective nature that allows investigations across many individuals at once. Once bats leave a roost, the primary task is to complete foraging and get to safety of the roosts before their risk of predation increases drastically i.e., in daylight. Emergence of flying foxes (*P. giganteus, P. alecto*, *P. poliocephalus*) have been studied with respect to day length, temperature, twilight, predation in isolation (Kumar et al., 2017; Welbergen

2006,2008; Sudhakaran et al., 2012). However, most of these have been in isolation, as many factors may affect such activity including clouds, moon-phases, humidity. Also, the initiation of emergence and return can periodically vary with changing season. Thus, the current study will attempt to investigate how such effects will determine emergence-return of *P.giganteus* with respect to twilight duration, day light, moon-phase, temperature, perceived predation and season. The study will add to the limited knowledge about giant flying fox emergence-return behaviour and its correlates.

1.1 Review of literature

Pteropus giganteus (Brünnich, 1782) commonly known as Indian flying fox is a large fruit bat belonging to the family Pteropodidae. It is listed as Least Concern by IUCN, in view of its wide distribution, presumed large population, tolerance to a degree of habitat modification, and unlikely fast decline. Its native countries are Bangladesh, Bhutan, China, India, Maldives, Myanmar, Nepal, Pakistan and Sri Lanka. However, it is well established like other fruit bats as a Keystone species. McConkey and Drake (2006) have suggested that flying foxes ecological function as seed dispersers cease to exist beyond certain threshold levels of their population decline. These may have very drastic effects on Tropical forest. The current population trend is decreasing, because of probable threats like cutting down of roosting trees, and hunting in several locations for meat and for medicine (IUCN redlist).

With over 50 species flying foxes, *Pteropus* is by the largest genus of Pteropodidae. Three species are already extinct and many more are threatened. Much work is done on their ecological function and they are well known as forest regenerators, pollinators etc. (Fujita et. al, 1991). Also much biological information is being gathered to aid conservation of some threatened species (Pierson et. al, 1992). Extensive work has been done on disease transmission and reservoir aspect of flying foxes. In last few years due to the Nipah virus outbreak by *Pteropus giganteus* a significant bloom in literature came up. However, the *Pteropus giganteus* remains as one of the most persecuted fruit bat in South Asia. The species is also listed in appendix II of CITES. There is also a need to determine major threats and overall decline of the species (Molur et. al, 2008)

Extensive work is done on bat activity rhythms as they are excellent models of circadian clocks. Emergence and return behaviour of Microchiropterans followed by megachiropterans have been studied around the globe. Some substantial work has been done on the emergence of *Pteropus poliocephalus*, and *Pteropus alecto* by Welbergen. Activity pattern of *P. alecto*, *P. polioicephalus*, *P. tonganus*, *P. dasymallus* with seasons has been discussed. Diurnal behaviour in *P. giganteus* and social organization was extensively but qualitatively described by Neuweiler (1969). Other works on behavioural aspects focused on copulatory behaviour (Koilraj et al., 2001), roost preference (Acharya, 1936), mating (Bhatt, 1942), local migration (Breadow, 1931; Nelson, 1965a) and general ecology and biology (Brosset, 1962). A recent quantitative approach to diurnal behaviour came up by Manandhar et al, (2017) in Nepal. The study of vigilance in roosting bats (*Pteropus poliocephalus*) by Klose et al, (2009) is a pioneer in its field. However, many aspects of the Indian Flying fox remain to be documented and related with its ecological significance. There have been limited or no studies on movement, foraging, vigilance and its role in specific role in seed dispersal.

Thirteen species of fruit bats occur in India, the Indian flying fox *Pteropus giganteus*, the dog-faced fruit bat *Rousettus leschenaultii* and the greater short-nosed fruit bat *Cynopterus* *sphinx* are distributed in the country. Two species, the Nicobar flying fox *Pteropus faunulus* and Salim Ali's fruit bat *Latidens salimalii* are endemic (Marimuthu 2009). There are two subspecies of Indian flying foxes present in India viz. *Pteropus giganteus leucocephalus* Hodgson and *Pteropus giganteus giganteus* (Brunnich 1782). In India, it is listed as vermin under Schedule V of the Indian Wildlife (Protection) Act, and is one of the most persecuted fruit bats. As elsewhere, the species is hunted extensively for meat as well as medicine. In terms of behavioral aspects of *P. giganteus* studies in India have been scarce. In India various aspects in terms of their population and distribution have been carried out. Nevertheless dramatic decrease of its population has been observed in the last few decades (Kumar et al. 2018). In India earlier studies on emergence of *Pteropus giganteus* suggests that it is related to seasonal and temperature fluctuations. However many other effects such as duration of twilight, predatory risk, foraging need and social context are yet to be determined. The ecological services provided by bats are not appreciated as they are still classified in Schedule V of the Indian Wildlife (Protection) Act, 1972 and amended Acts as vermin. Singaravelan and Marimuthu argues "it is now appropriate for the Government of India to revisit this issue and consider removing these pollinators and seed dispersers from the list of vermin in the Wildlife (Protection) Act" (Singaravelan et al. 2009).

1.2 Justification for the Study

A few studies on emergence behaviour of the genus *Pteropus* have suggested its relation with various factors such as twilight, predation, foraging and social needs. However, these studies have been restricted to *P. alecto* and *P. poliocephalus* (Welbergen 2006 and 2008) which occur in Australia and Pacific. Kumar *et al.* 2018 and Sudhakar *et al,* 2012 studied effects of day length sunset and temperature, but the compounding effects of various factors such as timing of sun rise and sunset, intensity of light, ambient temperature, humidity, precipitation, lunar phase, presence of predator or potential threat, and twilight duration need to be still determined. The current study adds value to such aspects in terms of understanding of circadian rhythms of bats and possible correlations with various factors.

Social structure of animal aggregation has been shown to vary in space and time. Nevertheless, little is known about how this is correlated with vigilance. Much of the literature on vigilance has been focused on primates, fishes, and other terrestrial mammals (Beauchamp 2015). In fruit bats limited studies on vigilance related behavior have been undertaken (Nelson 1965; Welbergen 2009). The current study is a novel study that will try to determine spatial and temporal variation in *Pteropus giganteus* in terms of social and environmental vigilance. The major gap in terms of Indian flying foxes lies in the area of its roosting architecture and environmental relations which the study will attempt to determine. The current study examines the various factors that also are associated with emergence, return and vigilance in North East India. Thus, it paves way for information in the context of a region known for biodiversity.

1.3 Objectives

Based on the above rationale I framed the hypothesis to investigate broadly two objectives

1. To determine activity time budget and emergence return pattern of flying foxes in Cachar district Of Assam, Northeast India

2. To determine the Spatial vigilance architecture with respect to its function (environmental and social) in roosting colony of *Pteropus giganteus*

Therefore, the current study proposes to investigate and test the following hypothesis

Hypothesis 1: Activity of flying foxes is determined by changing weather patterns hence emergence and return will change with changing environmental factors (Moon and Sun)

Research Question 1: What is the time activity budget of flying foxes?

Research Question 2: What are the patterns in emergence and return of flying foxes?

Research Question 3: What are the correlates that contribute to emergence and return?

Therefore, I will be testing the patterns of emergence and return across two seasons namely, late winter and early summer.

As roosting is key activity in the daily life cycle of roosting bats. I expect that vigilance will be a cost that is attached to attaining maximum fitness among such species. Therefore, roosting positions will be correlated with various types of vigilances the bats display. Hence, I hypothesize that,

Hypothesis 2: Extent of environmental vigilance or social vigilance of bats will be influenced on the spatial position (increasing towards periphery and core respectively) of the bats with respect to the group.

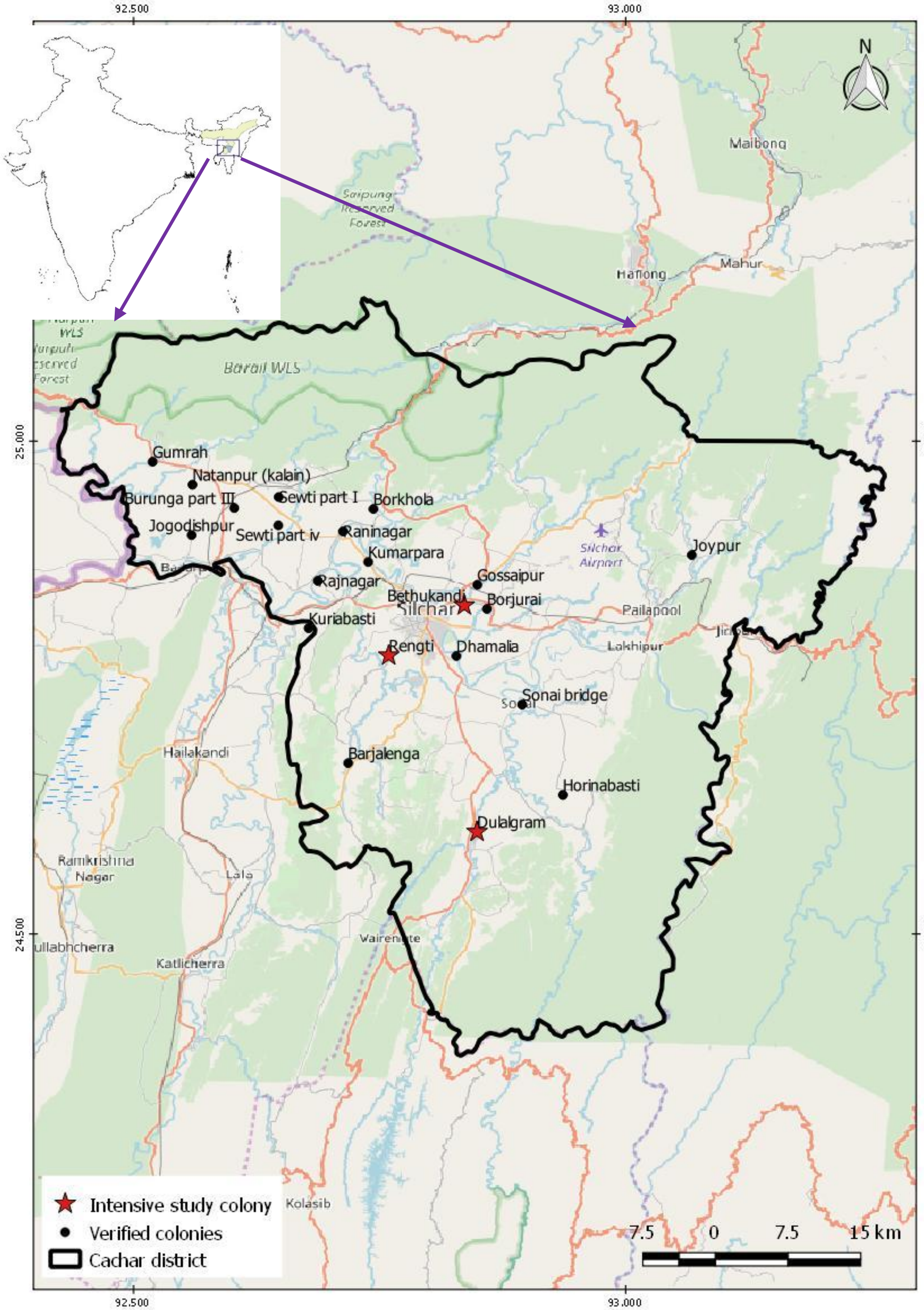
Research Question 1: Does environmental vigilance change (edge effect) with increasing distance from the center of the group?

Research Question 2: Does social vigilance change (guard effect) with increasing distance from the center of the group?

2. STUDY AREA

The proposed study area lies in Cachar district (Fig 1). It experiences very hot and humid climate during the major part of the year (April to October). Average rainfall of this area is about 2600-2700mm. Temperature ranges between 9-38°C. The district is bounded by state border with Mizoram in the South, Manipur in the south-east, North Cachar Hills and Jaintia Hills in the north and in the west by Hailakandi and Karimganj districts of Assam. Silchar is the head quarter of the district and is the second most important economic centre in the state, after Guwahati. The intensive study area was determined after reconnaissance survey following Rahman and Choudhury, 2017. Out of 21 verified Flying fox colonies three were selected based on colony age, permanency and population. This information was attained by questioning nearby villagers. All the three colonies were more than 20 years of age, and had a minimum of 500 bats from winter to summer. These three colonies are selected in the same landscape having similar habitat and degree of disturbance. Here each colony is comprised of multiple groups of bats roosting in multiple trees. A map showing the three *Pteropus giganteus* colonies is placed for reference (Fig 1). Three Google maps showing the intensive study colonies along with its surroundings are placed in plate 15, 16, and 17.

Fig 1. Map showing the study area of three colonies selected for the study (Red stars) along with other verified colonies



3. Methodology

1. To determine activity time budget and emergence return pattern of flying foxes in Cachar district of Assam

Flying foxes spend more than half of their life diurnal roosting. Their diurnal behavior is not as constant and simple as it is commonly perceived. A variety of different behaviours are shown in that time. Emergence behaviour implies their daily exodus to forage and return behaviour implies their returning to roost sites. Both emergence and return are manifestations of circadian rhythms. These endogenous rhythms are kept in phase using zeitgebers (Eckert *et al*., 1980). Furthermore, emergence and return of bats is fine-tuned using environmental variables. Therefore, I would be examining how these manifestations of the circadian rhythm vary with environmental factors in a tropical fruit bat.

Hypothesis 1: Activity of flying foxes is determined by changing weather patterns hence emergence and return will change with changing environmental factors (Moon and Sun)

Research Question 1: What is the time activity budget of flying foxes?

Research Question 2: What are the patterns in emergence and return of flying foxes?

Research Question 3: What are the correlates that contribute to emergence and return?

A preliminary ethogram of Diurnal roosting behavior is prepared by ad-libitum sampling. This is later finalized by comparing with an already published ethogram on *Pteropus alecto* by Markus and Blackshaw 2002.

An initial and thorough reconnaissance survey was carried out to standardize collection of emergence and return data. The emergence and return activity was attempted to be observed on a daily basis as well as on different moon phases regularly through winter to post winter and into early summer. The emergence and return was estimated by using method adapted from Welbergen, 2006 and Sudhakaran *et. al*, 2012 respectively. Observations were done mostly with naked eyes. Multiple observers (max. four) timed the emergence and return at vantage points outside or adjacent to the colony. Observers were stationed on certain positions that fulfilled two conditions: (a) One observer's field of vision does not overlap with the other (b) The colony gets monitored from all directions.

The emergence and return of flying foxes were timed with smart phone stop-watches. Observers are stationed at their respective positions by sunset. Each time a bat leaves the colony it gets timed using the stop-watch. Caution is taken while timing a bat because circling behavior can get confused with true emergence. True emergence is generally characterized by a straight head on flight. This way at least 15 observations were taken by all the observers. Now to time the emergence-end observers remained vigilant searching for the one minute gap between two successive bats. For ease of use this is abbreviated as GEM (timing of the bat after which the Gap Exceeded one whole Minute). From GEM the remaining emerging bats are again timed till a gap of 5 minutes is reached.

The onset of emergence is defined as the moment when at least ten bats could be seen flying above the canopy and dispersing. The end of emergence will be defined as the first entire minute when no bats can be seen flying above the colony (Welbergen 2006) i.e., GEM. Onset and end is finally obtained by comparing the readings of multiple observers.

Similarly, for return a protocol similar to emergence was used. Return behaviour was defined following Winchell and Kunz 1996. Return here is defined as an event post foraging at night beginning at most 90 mins before sunrise with minimum of 10 bats returning. End of return is the last GEM (timing of the bat after which the Gap Exceeded one whole Minute) recorded among observers.

Emergence and return are governed by many environmental factors, such as timing of sun rise and sunset, intensity of light, ambient temperature, humidity, precipitation, lunar phase, presence of predator or potential threat, and twilight duration (Welbergen, 2006, 2008; Kumar et. al, 2018). All these environmental variables will be collected along with emergence and return activity. Timings of sunset, sunrise, and lunar phase will be obtained from positional astronomical data (Ministry of Earth Sciences).

Data Analysis:

1. To obtain the activity time budget, total time spent in each state was calculated and divided by total sampling time. This proportion is then converted into percentage.
2. Descriptive statistics was used to get the mean and Standard error of emergence-initiation, emergence-duration, emergence-end, gap between sunset and emergence-onset, return-onset, return-duartion, return-end, and gap between return-end and sun rise.
3. To compare the readings of emergence and return between late winter and early summer, first a Kolmogorov-Smirnov (KS) test is performed to check normality of the data. Later, on finding the data to be normal a student's two tailed T-test for two independent means is done to compare readings between seasons. If at α=0.05 a

significant difference is found box plots are used to further compare the different distributions.

4. To find the correlation between emergence and return and different environmental variables such as sunrise, sunset, moonrise, moonset, and moon phase, Pearson correlation was used.
5. The above-mentioned analysis is performed using MS excel 2016 [version 1905 (Build 11629.20214)], XLSTAT 2019.2.1.58999, Oriana [Copyright © 1994-2011 Kovach Computing Services], and a website: Social Science statistics, 2018 © Jeremy Stangroom. Moonphase data is obtained from a software called Moonphase 3.3 (freeware) © 2009 Henrik Tingstron.

Objective 2: To determine the Spatial vigilance architecture with respect to its function (environmental and social) in roosting colony of *Pteropus giganteus*

Hypothesis 2: Extent of environmental vigilance or social vigilance of bats will be influenced on the spatial position (increasing towards periphery and core respectively) of the bats with respect to the group.

Research Question 1: Does environmental vigilance change (edge effect) with increasing distance from the center of the group?

Research Question 2: Does social vigilance change (guard effect) with increasing distance from the center of the group?

Vigilance behavior, can be described as scanning by an individual of its surroundings. It refers to an animal's state of readiness to detect certain specified events occurring unpredictably in the environment (McFarland). Vigilance has multiple functions (Hirsch 2002; Cameron and Du Toit 2005) and can be told apart (Klose et al., 2009; Jones 1998). In species forming stable colonies, temporal and spatial variation in the allocation of vigilance to social (targeted at conspecifics) and environmental (antipredatory) functions may be expected.

"It is predicted that environmental vigilance should be greater on the periphery because of increased risks of predation there, but social vigilance might be greater in more central positions due to increased competition for territories and mates or simply for social monitoring reasons" (Klose et al., 2009).

Study design and field methods

Three colonies were selected on the basis of availability. Colonies comprised of multiple roosting trees. Data is collected by focal behavior sampling. Collection of independent focal samples throughout the three colonies is done from 29th March to May 5th. Also, data on activity budget was determined using the same focal samples. (Fig 1. Study area and Plate 1, 2, 3, 4 and 5.)

Defining vigilance and differentiating between social and environmental vigilance

Vigilance is defined as "eyes open and looking beyond the immediate substrate or the animal's own body accompanied by any body movement (e.g. ear twitching) or change in body movement". Relating to the target of vigilance "social" and "environmental" vigilance are differentiated. An event is termed social when "individual was looking directly at another close-by individual (e.g., approaching, fighting, staring; typically individuals targeted are awake; mother-young interactions are not recorded)" [Plate 12]. An event is termed environmental when "individual's gaze was directed elsewhere (e.g., into foliage or distant vegetation, at the ground or into empty space)" [Plate 13]. When an event is confirmed as vigilance but the target cannot be determined it is categorized as "active vigilance". Vigilance is categorized "passive" when 'eyes are half open or eyes-open without any functionality' [Plate 11]. Vigilance is categorized "observer" when the event of vigilance is confirmed and directed towards observer. [Plate 14]

Determination of spatial position and Sampling framework:

A bat is categorized as peripheral or core depending on the relative position to its group of roosting bats. The distribution of roosting bats on a tree can be considered as a 3-D arrangement like a sphere. Here bats making up the surface area of this 3-D distribution are considered peripheral while bats located inner to the peripheral bats are categorized as core (Plate 6 and 7). If the no. of bats on a tree are less than 15 and scattered in distribution all of them were considered peripheral. This is because there is no effective core.

Vigilance data was collected using continuous focal animal samples, 300 s per sample (Martin and Bateson 1996). For each sample, the frequencies, durations, and types of vigilance events was recorded continuously. Observations were done using spotting scope, binoculars, and video camera. Samples are taken throughout the day, but between 1 h after flying foxes had arrived in the colony at dawn and 1 h before bats emerged from the colony at dusk. In each roosting tree two focal samples each of core and periphery are recorded along with sex and age group.

Data Analysis:

1. To check the normality of distribution of sampling durations (effort) in core and periphery K-S test is performed. Since both the distributions were normal a student's two-tailed T-test of independent means was performed between the efforts of core and periphery at $\alpha=0.05$.
2. Later K-S test was done to check normality of effort in all the three colonies. Since all the distributions of efforts belonging to three colonies were normal, a one way ANOVA for independent measures was performed across them at $\alpha=0.05$.
3. Since tested for normality the distribution of social/environmental vigilance durations were not normal, non-parametric test was opted. At $\alpha=0.05$ Kruskal-Wallis (KW) test on environmental and social vigilance was performed in different zones across colonies to confirm there was no significant difference between the systems (replicates).
4. The percentage of a vigilance category was calculated by dividing total vigilance duration with total sampling effort and multiplying it by 100. Descriptive statistics were used to calculate average social/environmental vigilance and standard error.
5. Normality of environmental vigilance and social vigilance durations was tested using K-S test. On not finding it normal vigilance-category between zones were compared using non-parametric two-tailed Mann-Whitney U test at $\alpha=0.05$. M-W U test specifically compares the duration of vigilance bouts in different zones.

6. To compare environmental/social vigilance as a whole between zones, a frequency distribution of vigilance events is created by taking hours of a day into consideration. These frequency distributions of different zones were tested to be normal.
7. At $\alpha=0.05$ a two-tailed student's t-test of independent means is performed to compare environmental/social vigilance in different zones.
8. The above-mentioned analysis is performed using MS excel 2016 [version 1905 (Build 11629.20214)], XLSTAT 2019.2.1.58999 and a website: Social Science statistics, 2018 © Jeremy Stangroom

4. RESULTS

Table 1. The Ethogram of Diurnal Roosting Behaviour in *Pteropus giganteus*			
Context	**Behavioral Unit**		**Description**
Asleep (AS)	1	Hang relaxed (HR):	Bat hanging bipedally or monopedally with wings folded across body or loosely by sides of body. Eyes are mostly closed or half open.
	2	Tight Sleep (TS):	Roosting position as in HR.; wings folded across body, head tucked in with nose underneath wings. Eyes are always closed.
	3	Wing-droop (WD):	Roosting while drooping one wing downward and grasping branch with other thumb for extra support. Thermoregulation. sleep with wings extended
Vigilant (VIG)	4	Hang Alert (HA)	Hanging in any roosting position, eyes are open and ears moving or directed towards a source of interest. Signifies a search mode. E.g., approaching observer, predator, con-specific, etc.
	5	Hang tense (HT)	Knees are angled giving an inverted 'hunched' appearance; wings folded by sides of body and slightly pulled back; head and ears inclined toward direction of perceived threat; often leads to SWY
	6	Sway alert (SWY)	Knees angled and body hunched as in 3.; head and body moving from side to side; wings relaxed, folded across body or extended forward; ears and eyes directed toward source of interest. Perceived threat, e.g., approach of large bird or ground predator
Locomotion on a Tree (LOT)	7	Crawl (CRL):	Quadrupedal movement along a branch, or up or down a trunk, by using thumb hooks and feet. It occurs by simultaneous grasping with alternate thumb and foot, i.e.,

			left thumb/right foot → right foot/left thumb; Hooks may be used simultaneously to pull the body up, with feet then following and grasping the trunk to push (climb). Usually used for faster movement through larger area of tree
	8	Bipedal (BP):	alternate placement of feet one in front of the other to move forward; wings folded loosely by sides. Short distance movement along branch
	9	Shuffle (SHF)	Short distance bipedal back-and-forth movement along branch
Position change (PC)	10	Swivel (SVL)	Rotation of body up to 180° while roosting relaxed and monopedally. Rejection of another bat; maximizing exposure to sun in winter"
	11	Turn (TRN)	Rotation of body while roosting alert (2.) with wings folded
Auto grooming (ATG)	12	General groom (GGR):	Cleaning of the front of the body (chest, stomach, genitalia), wing-bones, membranes and legs using a quick, vigorous licking motion. Also used on feet and in crevices such as between wrist-bones, toes etc.
	13	Wing groom (WG)	Apart from licking as described in GGR, this involves the rubbing of loosely extended wings over and around the head, particularly around the muzzle area, and across the scapular glands in the neck. During this action, eyes are often closed and the tongue protruding.
	14	Genital groom (GNG):	Licking of body and head of erect penis without urinating or ejaculating

	15	Clawing groom (CG):	Vigorous back and forth motion of foot claws across area of the body. It also includes grooming of back, face, head, shoulders and areas inaccessible by tongue. Teeth and ear canal grooming takes place with a much slow and careful raking motion.
	16	Scent Bath (SB)	Vigorous side-to-side rubbing of the neck across the erect penis while wings relaxed and open or wrapped loosely around head; results in dousing of body with odorous secretion which is then distributed over body and wings by dragging open wings across the head as in WG.
Stationary actions	17	Reach (RCH)	Extension of thumb-claw towards an object in an attempt to pull it close; usually followed by sniffing. Examination of object such as a branch or food item
	18	Fanning (FAN)	Wings extended loosely in front of body; rhythmic extension and contraction of one or both open wings effecting the movement of air towards the body and across the wing membrane. Cooling action in hot conditions or sign of agitation such as after rejected courtship attempts.
	19	Wing extension (WE):	Full or half extension of wing(s) from shoulder(s) and of fingers from wrist; wing(s) tensed and extended sideways or forward of body for a few seconds before relaxing.
	20	Wing flick (WFL):	jerking, followed by keeping it in a relaxed position. Sudden extension of wings often causing a snapping sound before retraction and relaxation of wings. E.g., at conclusion of an auto-grooming session

	21	Yawn (Y):	Slow wide opening of the mouth with tongue slightly protruding and often ‘snapping’ toward lower jaw before closing of mouth.
	22	Urination (URN)	Suspension of body only with the help of thumbs and release of feet to pass urine.
	23	Defecation (DF)	Suspension of body only with the help of thumbs and release of feet to pass faeces.
Social Interaction (SI)	24	Reach (RCH):	Extension of thumb-claw towards an object or an individual in an attempt to pull it close; usually followed by sniffing. Examination of object such as a branch or food item. In case of social interaction being reached by another individual is RCH-R.
	25	Threat (THR):	Opening and flexing of wings forward with body and head angled forward; may be accompanied by loud vocalizations and movement towards perceived source of threat; Mouth open showing teeth.
	26	Lean towards (LNT):	" Wings folded by sides or across body; body actively inclined forward, apparently to identify olfactory signals. E.g., identification of another bat.
	27	Sniff (SNF)	Forward tilt of head towards of object or other bat as in LNT to inhale and assess scent. Identify neighbors; assess reproductive status. Being sniffed, SNF-R. Sniffing, SNF.
	28	Chase (CHS)	Bipedal or quadrupedal active pursuit of intruder through branches of tree in defense of territory; may involve loud

			vocalization and hooking but often does not involve any physical contact.
	29	Escape (ESC)	locomotion following a fight that is directed away from the opponent; locomotion when one is chased
	30	Hook (HOK)	Rapid swiping of thumb claw in direction of aggressor with apparent intent to threaten or scratch
	31	Wrestle (WRS)	Use of folded wings and wrists in combat to fend off another bat; usually restricted to brief bouts of several seconds in length
	32	Bite (BIT)	Used in combat; usually directed at head of opponent. Aggressive defense of territory.
	33	Mock-biting (MBI)	Action as in BIT, but implemented in an affiliative context.
	34	Play-wrestle (PWR)	Action as in wrestle but without vocalization and usually of a longer duration than during combat.
Mother Infant Interaction (MII)	35	Infant groom (IG)	Extensive and thorough licking of an infant by its mother
	36	Suckle (SUC)	Extraction of milk from mammary glands in the females' wing-pit. This may continue for three to four months or longer.
	37	Infant wrestle (IW)	Basic mother infant physical interactions. Mother adjusting the infant clinging to her; Like play-wrestle by a mother with her young.
Mating/ Courtship	38	Follow	Male chasing a female. Associated to courtship/mating.
	39	Approach/scream	Approach towards female with head angled forward and while emitting loud, harsh, continuous vocalisations towards her ears. Vocalisations may last up to several minutes.

	40	Uro-genital sniff	Action as in SNF, directed by male toward genital opening of female
	41	Uro-genital lick	Intensive licking of female genital opening by courting male, ostensibly to arouse and subdue female for copulation; may occur in several bouts prior to attempted copulation
	42	Grasp-restraint	Extension of wrists with wings relaxed or loosely folded to forcibly hold another. Courting male attempts to manipulate female into a dorsoventral position for mating
	43	Scruff bite	Male biting scruff of female to subdue her during copulation; behaviour used in conjunction with the grasp-restraint
	44	Copulation	Successful copulation with male penis inserted into female vaginal opening, or an attempt to do so. Male vocalizes loudly and restrains the struggling female.
	45	Break	Cessation of copulation bout or attempt, indicated by the release of the female by the male
	46	Face-reject	Opposite action of swivel-reject; deliberate facing of courting male by female to prevent copulation.
	47	Push away	Physical distancing of proximate male by female using her wrists
Flying	48	Take off (TO):	Standard bipedal roosting position with head tilted towards ground and back slightly arched; this is followed by one or two beats of the extended wings to raise body from vertical position, release of the branch and a slight drop in altitude until wing motion sustains body in flight.
	49	Land (LND):	Transition from flight to suspension from an object or branch; may be preceded by a brief, vigorous hover of 3–4

			wing beats before connection is made. Having passed over the top of the branch and feet connected with it, wings are folded and body swings into a vertical roosting position.
	50	Flight (FLT):	Simultaneous up and down motion of wings to sustain body in a horizontal position (head facing forward) and propel it forward.
	51	Glide (GLD):	Smooth forward flight motion with decreasing altitude, involving outstretched wings but no flapping. Approach of landing site, leading up to LND.

4.1 Objective 1: To determine activity time budget and emergence return pattern of flying foxes in Silchar, Northeast India

Research Question 1: What is the time activity budget of flying foxes?

Using the above-mentioned ethogram six different states are selected which covers all the diurnal roosting behavioural units. During the total sampling period of 764.91 minutes (12:44:55) spanning from 07:41 to 17:10, it has been found that 45.67% (SE=8.57) of *Pteropus giganteus* diurnal roosting behavior comprises of "Hang relaxed" state. This state is followed by 'Tight sleep' (24.57%, SE=7.57) and 'Wing droop' (11.57%, SE=3.11). Vigilance occupies 8.50% (SE=2.57) of its total activity while 'Locomotion on tree' occupies only 0.47% (SE=0.15).

Since there were more samples in mid-day, separate activity budgets of early day (7:30-10:29), mid day (10:30-13:29) and late day(13:30-5:30) have been made. In mid-day and late day most time was spent hanging relaxed (66.23% and 55.65% respectively) while least in locomotion on tree (0.34% and 0.29%). In early-day bats were mostly in 'tight sleep' (43.30%) and least in 'locomotion on tree' (0.59%). According to the time budgets bats were most vigilant early-day (14.80%) and least mid-day (2.94%).

Table 2. Time Activity Budget of Diurnal Roosting behaviour in *Pteropus giganteus*								
Day of sampling	Proportion of Behavioural states in percentage							
	Auto-grooming	Vigilant	Hang relaxed	Locomotion on tree	Mother-infant interaction	Social Interaction	Tight Sleep	Wing droop
03.04.2019	2.97	0.05	25.78	0.57	5.80	0.00	58.41	6.42
06.04.2019	1.93	8.94	15.71	0.00	0.00	0.00	61.31	12.10
12.04.2019	2.83	1.54	56.27	1.64	0.72	0.00	29.50	7.50
14.04.2019	23.87	13.46	29.72	0.83	0.00	16.68	1.11	14.33
17.04.2019	2.60	5.99	70.21	1.00	3.42	4.08	0.00	12.70
21.04.2019	10.91	27.38	39.88	0.64	0.00	0.00	16.52	4.67
22.04.2019	5.91	8.81	10.58	0.44	2.50	0.00	69.38	2.37
26.04.2019	0.55	0.85	52.21	0.00	9.69	0.00	0.00	36.71
27.04.2019	4.41	17.78	29.55	0.30	0.00	3.07	21.50	23.38
29.03.2019	5.36	17.13	23.26	0.14	0.00	0.70	34.75	18.66
29.04.2019	0.33	0.00	99.67	0.00	0.00	0.00	0.00	0.00
30.04.2019	0.32	0.02	95.17	0.02	2.10	0.00	2.37	0.00
Mean	5.17	8.50	45.67	0.47	2.02	2.04	24.57	11.57
SD	6.60	8.90	29.69	0.51	3.04	4.81	26.21	10.76
SE	1.91	2.57	8.57	0.15	0.88	1.39	7.57	3.11

Fig 2. Time Activity budget of Diurnal roosting behaviour in *Pteropus giganteus* (29th March to 30th April 2019)

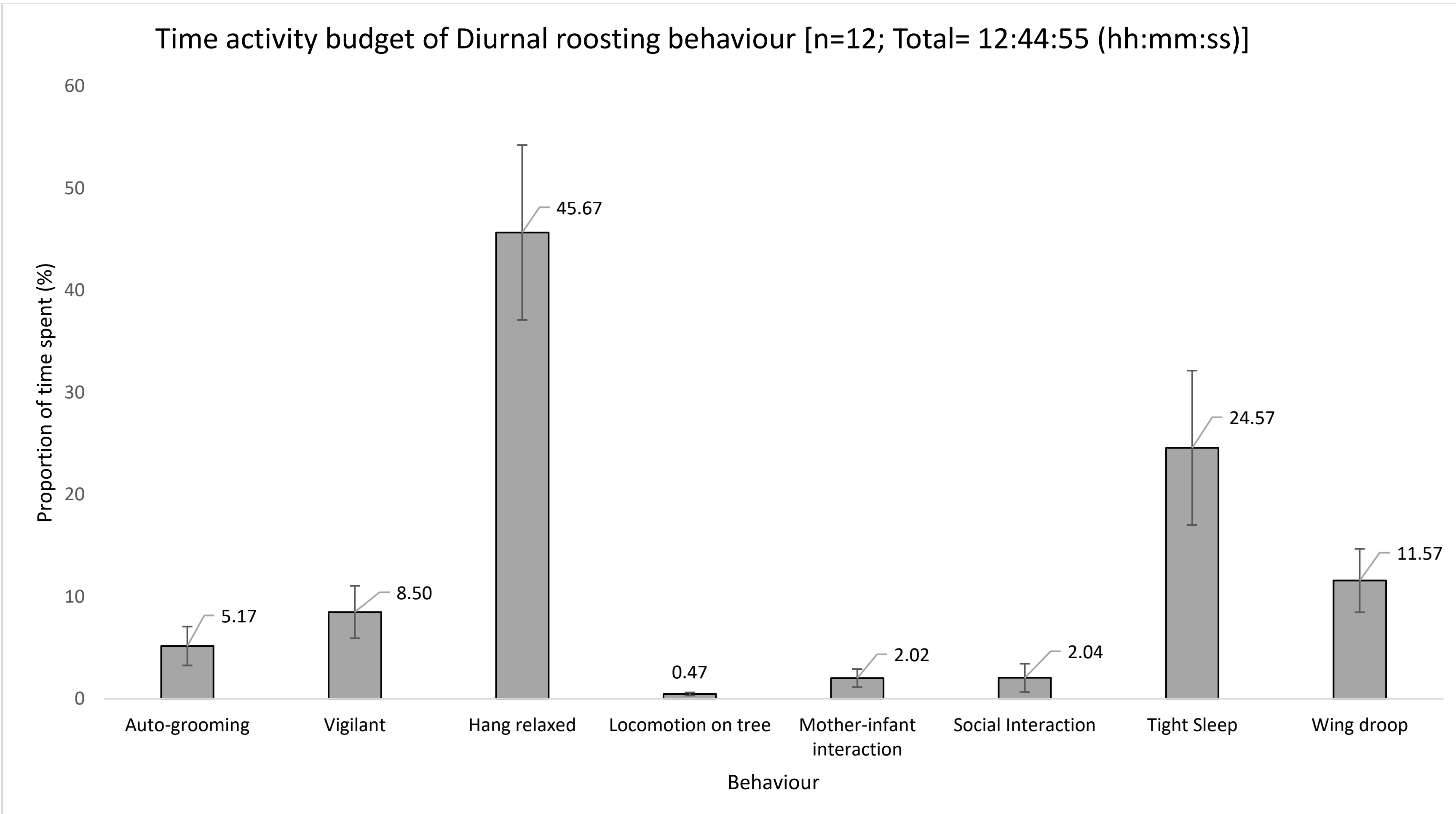
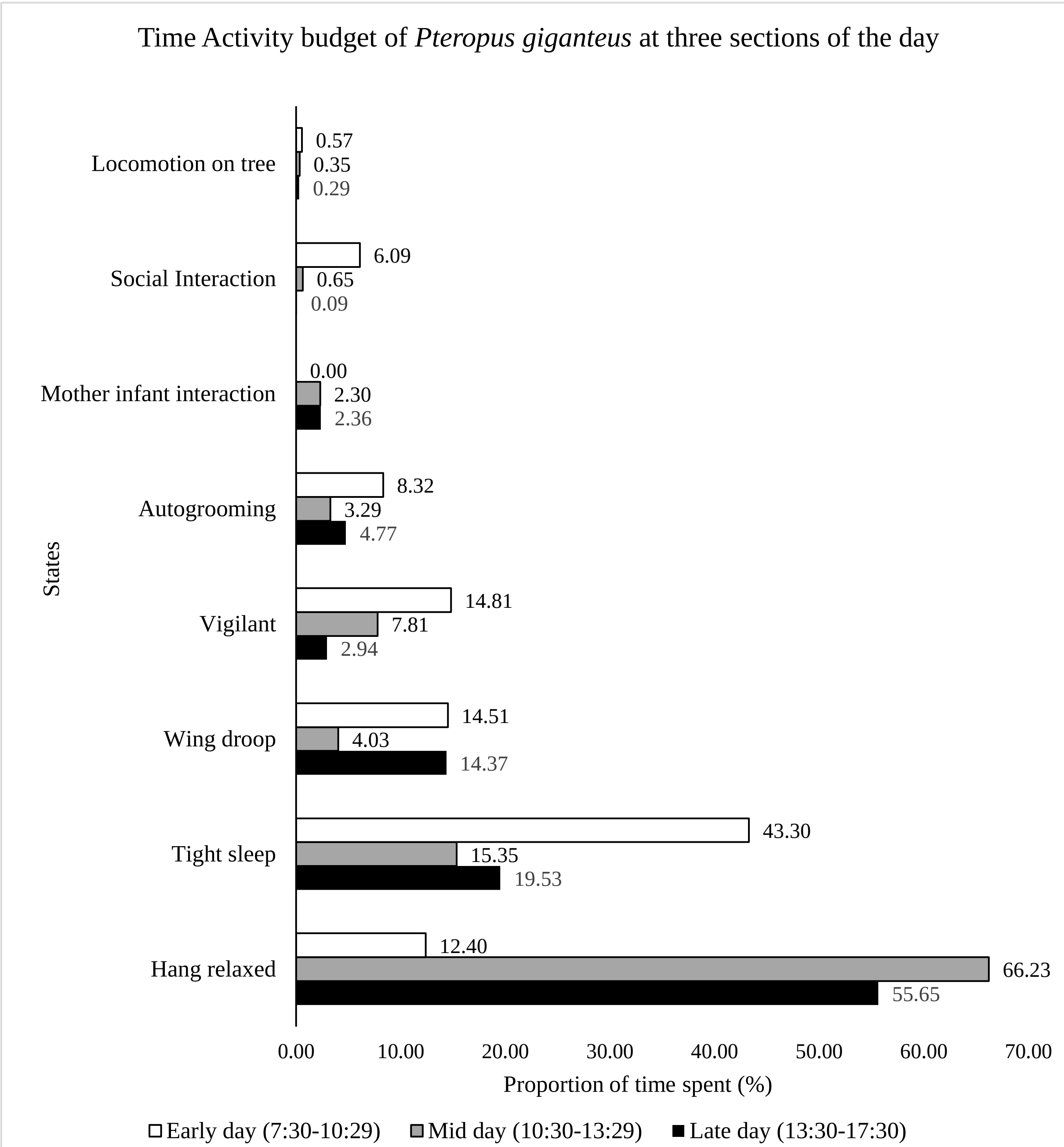


Table 3. Time Activity Budget of different Periods in a day						
Early day (7:30-10:29)			**Mid day (10:30-13:29)**		**Late day (13:30-17:30)**	
State	**Duration (hh:mm:ss)**	**Percentage**	**Duration (hh:mm:ss)**	**Percentage**	**Duration (hh:mm:ss)**	**Percentage**
Hang relaxed	0:16:43	12.39	4:49:30	66.23	1:47:24	55.65
Tight sleep	**0:58:23**	**43.30**	**1:07:06**	**15.35**	**0:37:41**	**19.52**
Wing droop	0:19:34	14.51	0:17:38	4.03	0:27:44	14.37
Vigilant	**0:19:58**	**14.80**	**0:34:07**	**7.81**	**0:05:41**	**2.94**
Auto-grooming	0:11:13	8.31	0:14:22	3.29	0:09:12	4.76
Mother infant interaction	0:00:00	0.00	0:10:02	2.30	0:04:33	2.35
Social Interaction	0:08:13	6.09	0:02:50	0.65	0:00:10	0.086
Locomotion on tree	0:00:46	0.56	0:01:31	0.35	0:00:34	0.29
Total sampling duration	**2:14:50**	**100.00**	**7:17:06**	**100.00**	**3:12:59**	**100**

Table 4. Comparison between Early day (ED) Mid day (MD) and Late day (LD)	
State	*Proportion of time spent in that period*
Hang relaxed	ED<LD<MD
Tight sleep	MD<LD<ED
Wing droop	MD<LD~ED
Vigilant	LD<MD<ED
Auto-grooming	MD<LD<ED
Mother infant interaction	ED<MD~LD
Social Interaction	LD<MD<ED
Locomotion on tree	LD<MD<ED

Fig. 3. Time Activity Budget of *Pteropus giganteus* at different periods of the day.



Research Question 2: What are the patterns in emergence and return of flying foxes?

In the time period spanning from 29th December 2018 to 27th April 2019 the mean emergence time was 17:30:47 (SE 00:02:38) and mean duration was 00:17:23 (SE 00:00:50). Mean emergence-initiation for late winter was 17:17:32 (SE 00:02:32) and for early summer was 17:45:59 (SE 00:01:12). Comparing the emergence-initiation readings of late winter and early summer a significant difference was found (t-value=-9.65, p-value < 0.0001). When we compared the emergence-end readings of late winter and early summer again a significant difference was found (t-value= -9.22, p-value < 0.0001). Also, when late winter and early summer readings of "gap between sunset and emergence-onset" were compared a significant difference came up (t-value=3.26; at α=0.05, p-value=0.002265). The gap is more in late winter than in early summer (fig. 5). But when late winter and early summer readings of emergence-duration were compared no significant difference was found (t-value=0.43. At α=0.05, p-value=0.66972)

Table 5. Emergence summary from 29th December 2018 to 27th April 2019

Initiation	Time	*end*	Time	*Duration*	Time
Mean	17:30:46	Mean	17:48:09	Mean	00:17:23
Standard Error	00:02:38	Standard Error	00:02:36	Standard Error	00:00:50
Standard Deviation	00:17:14	Standard Deviation	00:17:02	Standard Deviation	00:05:30
Minimum	16:50:00	Minimum	17:11:00	Minimum	00:05:17
Maximum	18:00:39	Maximum	18:21:57	Maximum	00:32:58
Count	43	Count	43	Count	43

Table 6. Emergence summary of late Winter (Late December, January February)

initiation	Time	*end*	Time	*Duration*	Time
Mean	17:17:32	Mean	17:35:15	Mean	00:17:43

Standard Error	00:02:32	Standard Error	00:02:13	Standard Error	00:00:47
Standard Deviation	00:12:10	Standard Deviation	00:10:37	Standard Deviation	00:03:47
Minimum	16:50:00	Minimum	17:11:00	Minimum	00:08:00
Maximum	17:35:41	Maximum	17:48:47	Maximum	00:26:30
Count	23	Count	23	Count	23

Table 7. Emergence summary of early Summer (March, April, early May)					
initiation	Time	*end*	Time	*Duration*	Time
Mean	17:45:59	Mean	18:02:59	Mean	00:17:00
Standard Error	00:01:12	Standard Error	00:01:59	Standard Error	00:01:35
Standard Deviation	00:05:23	Standard Deviation	00:08:50	Standard Deviation	00:07:05
Minimum	17:36:00	Minimum	17:49:14	Minimum	00:05:17
Maximum	18:00:39	Maximum	18:21:57	Maximum	00:32:58
Count	20	Count	20	Count	20

Table 8. Gap between sunset & emergence initiation					
Overall		*Late winter (Late December, January February)*		*early summer (March and April)*	
Mean	00:14:21	Mean	00:16:40	Mean	00:11:41
Standard Error	00:00:51	Standard Error	00:00:43	Standard Error	00:01:25
Standard Deviation	00:05:32	Standard Deviation	00:03:27	Standard Deviation	00:06:20
Minimum	00:01:02	Minimum	00:10:40	Minimum	00:01:02
Maximum	00:22:54	Maximum	00:22:54	Maximum	00:22:13
Count	43	Count	23	Count	20

Fig 4. Box Plot of emergence-onset in Late Winter and Early Summer.

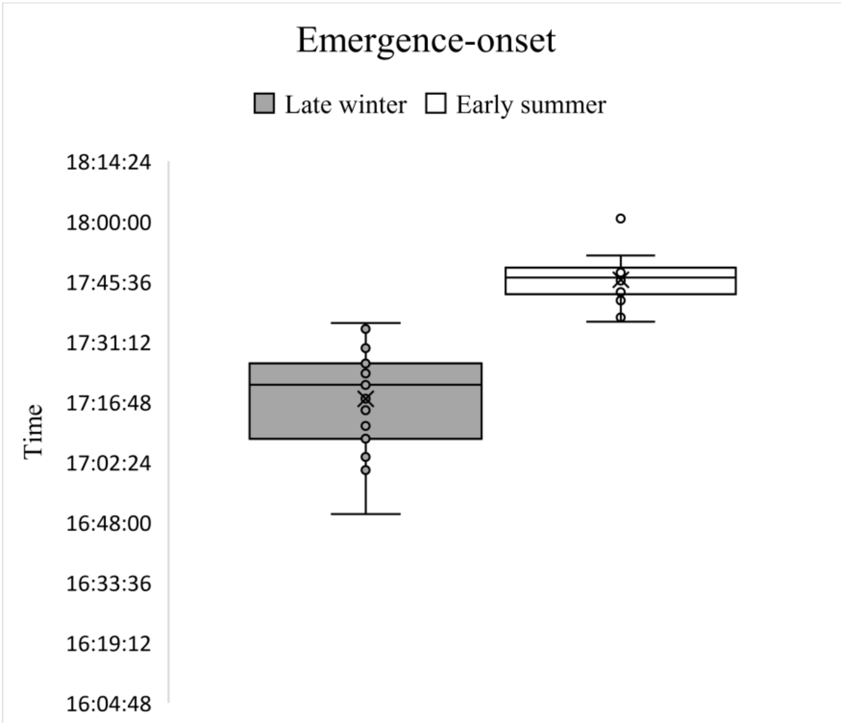


Fig 5. Box Plot of emergence-end in Late Winter and Early Summer.

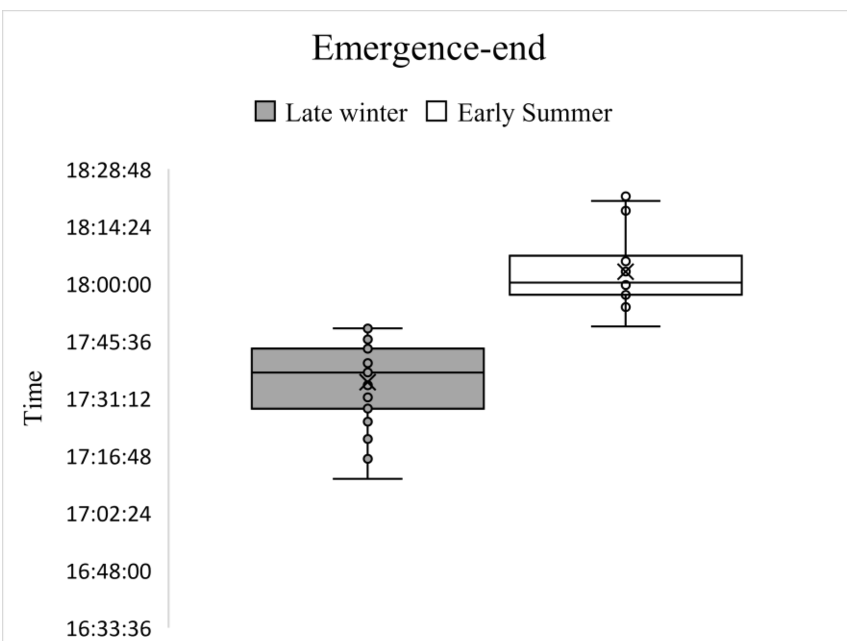
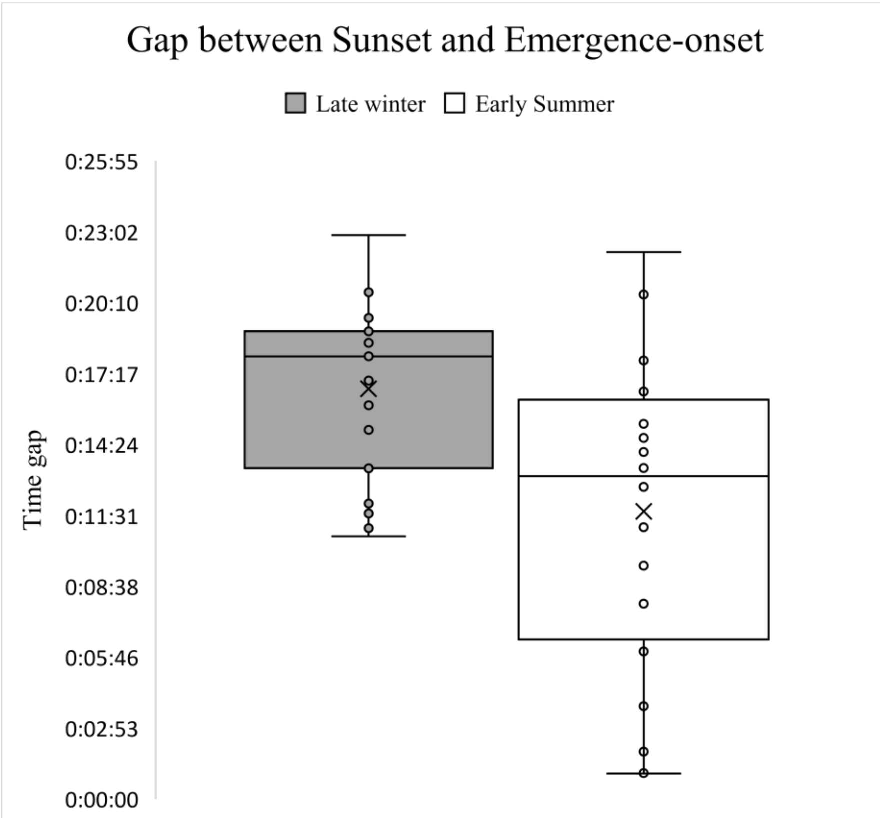


Fig 6. Box plot showing gap between sunset and emergence initiation in different seasons



In the time period spanning from 2nd January 2018 to 1st May 2019 the mean return-initiation time was 04:44:10 (SE 00:05:39) and mean duration was 00:30:41 (SE 00:01:59). Mean return-initiation for late winter was 05:01:00 (SE 00:03:18) and for early summer was 4:16:35 (SE 00:06:40). Comparing the return-initiation readings of late winter and early summer a significant difference was found (t-value=6.51; at α=0.05, p-value < 0.00001). Comparing the return-end readings of late winter and early summer again a significant difference was found (t-value= 9.50; at α=0.05, p-value < 0.00001). But when the late winter and early summer readings of "gap between sunrise and return-end" were compared no significant difference came up (t-value= 1.85. At α=0.05, p-value=0.07). Even when late winter and early summer readings of return-duration were compared no significant difference was found (t-value= 0.91. At $\alpha=0.05$, p-value=0.37)

Table 9. Return summary from 2nd January to 1st May 2019					
initiation (10th)	Time	*end*	Time	*Duration*	Time
Mean	04:44:10	Mean	05:13:10	Mean	00:30:41
Standard Error	00:05:39	Standard Error	00:05:31	Standard Error	00:01:59
Standard Deviation	00:28:16	Standard Deviation	00:27:01	Standard Deviation	00:09:44
Minimum	03:35:00	Minimum	04:20:33	Minimum	00:17:45
Maximum	05:24:36	Maximum	05:44:00	Maximum	00:58:35
Count	25	Count	24	Count	24

Table 10. Return summary of late Winter (January and February)					
initiation (10th)	*Time*	*end*	*Time*	*Duration*	*Time*
Mean	05:01:00	Mean	05:33:13	Mean	00:32:13
Standard Error	00:03:18	Standard Error	00:02:03	Standard Error	00:02:44
Standard Deviation	00:12:20	Standard Deviation	00:07:40	Standard Deviation	00:10:12
Minimum	04:40:03	Minimum	05:22:41	Minimum	00:20:33
Maximum	05:17:43	Maximum	05:44:00	Maximum	00:58:35
Count	14	Count	14	Count	14

Table 11. Return summary of early Summer (March and April)					
initiation (10th)	*Time*	*end*	*Time*	*Duration*	*Time*
Mean	04:16:35	Mean	04:45:07	Mean	00:28:32
Standard Error	00:06:40	Standard Error	00:05:18	Standard Error	00:02:53
Standard Deviation	00:21:04	Standard Deviation	00:16:46	Standard Deviation	00:09:08
Minimum	03:35:00	Minimum	04:20:33	Minimum	00:17:45
Maximum	04:39:26	Maximum	05:09:32	Maximum	00:49:50
Count	10	Count	10	Count	10

Table 12. Gap between sun rise and return-end					
Overall		*Late Winter (Late December, January February)*		*Early Summer (March and April)*	
Mean	00:21:15	Mean	00:22:55	Mean	00:18:53
Standard Error	00:01:08	Standard Error	00:01:23	Standard Error	00:01:41
Standard Deviation	00:05:32	Standard Deviation	00:05:12	Standard Deviation	00:05:21
Minimum	00:12:22	Minimum	00:12:22	Minimum	00:14:00
Maximum	00:33:19	Maximum	00:33:19	Maximum	00:29:27
Count	24	Count	14	Count	10

Fig. 7 Box plot showing Return-initiation time between late winter and early summer

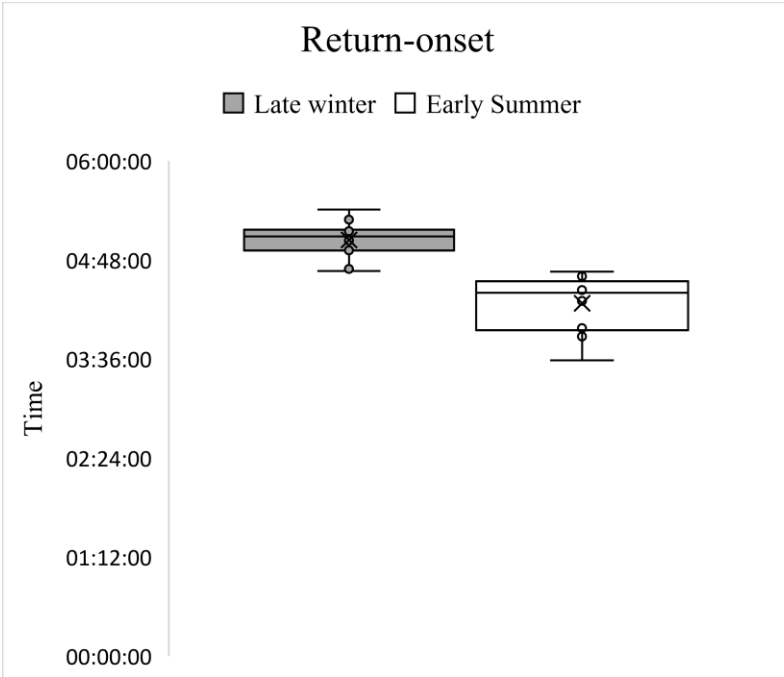
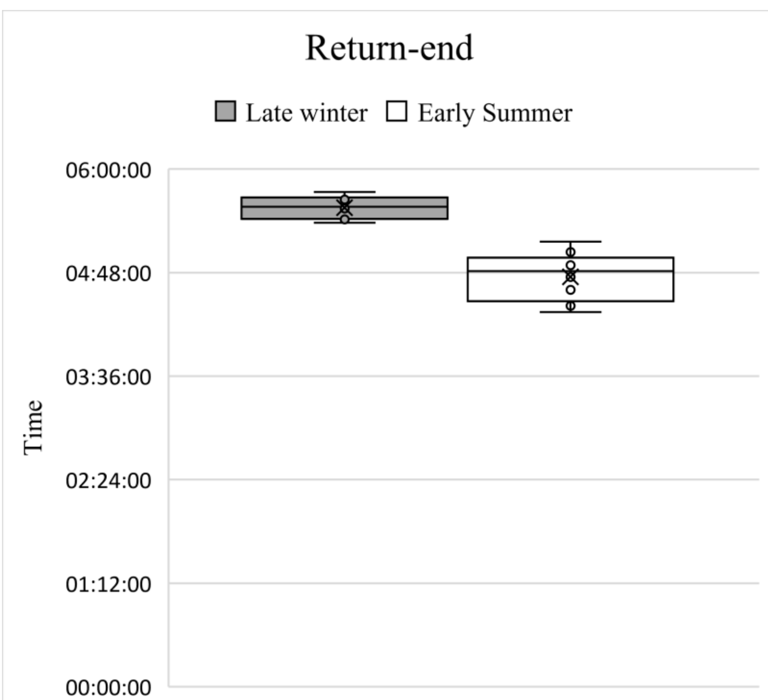


Fig. 8 Box plot showing Return-end time between late winter and early summer



Research Question 3: What are the correlates that contribute to emergence and return?

Among sunset timings, moon-rise, moon-set timings and moon phase (%), emergence-initiation and emergence-end correlates mostly with sunset i.e., 0.96 and 0.95 respectively. Emergence-end also shows positive correlation with temperature (r=0.54) while ‘gap between onset and sunset’ shows negative correlation with sunset (r=-0.51) [Table 13]. Among sunrise, moon-rise, moon-set and moon phase, return-initiation and return-end correlates mostly with sunrise i.e., 0.92 and 0.98 respectively. However, return onset and return-end negatively correlates with temperature i.e, -0.68 and -0.75 respectively [Table 14].

Table 13. Correlation matrix (Pearson): Between Emergence and environmental variables														
Variables	ONSET temp.	ONSET humidity	End temp	END humidity	Twilight (duration)	Sun set	Moon phase	Moon rise	Moon set	Onset	Onset lux	End	Duration	gap
ONSET temp.	1.00													
ONSET humidity	-0.47	1.00												
End temp.	0.96	-0.40	1.00											
END humidity	-0.46	0.95	-0.47	1.00										
Twilight (duration)	-0.12	0.16	-0.06	0.12	1.00									
Sun set	0.48	0.27	0.49	0.25	-0.58	1.00								
Moon phase	0.09	0.11	0.12	0.08	0.01	0.08	1.00							
Moon rise	-0.16	0.22	-0.12	0.20	0.01	-0.07	0.73	1.00						
Moon set	-0.26	0.00	-0.27	0.04	0.09	-0.14	-0.83	-0.46	1.00					
Onset	0.43	0.18	0.45	0.16	**-0.65**	**0.96**	0.04	-0.15	-0.10	1.00				
Onset lux	0.39	0.11	0.43	0.07	**0.75**	0.48	0.24	0.21	-0.31	0.11	1.00			
End	**0.53**	0.17	**0.55**	0.15	**-0.52**	**0.95**	0.13	-0.08	-0.15	**0.95**	0.36	1.00		
Duration	0.27	-0.02	0.27	-0.01	0.42	-0.08	0.27	0.20	-0.15	-0.20	**0.60**	0.13	1.00	
gap	-0.32	-0.34	-0.31	-0.35	0.03	**-0.51**	-0.15	-0.20	0.17	-0.25	**-0.91**	-0.36	-0.33	1.00

Table 14. Correlation matrix (Pearson): Between Return and environmental variables														
Variables	ONSET temp.	ONSET humidity	END temp.	END humidity	Twilight duration	Sun rise	Moon phase	Moon rise	Moon set	Onset	End	lux	Duration	gap
ONSET temp.	1.00													
ONSET humidity	-0.25	1.00												
END temp.	0.94	0.02	1.00											
END humidity	-0.25	0.53	-0.26	1.00										
Twilight duration	0.25	0.46	0.35	0.29	1.00									
Sun rise	-0.80	-0.18	-0.82	-0.20	-0.18	1.00								
Moon phase	0.28	0.12	0.22	0.29	-0.06	-0.10	1.00							
Moon rise	0.27	0.14	0.19	0.38	-0.02	-0.16	0.77	1.00						
Moon set	-0.24	0.01	-0.22	-0.26	0.05	0.18	-0.77	-0.46	1.00					
Onset	**-0.74**	-0.15	**-0.68**	-0.37	-0.23	**0.92**	-0.21	-0.36	0.18	1.00				
End	**-0.73**	-0.33	**-0.76**	-0.32	-0.27	**0.98**	-0.12	-0.19	0.18	**0.94**	1.00			
lux	0.18	-0.42	0.08	-0.10	-0.34	-0.21	-0.62	0.04	0.54	**-0.54**	-0.02	1.00		
Duration	-0.06	-0.10	-0.20	0.13	-0.05	0.12	0.11	0.38	0.07	-0.23	0.12	0.63	1.00	
gap	-0.40	0.22	-0.40	0.53	0.34	0.28	0.26	0.29	-0.07	0.07	0.08	**-0.75**	0.02	1.00

4.2 Objective 2: Determination of Spatial vigilance architecture with respect to its function (environmental and social) in roosting colony of *Pteropus giganteus*.

Out of 21 colonies, three colonies were chosen to be monitored for vigilance. The details of the colonies are given in the Fig. 1. A total of 50257 seconds of focal sampling was done, where 16967 seconds were in core and 32851 seconds were in periphery. The details of it are given in table no. 15

Table 15. Focal Sampling effort (in Secs) . Table shows effort in various colonies in seconds			
Colony	**Core**	**Periphery**	**Total Effort**
Bethukandi	5423	8019	13881
Dulalgram	6566	12229	18795
Rengti	4978	12603	17581
Grand Total	16967	32851	50257

It was observed that the sampling effort between core and periphery was not significantly different (At $\alpha=0.05$, t-value=1.86, p-value=0.06). Sampling effort across colonies was also found to be non-significant (f-ratio=0.61; at $\alpha=0.05$, $p=0.54$, $df = 2$). Considering all vigilance types viz., Passive vigilance (PV), Active vigilance (AV), Social vigilance (SV), Environmental Vigilance (ENV), and Observer vigilance (ENV-O), bats are most vigilant in Rengti and least in Dulalgram. For Rengti the percentage of overall vigilance is 18.44 and for Dulalgram is 4.97.

Table 16. Overall Vigilance. Table shows records of vigilance across colonies in proportion to effort spent	
Colony	Percentage of Vigilance
Bethkundi	8.57

Dulalgram	4.97
Rengti	18.44

Distributions of ENV durations did not significantly differ among the three colonies (Kruskal-Wallis test: H statistic= 0.45; at $\alpha=0.05$, $p=0.79$). Neither did distributions of SV durations (Kruskal-Wallis test: H statistic= 4.67; at $\alpha=0.05$, $p=0.09$). Hence confirmed there is no significant difference between the systems (replicates).

Research Question 1: Does environmental vigilance change (edge effect) with increasing distance from the center of the group?

The total number of ENV events recorded were 81 in periphery and 10 in core zone of the roosting sites. The average percentage of ENV in periphery is 5.26% (SE=0.67) and core was found to be 0.93% (SE=0.38). It was observed that ENV in periphery was higher than in core [table 17]. However, the "duration of ENV" was not significantly different between core and periphery (Two tailed Mann-Whitney U Test:U=323.5; Z-score=1.02. $\alpha=0.05$, $p=0.30$).

Table 17. Percentage of Environmental Vigilance (ENV). Table shows the percentage of vigilances that were displayed by bats at various colonies**.**

Sl. No	Colony	Core	Periphery
1	Bethkundi	1.12	6.43
2	Dulalgram	0.18	4.08
3	Rengti	1.48	5.26
4	average	0.93	5.26

5	SD	0.67	1.17
6	SE	0.38	0.67
7	CI	0.76	1.32

It was observed that the environmental vigilance counts or bouts were much greater in the periphery than in the core areas of the roosting sites (Fig 9). Only, 10 vigilance counts were recorded in the core area with respect to environmental vigilance. The frequency of ENV events at different hours of the days showed average ENV in core was 0.90 (SE=0.41) and in periphery was 6.63 (SE=1.79). It was recorded that ENV was significantly different in core from the periphery (t-value= -3.10; At α=0.05, p=0.005).

Fig 9. Pie chart showing Environmental Vigilance counts in Core and Periphery

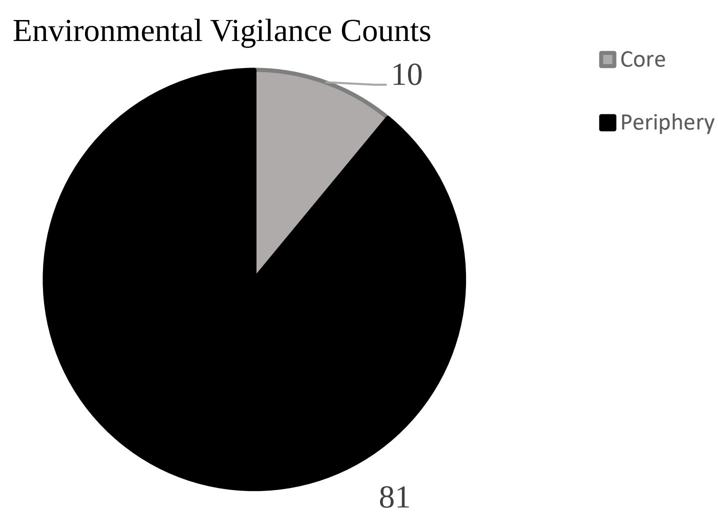


Fig 10. Percentage of Environmental Vigilance between Periphery and Core

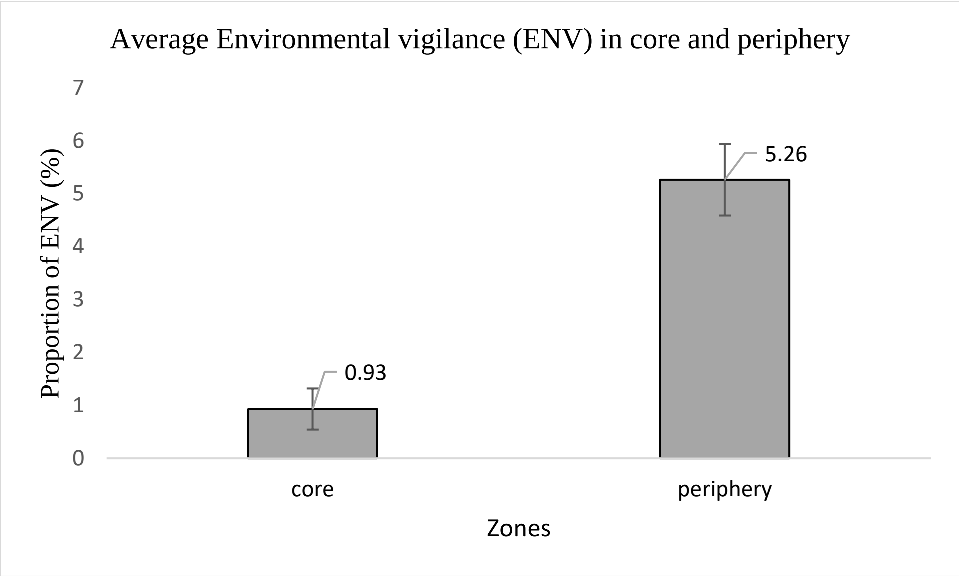
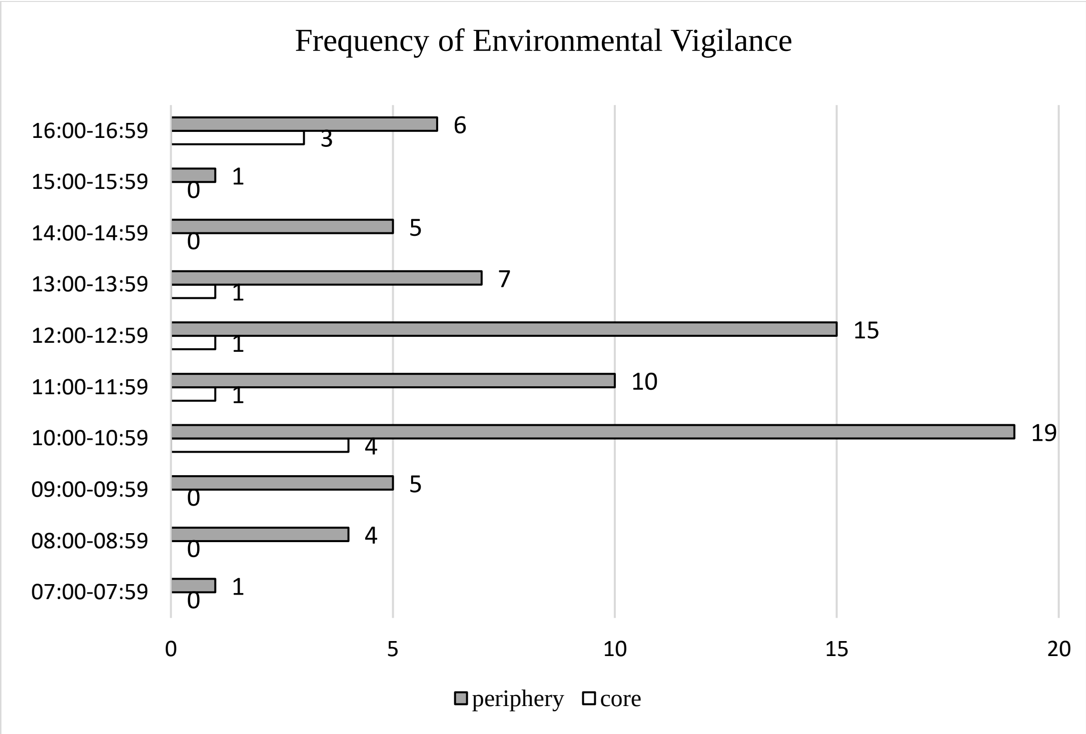


Fig 11. Comparison of frequency of Environmental vigilance across core and peripheral zones. Zones show marked differences in vigilance bouts across various time periods.



It was found that vigilance did not vary across sites with respect to environmental vigilance. It was observed that ENV was markedly different in periphery than core zones in terms of proportion and frequency. It was also observed that vigilance was higher and found to increase as observed from core to periphery. Thus, it was observed that Environmental Vigilance was influenced by 'Edge Effect'.

Research Question 2: Does social vigilance change (guard effect) with increasing distance from the centre of the group?

The numbers of Social Vigilance (SV) events recorded were 41 in periphery and 11 in core zones. The average percentage of SV in periphery was found to be 1.95 % (SE=0.80) and core was 0.93% (SE=0.80). It was observed that SV in periphery was higher than in core [table 18, Fig. 13]. However, the "duration of SV" was not significantly different between core and periphery (Two

tailed Mann-Whitney U Test:Z-score= -0.54;at $\alpha=0.05$, p-value=0.58).The frequency of SV events at different hours of the day, the average SV in core was 1%(SE=0.53) and in periphery is 3.363% (SE=1.45). It was found that SV was not significantly different in core and periphery (t-value= -1.52; At $\alpha=0.05$, p-value= 0.14).

Fig 12. Pie chart showing social vigilance counts in core and periphery

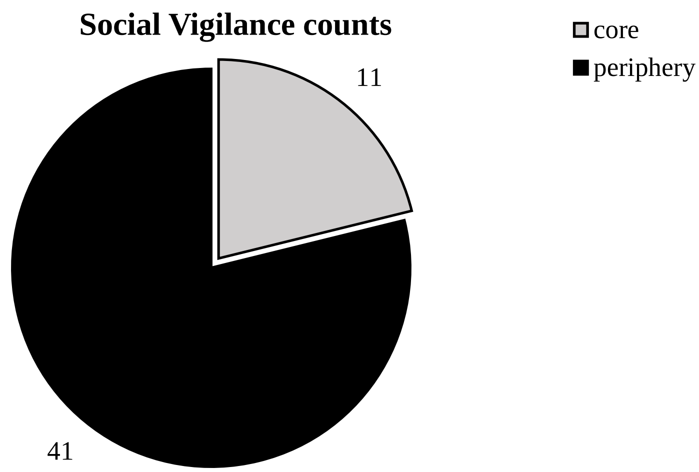


Table 18. Percentage of Social Vigilance (SV). Table shows proportion of vigilance with respect to the total effort spent on observing vigilance.		
Colony	Core	periphery
Bethukandi	2.54	3.20
Dulalgram	0.27	0.44
Rengti	0	2.20
average	0.93	1.95
SD	1.39	1.39
SE	0.80	0.80
CI	1.58	1.57

Fig 13. Percentage of Social Vigilance between periphery and core. Social vigilance is more towards the periphery

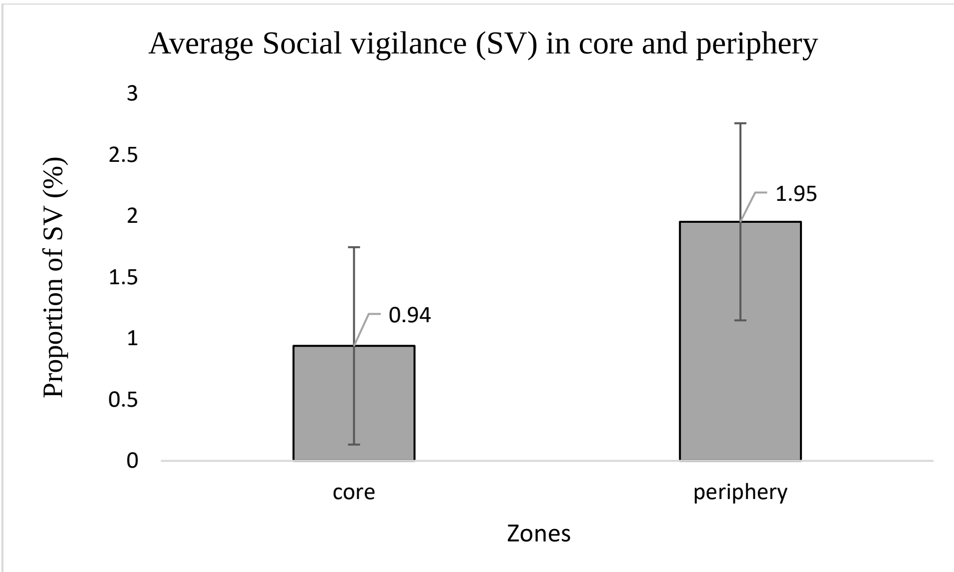
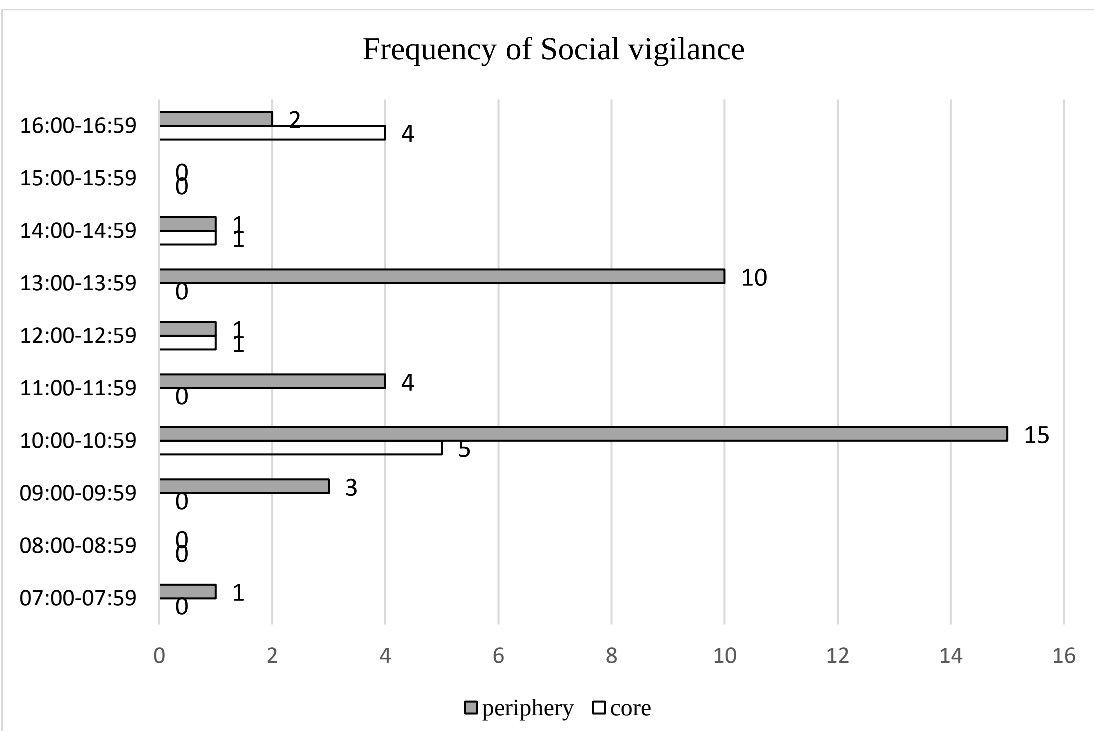


Fig 14. Frequency of Social vigilance across core and peripheral zones at different periods.



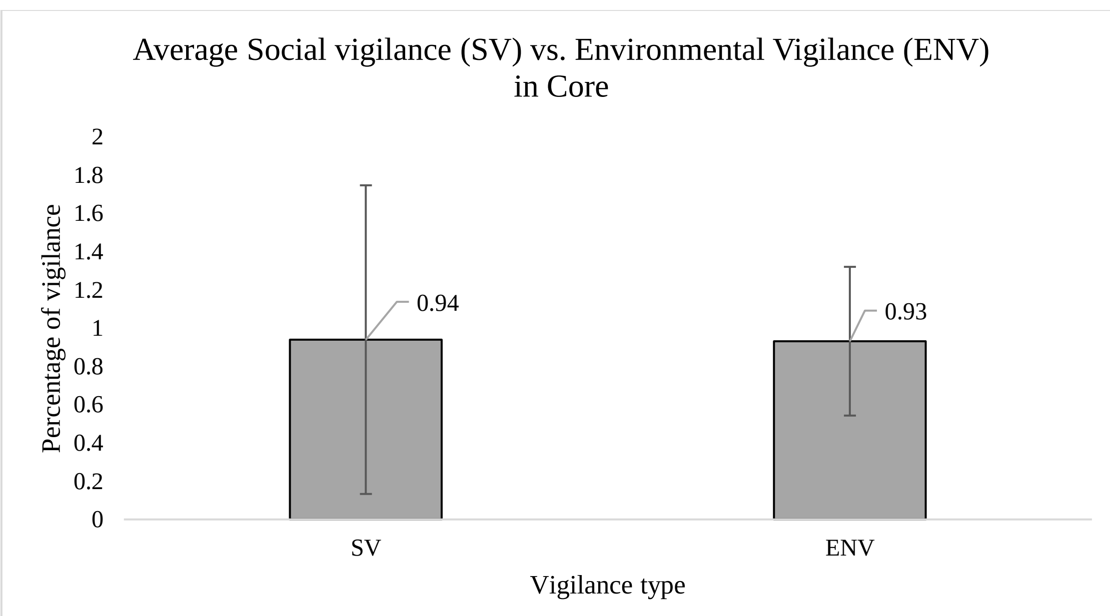
Variation in vigilance type within sites

The average percentage of SV was 0.93 (SE=1.39) and ENV was 0.93 (SE=0.381) in core zones. However, when Rengti was excluded the SV was observed to be 1.40 (SE = 1.13).

Table 19. Social vigilance (SV) vs. Environmental Vigilance (ENV) in Core.

Sl.No	Colony	SV	ENV
1	Bethukandi	2.54	1.12
2	Dulalgram	0.27	0.18
3	Rengti	0	1.49
4	Average	0.94	0.93
5	SD	1.39	0.67
6	SE	0.80	0.38
7	CI	1.58	0.76

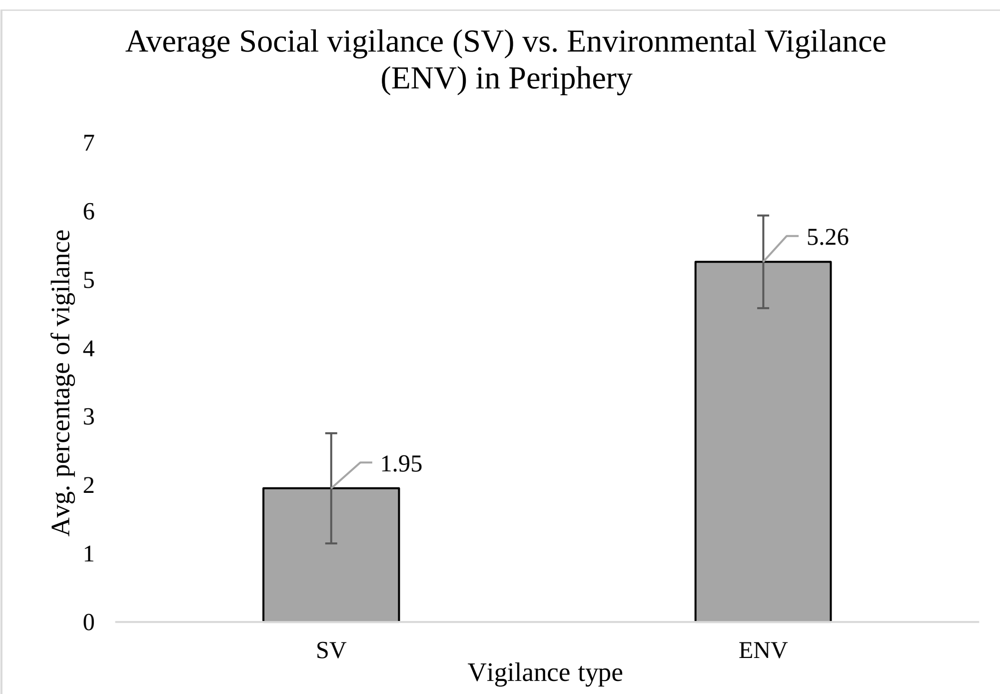
Fig 15. Social and Environmental vigilance in core



Difference between environmental vigilance (ENV) and Social vigilance (SV) in peripheral bats of a roosting tree was observed to be different. The average percentage of SV was 1.95% (SE=0.80) and ENV is 5.26 % (SE=0.67). In all the colonies it is found that the percentage of ENV is always higher than SV in peripheral bats.

Table 20. Social vigilance (SV) vs. Environmental vigilance (ENV) in Periphery			
Sl.No	Colony	SV	ENV
1	Bethukundi	3.20	6.43
2	Dulalgram	0.44	4.08
3	Rengti	2.20	5.26
4	average	1.95	5.26
5	SD	1.39	1.17
6	SE	0.80	0.67
7	CI	1.57	1.32

Fig 16. Social and Environmental Vigilance in Periphery



5. DISCUSSION

Cachar has 23 verified *Pteropus giganteus* colonies out of which 18 are permanent colonies and rest 4-5 temporary colonies. All of these colonies were characterized by tall trees like *Bombax ceiba, Samanea saman, Lagerstroemia sp., Albizia acle*, *Mangifera indica*, etc., hillocks with thick shrub-cover, or grave-yards, or a combination of all. The sites have two things in common that is they are not much frequented by humans and all of them are situated near a river or a big water body. Flying foxes in cachar seemed to be relatively more active and vigilant compared to Kachari ghat colony near DC office Guwahati. This can be a reflection of anthropogenic disturbance and hunting pressure. 51 distinct behavioural units were identified and all of them were concurrent with the units described in the ethogram of *Pteropus alecto*. Time activity budget reflects the dominance of resting characterized by states of 'hang relaxed', 'tight sleep' and 'wing droop'. Locomotion on a tree was very limited as most of the time they fly off to a new roosting spot if need arises.

Vigilance in bats occupies a relatively high proportion of non-resting behavior. Emergence-initiation and end was strongly correlated with sun set whereas return-initiation and end was with sun rise. Thus, when sunset timing moves forward with transition from winter to summer so does emergence (initiation & end). A similar trend is evident with return, i.e. as sunrise timing got earlier from winter to summer so did return (initiation and end). Interestingly the gap between sunset and emergence-initiation decreased from late winter to early summer. But no such seasonal difference was found for emergence and return duration. Now while studying vigilance it was observed that both environmental and social vigilance was higher in peripheral bats than in core bats on a roosting tree(s). This difference was drastic for environmental vigilance but moderate for social vigilance. The intensity of social or environmental vigilance in terms of duration of a vigilance bout was similar in both core and periphery. Environmental vigilance was much higher than social vigilance in periphery while social vigilance and environmental vigilance did not show much difference in core.

Out of 74 behavioral units mentioned in the ethogram of *Ptreropus alecto* (Markus and Blackshaw 2002), 53 (50 confirmed, 3 doubtful) were witnessed in *Pteropus giganteus* during the provided study period. These 53 units belonged to Roosting, Stationary action, Locomotion, Auto-grooming, Territoriality, Courtship/mating, Mother Infant interaction and play behavior. Though not observed in field condition, feeding behavior observed in a rescued Indian flying fox was concurrent to the behavioural units described for *Pteropus alecto*. Courstship/ mating behavior was observed only once but outside the sampling protocol. Behavioural units of *P.giganteus* also corresponds to that of *P. vampyrus* (Cayunda et al. 2004). A new behavior very similar to 'scent bath' (an exclusively male behaviour) was observed in a female accompanied by urinating on itself. Following the ad hoc event of a huge storm a completely different kind of vocalization by females became very frequent. This vocalization can be considered as a search call to locate lost infants, which in turn respond by distress calls.

The states of hanging relaxed and wing droop did not necessarily mean bats were asleep. Events like fanning and other stationary actions viz. wing extension, wing flick, swivel, turn, yawn, etc. were commonly associated. The state of 'tight sleep' is a true indication of being asleep. 'Tight sleep' is more dominant early day and late day. It was observed that when it rains most bats remain in tight sleep. Fanning occurs mostly in the state of 'Hang relaxed' and this state is highest during mid day when temperature is generally high. Most non resting activities seem to be higher in early part of the day than mid day or late day. Vigilance decreases from early day to late day. Social interaction bouts except for play behavior were of very short duration lasting less than 50 seconds. Bouts of mother infant interactions are generally prolonged exceeding a minute. Auto grooming can be both prolonged or in bursts.

Emergence-return of *Pteropus giganteus* and other *Pteropus* species are strongly correlated with sun set and sun rise respectively. Following this, the logical expectation that the gap between sunset and emergence or the gap between return-end and sunrise should remain fairly constant with changing season was not true. This issue may be approached by considering the seasonal change in twilight and its associated rate of change in illuminance (Welbergen 2008). Also, there were observations of emergence getting earlier and return getting delayed in cloudy or rainy days but never before sunset or after sunrise respectively. Considering the above mentioned points it can be suggested that after sunset the exact initiation of emergence was governed by a threshold illuminance. Similarly, prior to sunrise the exact end of return was governed by a threshold illuminance. Ambient temperature also has an effect on emergence and return. On warmer days emergence-end may delay while on cooler days return may shift earlier.

Now, while studying vigilance it was observed that both environmental and social vigilance was higher in peripheral bats than in core bats on a roosting tree(s). This difference was drastic for environmental vigilance but moderate for social vigilance. The intensity of social or environmental vigilance in terms of duration of a vigilance bout was similar in both core and periphery. Environmental vigilance was much higher than social vigilance in periphery while social vigilance and environmental vigilance did not show much difference in core.

Coming to the vigilance study, environmental vigilance increased 5.65 times from core to periphery while Social vigilance increased 2.1 times. The moderate increase in social vigilance from core to periphery may be an outcome of more individuals at periphery than core. Another important thing to note was that environmental vigilance is higher than social vigilance in periphery, while environmental and social has no significant difference in core. Only if 'Rengti' is not considered, social vigilance becomes higher than environmental in core. There were no readings of social vigilance in core bats of Rengti. This can be addressed by considering the trees in Rengti which provide less core space. Hence from the above discussed points, social or environmental vigilance of a bat did depend on the spatial position with respect to the group. Environmental vigilance increased significantly towards periphery and decreased towards core showing Edge effect. However social vigilance increased towards periphery and decreased towards core – Reverse Guard effect. In totality Environmental vigilance is more than social vigilance irrespective of core or peripheral bats on a tree(s). This is additionally due to prevalent hunting pressure in all the three colonies. Overall vigilance was highest in Rengti. The physical characteristic of the colony and its surrounding disturbance might be the answer to it. This colony is on a hillock with heterogeneous composition of both short and tall roosting trees. Villagers used this hillock to collect firewood and the hillock was undergoing massive earth excavation. Though most verified colony sites were traditional-permanent roost sites they were under constant threat of turning into temporary or even losing the site completely, because of anthropogenic disturbance. The fruit bats are a family that have well adapted to human conditions. However, with the passing of time such gregarious species may well be vanishing.

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ANNEXURES

Plate 1. Roosting tree at Rengti

Plate 2.: Rengti colony

Plate 3: Dulalgram colony

Plate 4: Dulalgram roosting tree

Plate 5: Bethukandi roosting tree

Plate 6 (a): Yellow circle indicates peripheral bats. Red circle indicates core bats. [Lateral view of the tree]

Plate 6 (b): Yellow circle indicates peripheral bats. Red circle indicates core bats [View from under the tree]

Plate 7: An infant *Pteropus giganteus* which got detached from its mother

Plate 8: Mother *Pteropus giganteus* with two pups (very rare). Both may not be her own.

Plate 9: Mother *Pteropus giganteus* with a single pup (general case)

Plate 10. Adult male *Pteropus giganteus*

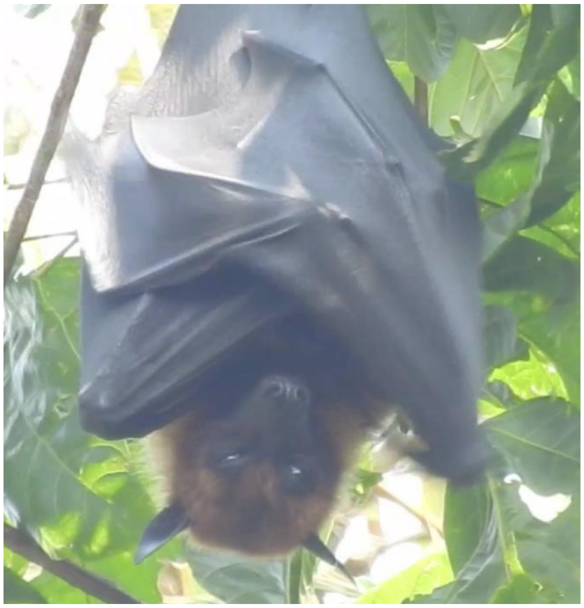

Plate 11: *P. giganteus* showing passive vigilance

Plate 12: *P. giganteus* showing social vigilance (looking at a nearby individual)

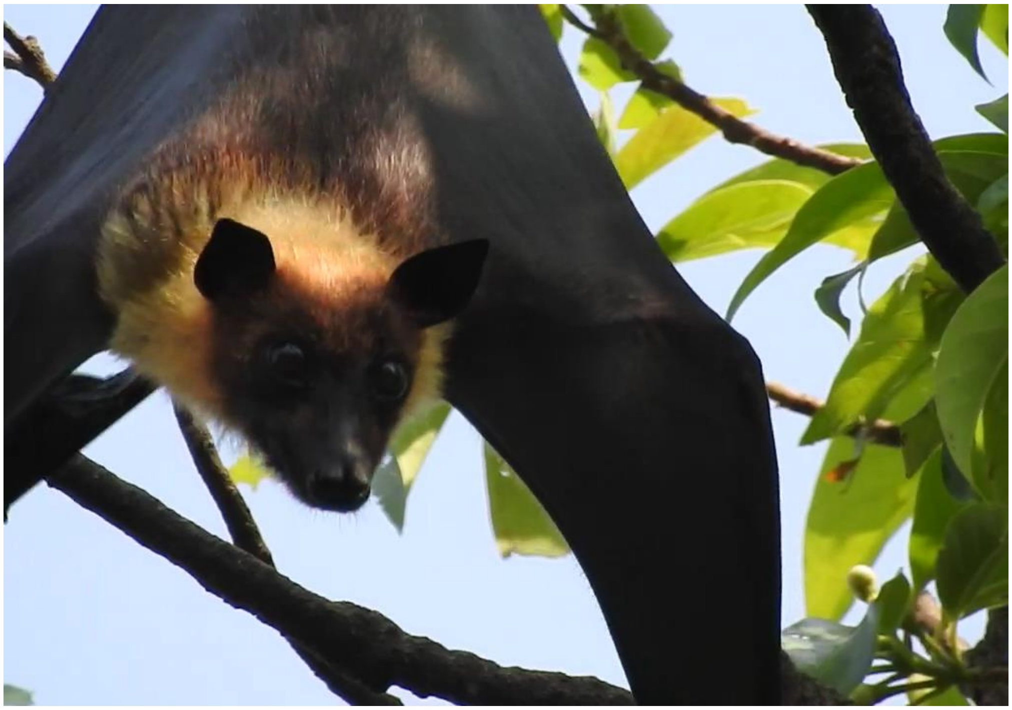

Plate 13: *P. giganteus* showing environmental vigilance

Plate 14: *P. giganteus* showing observer vigilance

Plate 15: Bethukandi colony and its surrounding

Plate 16: Dulalgram colony and its surroundings

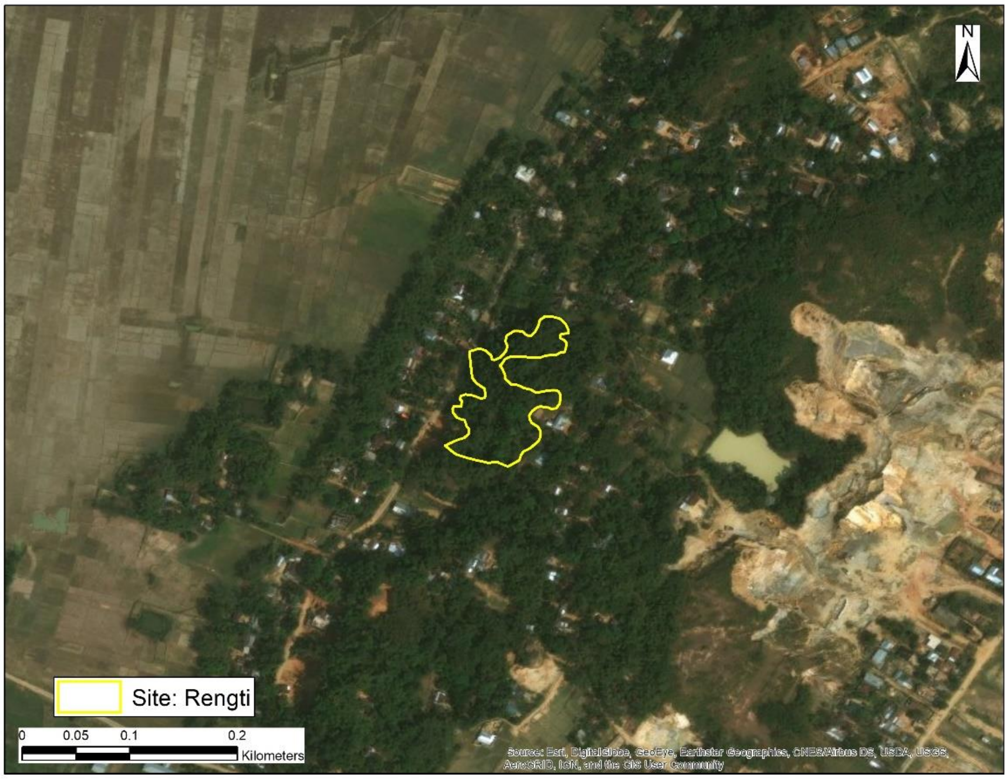

Plate 17: Rengti colony and its surroundings